

POTENTIAL PALEOECOLOGIC BIASES FROM SIZE-FILTERING OF FOSSILS: STRATEGIES FOR SIEVING

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ABSTRACT

The methods by which fossils are extracted from sediments can alter their observed size-frequency distributions, which can in turn alter observed paleoecologic patterns. Building on previous work, this study uses virtual sieving (i.e., replicated via subsampling on a computer) to test the effects of size filtering on the apparent ecologic composition of a database of Miocene mollusks in which the size of every specimen was measured. When simulated mesh sizes varied by nearly an order of magnitude (2–10 mm), the apparent relative abundances of tiering, motility, and feeding categories varied substantially in some individual bulk samples. Not surprisingly, the extent to which variations in mesh size affected the ecologic proportions of a sample depended in part on its size-frequency distribution. If the goal is to characterize the ecology of adult assemblages, the chosen mesh size should not be so small that juveniles dominate the results or so large that a majority of specimens are excluded. For many molluscan assemblages, 2–4 mm should often be appropriate. For preexisting data sets composed of heterogeneously collected data, there is a positive result: averaging samples together to produce a mean view of ecologic composition tends to remove the more egregious effects of the size-filtering bias. Thus, comparisons of the ecologic composition of single samples may be sensitive to mesh-size effects, but comparisons of regional or global faunas are likely more robust, and variations in size filtering may not be an obstacle to large-scale, secular comparisons of ecospace use. Measuring ecologic importance using biomass instead of abundance also reduced the effects of the mesh-size bias by reducing the influence of small-bodied individuals on ecologic proportions.

INTRODUCTION

Patterns of ecology, evolution, and diversity observed in the fossil record can be distorted by the ways in which fossils are preserved, collected, and analyzed on local to global scales (e.g., historical work by Raup, 1972; Sepkoski et al., 1981; Signor and Lipps, 1982; see also recent work by Cherns and Wright, 2000; Holland, 2000; Alroy et al., 2001; Kidwell, 2002a; Kowalewski and Bambach, 2003; Bush and Bambach, 2004a; Peters 2006). Separating biological signals from preservational and methodological distortions has become increasingly important in recent decades as paleontologists try to achieve an ever more detailed understanding of the history of life.

Biases can be introduced into a study simply by heterogeneities caused by how fossil assemblages were collected in the field or processed in the lab. For example, fossils from unlithified sediments, common in the late Mesozoic and Cenozoic, can be extracted from bulk samples by sieving

(e.g., Kosnik, 2005), which may exclude small specimens. This can introduce a bias into further analyses by altering the size-frequency distributions of samples, which can change other parameters related to body size. The paleontologist, however, can at least choose the mesh size and control the strength of the size-filtering bias, although mesh sizes used in studies of a single taxon can vary by more than an order of magnitude (Kidwell et al., 2001; Kowalewski and Hoffmeister, 2003), so the strength of the size-filtering bias can vary greatly. Size filtering may also occur when extracting fossils from lithified sediments (e.g., Hendy, 2005; Kowalewski et al., 2006), but the exact nature of the filtering requires further documentation.

Several recent studies have highlighted the effects of size filtering on various paleontological patterns based on quantitative data (abundance counts). Peeters et al. (1999) found that the species composition and richness of foraminiferal samples varied with sieve size, with implications for paleoceanographic interpretations. In a meta-analysis, Kidwell (2001, 2002b) found that modern molluscan death assemblages best reflected the rank-order abundances of the species in the living assemblages from which they formed for mesh sizes >1.0 mm. The live-dead agreement was poorer for samples sieved with smaller mesh sizes. Thus, both the taxonomic composition and fidelity of fossil assemblages can vary with mesh size. Kidwell et al. (2001) found that measures of the rates of taphonomic damage on mollusk shells can vary depending on the mesh size used in sieving.

In another study, Kowalewski and Hoffmeister (2003) measured every specimen in a set of molluscan samples from the Miocene of Europe and simulated the effects of sieving on a number of paleobiological parameters. As mesh sizes varied between 2–10 mm, many measured parameters changed significantly (e.g., species richness, evenness, encrustation rate, taxonomic composition, drilling intensity, etc.). Furthermore, they found that comparisons between samples with regard to these parameters sometimes yielded different results depending on the mesh size used. Biologists have also found that mesh-size biases can affect a number of parameters relating to ecology and diversity (Muus, 1973; Livesley et al., 1998; Tanaka and Leite, 1998; Crewe et al., 2001; Gage et al., 2002).

This paper follows that of Kowalewski and Hoffmeister (2003) in using computer routines to test the effects of size-filtering biases on the Miocene molluscan data collected by Kowalewski et al. (2002) and Hoffmeister and Kowalewski (2001), but it expands on their previous work in several key ways. First, it tests the effects of mesh-size variations on the ecologic composition of fossil assemblages, which has played an important role in discussions of Phanerozoic diversity trends (Bambach, 1983, 1985; Bush and Bambach, 2004b; Bush et al., 2007). The ecologic composition of fossil samples can also be used in the multivariate ordination of paleoecologic data (e.g., Kowalewski et al., 2002). Second, this work considers the effects of mesh-size biases on individual bulk samples, not just pooled regional data, which is directly relevant to the collection and comparison of fossil assemblages by other paleontologists

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TABLE 1—Descriptions of samples and localities, based on table 1 of Kowalewski et al. (2002). Samples listed on the same row were collected from different sites at the same outcrop. Sample numbers in bold are those shown in Fig. 2; others are shown in Fig. 3. Median sizes include only specimens >2 mm.

Sample	<i>n</i>	Median size (mm)	Country	Province	Facies
1	243	7.0	Germany	Boreal	Shell-rich dark clay
2	331	4.5	Germany	Boreal	Shell-rich dark clay
3, 4, 5, 6	238, 267, 437, 256	6.0, 6.9, 5.2, 5.0	Netherlands	Boreal	Bioclastic sand
8	141	4.5	Belgium	Boreal	Bioclastic sand
9	160	3.5	France	SE North Atlantic	Bioclastic sand
13	275	8.0	Austria	Paratethys	Bioclastic sand
14, 15	234, 246	3.0, 3.1	Hungary	Paratethys	Bioclastic sand
16	119	4.1	Hungary	Paratethys	Bioclastic sand
17, 18	229, 253	3.3, 3.15	Austria	Paratethys	Shell-rich light sandy marl

(see Zuschin et al., 2005). Third, it relates the effects of mesh-size biases to the size-frequency distributions of specimens in the samples studied. Fourth, this study links patterns at the local and regional scale by testing the ability of spatial pooling to ameliorate the mesh-size bias. Finally, it demonstrates the effects of using biomass instead of relative abundance on the mesh-size bias.

DATA AND METHODS

The data and methods used here follow those of Kowalewski and Hoffmeister (2003), which are summarized below. The data set consisted of 3868 molluscan specimens from 17 individual bulk samples collected from two marine bioprovinces of Europe (Kowalewski et al., 2002; see also Hoffmeister and Kowalewski, 2001). To maintain adequate sample sizes throughout the sieving process (see below), only 14 bulk samples were used here (Table 1 and Supplementary Data¹). Most of these samples were collected from bioclastic sands, with several from clays or marls (Table 1; Kowalewski et al., 2002). A number of samples were collected from multiple sites from the same bed at the same outcrop, and thus they constitute replicate samples (Table 1). Fossils were extracted from the matrix with fine-meshed sieves (≤ 1 mm) and were identified to the lowest taxonomic level possible, typically species or genus, although all analyses shown here were performed at the genus level. Counting methods were discussed by Kowalewski and Hoffmeister (2003; see also Gilinsky and Bennington, 1994; Bambach and Kowalewski, 2000). The size of each specimen was measured to the nearest 0.1 mm; gastropod size was estimated as shell height, and bivalve size was estimated as the greater of the anterior-posterior length and the dorsal-ventral height.

Each genus was classified ecologically according to three variables (tiering, motility, and feeding mechanism), and assignments were made by functional morphology and by reference to living taxa. Genera were used instead of species for several reasons. First, this is one in a series of papers in which the data are analyzed at the genus level (Bush and Bambach, 2004a, 2004b; Bambach et al., 2007; Bush et al., 2007). Second, not all species in the data set were identified to the species level, so species-level assessments were not always possible. Third, not all the species are extant, so ecologic assignments are often based on extrapolation to some extent, and working at the genus level is a conservative approach. Fourth, these ecologic categories are rather broad, limiting the amount of species-specific variation within genera. Working at the genus level may nonetheless conceal some amount of variation within genera, but given the points above, it is a relatively minor source of variation.

The ecologic categories are the same as those used by Bush and Bambach (2004b), Bush et al. (2007), and Bambach et al. (2007); the raw data and ecologic assignments are listed in the Supplementary Data¹. Tiering refers to the position of an animal's body relative to the sediment-water interface (Ausich and Bottjer, 1982, 1985), and includes the following categories: pelagic (in the water column, free of the substrate),

erect (extending from the substrate surface into the water column), surficial (on the sediment surface, not extending appreciably upward), semi-infaunal (part of the body buried, part exposed to the water), shallow infaunal (burrowing, living in the top ~5 cm of the sediment or substrate), and deep infaunal (burrowing, living more deeply). Motility refers to the ability of an animal to move under its own power (Bambach et al., 2002) and is divided into the following categories: nonmotile, facultatively motile (able to move if disturbed or threatened), and fully motile (moving routinely). The nonmotile and facultatively motile categories are split into attached and unattached forms, and the fully motile category is split into fast-moving (swimming, walking) and slow-moving (creeping, burrowing) forms. Feeding mechanism is the process by which an animal collects food, as opposed to diet, which is the type of food eaten (Bambach et al., 2007; Bush et al., 2007). Feeding mechanism is often more easily determined than diet for extinct organisms and includes the following categories: suspension feeding (trapping suspended food from the water column), surface deposit feeding (eating food deposited on the sediment surface), mining (eating buried particles), grazing (scraping or nibbling of nonmotile organisms of any sort that are incapable of significant resistance), predation (hunting or ambushing prey that are capable of mechanical resistance; includes scavenging), and other (in this case, parasitism).

Some mollusks change mode of life as they pass from juvenile to adult life stages, but only adult life habits are coded here. In part, this reflects practical considerations, not the least a lack of information about the juvenile life habits of many extinct species. For some extinct species, adult and juvenile modes of life could be designated based on differences in shell morphology, but nonarbitrary criteria for assigning individual specimens to the adult or juvenile category are often lacking. One could pick a boundary based on size for each species, but this would be somewhat speculative and arbitrary, especially for extinct species. Instead, the problem of ontogenetic shifts in autecology is simply acknowledged.

The smallest sieve size presented is 2 mm, which excludes size classes that may have extremely large numbers of larval and juvenile forms for many common species (thus, this study does not address the effects of sieving on assemblages of juveniles or very small adults). To explore the additional effects of not coding juvenile life habits, a survey of the literature on juvenile bivalve life habits is presented below. Bivalves were targeted because there are many documented examples of bivalve taxa with separate juvenile and adult life habits. The taxa discussed below are not necessarily represented in this data set but are well-documented examples from the literature.

In general, a planktonic bivalve larva secretes a byssal thread, attaches to the substrate during metamorphosis, and (often) lose the byssus soon after. In many species, however, juveniles can resuspend and relocate by byssal drifting, in which a long byssal thread is used as a sail or parachute. The juveniles employing byssal drifting are generally less than 2–3 mm in shell length (Sigurdsson et al., 1976; Lane et al., 1985; Cummings et al., 1993, 1995; Baker and Mann, 1997; de Montaudouin, 2004).

In some cases, bivalve species exhibit adult life habits by the time the

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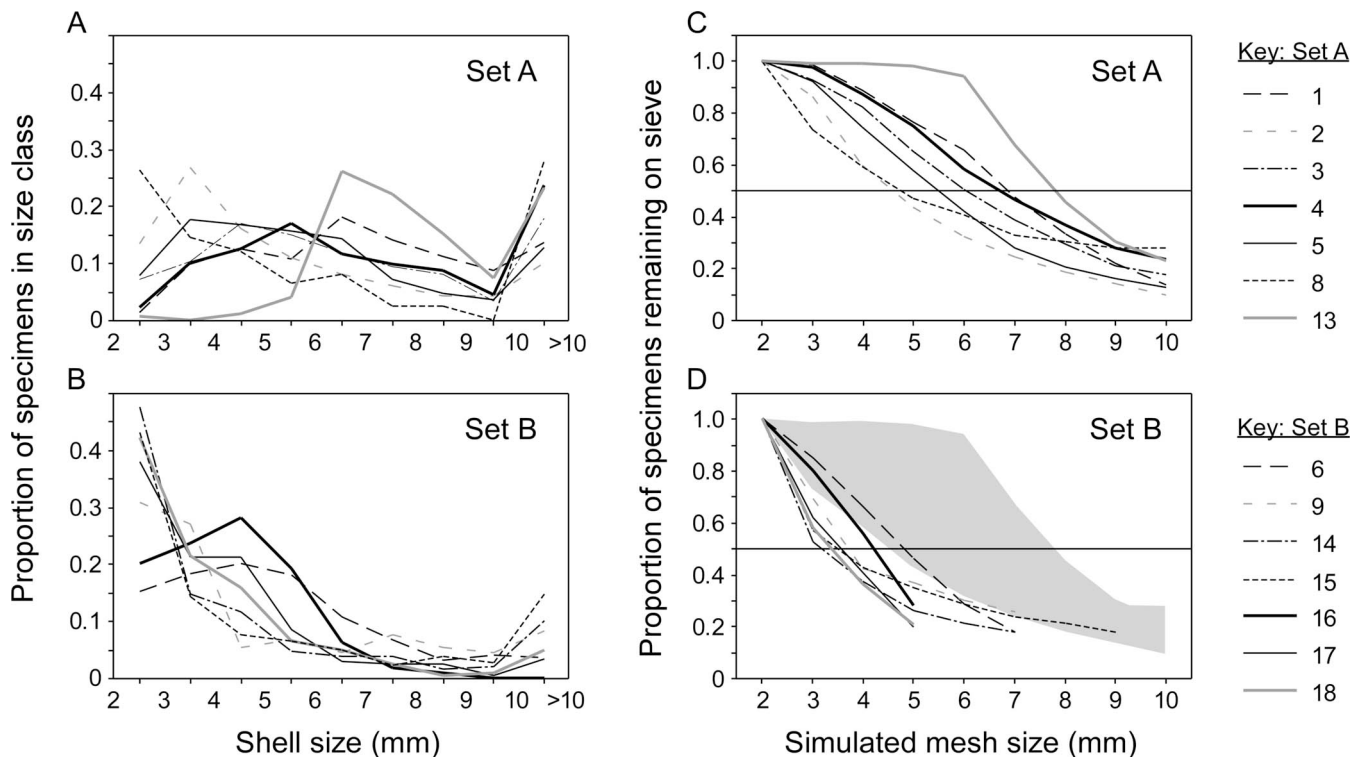


FIGURE 1—Size-frequency information for set A (seven samples with ≥ 30 specimens ≥ 10 mm) and set B (seven additional samples with ≥ 30 specimens ≥ 5 mm). A–B) Size-frequency distributions. C–D) Proportional sample-size decay curves. Gray field shows range of values from C.

shell reaches 2 mm in length. *Crassostrea virginica* (Ostreidae) cements immediately upon settling at a size of 0.3–0.4 mm (Kennedy, 1996); likewise, *Chama congregata* (Chamidae) attaches by a byssus at a length of 0.2 mm and is permanently cemented at a length of 0.35 mm (LaBarbera and Chanley, 1971). Juvenile *Mytilus* reach the heteromyarian configuration associated with attachment by a size of 1–2 mm (Fuller and Lutz, 1989). Some free-living bivalves also attain adult life habits at small shell sizes. For example, the tellinids *Macoma balthica* and *Macomona liliana* start burrowing by the time their shell length reaches 2 mm (Caddy, 1969; Cummings et al., 1993). The pholad *Barnea manilensis* begins boring before its shell reaches 2 mm (Ito, 1999). After settling, young *Venus striatula* quickly develops an exhalant siphon and burrows, often to a depth greater than the length of the siphon, drawing water from between sand grains (Ansell, 1962).

Some modern bivalve taxa do shift life habits at sizes greater than 2 mm. A classic case is *Mercenaria mercenaria* (Veneridae), which is a shallow, unattached burrower as an adult. Juveniles alternate between byssal attachment and active crawling, with the byssus lost at an average shell length of 7 mm (Carriker, 1961, p. 184). The clam's siphons form while the animal is a juvenile, with definite inhalant and exhalant siphons at a shell length of about 4 mm. In the related *Meretrix lamarckii*, byssal threads are used before the clam achieves a shell length of approximately 5 mm (Narihara and Morisue, 1991). Similarly, juveniles of *Mya arenaria* can be quite active until a length of 15 mm—alternately attaching with the byssus, crawling, and burrowing—before settling down to a permanently infaunal existence (Baker and Mann, 1991). The geoduck *Panope abrupta* stays on or near the sediment surface until a shell length of about 15 mm, at which point the siphons lengthen and it begins to shift toward deep burrowing (Strathmann, 1987). Juvenile bay scallops, *Argopecten irradians*, attach to eelgrass well above the sediment surface, probably to avoid predation. At shell lengths of 11–31 mm, however, they relocate and live unattached on the seafloor (Garcia-Esquivel and Bricelj, 1993). *Chlamys gigantea* (= *Hinnites multirugosus*; see Strathmann, 1987) first

attaches by byssal threads and is capable of facultative motility, cementing to rocks at a shell size of 2.2–4.2 cm (Yonge, 1951).

Many of these cases of ontogenetic shifts at sizes greater than 2 mm occur in large, long-lived species. For example, *Mercenaria mercenaria* spends only a few weeks in its unique juvenile lifestyle before entering up to a decade or more of life as an unattached burrower (Carriker, 1961). Most of the species discussed here spend the majority of their lives as adults. Therefore, assigning the adult autecology to the occasional juvenile probably has little effect on the analysis of the net contribution of a species to an ecosystem in terms of time and energy flow.

To simulate the effects of sieving, those specimens whose measured sizes were greater than the specified mesh size were retained in a subsample, while the remainder were removed. As noted by Kowalewski and Hoffmeister (2003), this is not an entirely realistic simulation of real-world sieving because the estimated sizes used here are maximum values, and many specimens whose maximum dimensions were greater than the mesh size could pass through an actual sieve if their other dimensions were less. These authors also tried two additional sieving protocols for bivalves, for which more than one linear dimension was measured. In one of these protocols, a specimen was allowed to pass through the mesh if its minimum measured length was less than the mesh size, even if its maximum length was greater. These end-member recreations of physically plausible sieving scenarios produced highly similar results, indicating that the simulation performs consistently across a range of sieving protocols.

As one sieves a finite sample with progressively larger mesh sizes, the sample size drops as progressively larger specimens are excluded, as demonstrated by Figures 1C and 1D and by Kowalewski and Hoffmeister (2003, fig. 2). In calculating the proportional abundances of different ecologic groups, proportions were only calculated for subsamples that retained ≥ 30 specimens. All diversity analyses were performed after rarefying to 100 specimens (Hurlbert, 1971; Raup, 1975), so only subsamples that retained ≥ 100 specimens were used in these analyses. Rarefac-

tion or other subsampling methods were not needed for calculating proportions because proportions are unbiased with respect to sample size.

RESULTS

Individual Bulk Samples

Figures 1A and 1B show the size-frequency distributions of the 14 bulk samples considered here, and Figures 1C and 1D show the proportional sample-size decay curves that specify the proportion of each sample that would be retained on a sieve of each mesh size. Kidwell (2001, 2002b) suggests using mesh sizes of at least 1.5–2 mm to maximize live-dead taxonomic agreement, so only mesh sizes and specimens ≥ 2 mm are considered. In Figure 1, the samples are split into two sets: set A (Figs. 1A, 1C) contains the seven samples that retained 30 or more specimens at a mesh size of 10 mm, allowing the calculation of ecologic proportions at this mesh size (shown in Fig. 2) according to the strictures outlined above. Set B (Figs. 1B, 1D) contains seven additional samples that had at least 30 specimens at a mesh size of 5 mm (shown in Fig. 3). To a great degree, this division reflects underlying differences in size-frequency distribution. The samples from set B are generally dominated by small specimens (average median size = 3.6 mm; see Table 1), and many have a strong mode in the 2–3 mm category (Fig. 1B). In contrast, the samples from set A have a more even distribution of size classes on average (Fig. 1A) and, as a result, retain a higher proportion of their specimens on coarser sieves (Fig. 1C). Thus, they maintain a reasonable number of specimens in the larger size classes (average median size = 6.0 mm; see Table 1).

Figure 2 shows the proportional abundances of the tiering, motility, and feeding categories as mesh size changed for the samples in set A (≥ 30 specimens at a mesh size of 10 mm), and Figure 3 shows the results for set B (≥ 30 specimens at a mesh size of 5 mm). As an example showing that these effects are significant, the feeding data for sample 5 are replotted in Figure 4 with 95% confidence intervals (CIs) calculated using two sets of assumptions with a naïve bootstrap (Efron, 1981) run at 1000 iterations. For the solid lines, CIs were calculated for each ecologic group and mesh size by resampling with replacement based on the proportion of the ecologic group and the sample size remaining at that mesh size. The dashed lines provide another way of looking at the sampling error. Say 15 large specimens out of a total of 300 belong to an ecologic group at the 2 mm mesh size. This is 5%, with bootstrapped CIs of 2.6–7.6%. If all 15 specimens remain after sieving with the 10 mm mesh and the total sample size is reduced to 30, then normal bootstrapping would give CIs of 33%–66% around the estimated proportion of 50%. Relatively speaking, the width of the CIs has shrunk. The dashed lines merely scale up the sampling error calculated at finer mesh sizes, providing slightly wider (and thus more conservative) CIs in some cases, addressing the concern that sieving is underestimating the appearance of statistical sampling error. The two methods do not yield greatly different results (Fig. 4).

For some samples and some variables in Figures 2 and 3, the proportional representations of the ecologic groups were fairly constant as mesh size changed. As one example, the motility categories did not vary appreciably with mesh size in sample 4 (Fig. 2B). For other samples and variables, however, there were considerable changes in apparent ecologic structure as mesh size varied. In some cases, some ecologic categories within a variable were stable as others changed dramatically in relative abundance, and some samples were stable for one of the three ecologic variables but not for the others.

The ecologic proportions in Figure 2 are largely stable at small mesh sizes, and only begin to change dramatically above about 6–7 mm, when the majority of the specimens in the samples have been sieved away (Fig. 1C). Above mesh sizes of about 6–7 mm, some samples contained an ecologic group that “exploded” in relative abundance with only small changes in mesh size owing to the loss of common smaller specimens belonging to other ecologic groups. Examples include samples 1 and 2

for motility (Fig. 2B) and samples 1–5 for feeding type (Fig. 2C). Although ecologic composition was not always stable as mesh size changed between 1–6 mm, the changes were on average less pronounced than those observed at larger mesh sizes. A simple decrease in sample size could also cause the patterns to be more volatile at coarser mesh sizes (even if bigger specimens were representative of smaller ones), but the widths of the confidence intervals (e.g., Fig. 4) suggest that this is not the case. Notably, the two samples in Figure 2 that were least stable in ecologic proportions at mesh sizes < 6 mm were samples 2 and 8, and these samples lost specimens most rapidly in Figure 1C.

In contrast, the samples shown in Figure 3 are more volatile in ecologic proportions as mesh size changes among low values (2–6 mm), and these samples were dominated by specimens smaller than 6 mm. In fact, all of these samples had 30% or fewer of their specimens remaining on the 6 mm sieve (Fig. 1D).

Hierarchical Spatial Analysis

Kowalewski et al. (2002) collected this data set so that it could be analyzed hierarchically at a number of spatial scales, and this structure can be employed to test the effects of spatial averaging on mesh-size effects. If changes in mesh size elicit similar changes in ecologic composition in two or more samples, then averaging them together will not ameliorate the effects of the mesh-size bias. If, however, the samples change in composition in opposite directions as mesh size changes, then these changes will cancel out during averaging, resulting in an observed ecologic composition that is more invariant with respect to mesh size. This amelioration of the bias is a natural consequence of averaging, but how much bias does it remove, and at what spatial scale?

Figure 5A shows the average of samples 3–5, which were replicates of the same bed at the same outcrop. In Figure 2, these replicates had similar relationships between mesh size and ecologic composition, and these patterns hold in Figure 5A. Not surprisingly, averaging together several extremely similar profiles did little to damp the mesh-size bias that was present for these samples in the feeding categories. Sample 6 was also collected from this bed, although it was not averaged in because it did not have a sufficient sample size at coarse mesh sizes, and it is quite distinct ecologically (Fig. 3). Clearly, this bed captured an ecologic (or taphonomic) patch, and if it had been averaged in, it could have damped some of the mesh-size-related variability in the feeding categories. The sample pairs 14–15 and 17–18 were also collected from the same lithostratigraphic units at the same outcrops (Kowalewski et al., 2002), and plots of ecologic proportions against mesh size show clear variation within the pairs (Fig. 3). Averaging within these pairs, shown for motility as an example (Fig. 6), removes some of this volatility, despite having only two samples.

These results show the (unsurprising) fact that the effects of averaging at the outcrop scale depend on how much ecologic patchiness is captured. Still, it is notable that a great deal of mesh-size-related variation in ecologic proportions can still remain. The effects of sieving on outcrop-scale patterns (including both ecologic and taxonomic composition), however, deserve a much more detailed treatment using a sampling scheme designed specifically to test these patterns (e.g., Bennington and Rutherford, 1999). Furthermore, patchiness may have a more subtle effect on comparisons of ecologic parameters. To get an adequate sample size of large-shelled specimens, one may have to sample a larger volume of sediment than if one were studying small-shelled specimens. More voluminous samples may incorporate greater patchiness, which could affect ecologic parameters. Future collectors should bear this effect in mind.

Figure 5B shows the average of all of the samples taken from the sandy facies for which data were available for all size classes (samples 3–5, 8, 13). Samples 3–5 were averaged together first because they were replicates of the same bed and would swamp the signal otherwise. For the tiering, motility, and feeding categories, this small amount of averaging removed a large amount of variation in ecologic proportions. It might be

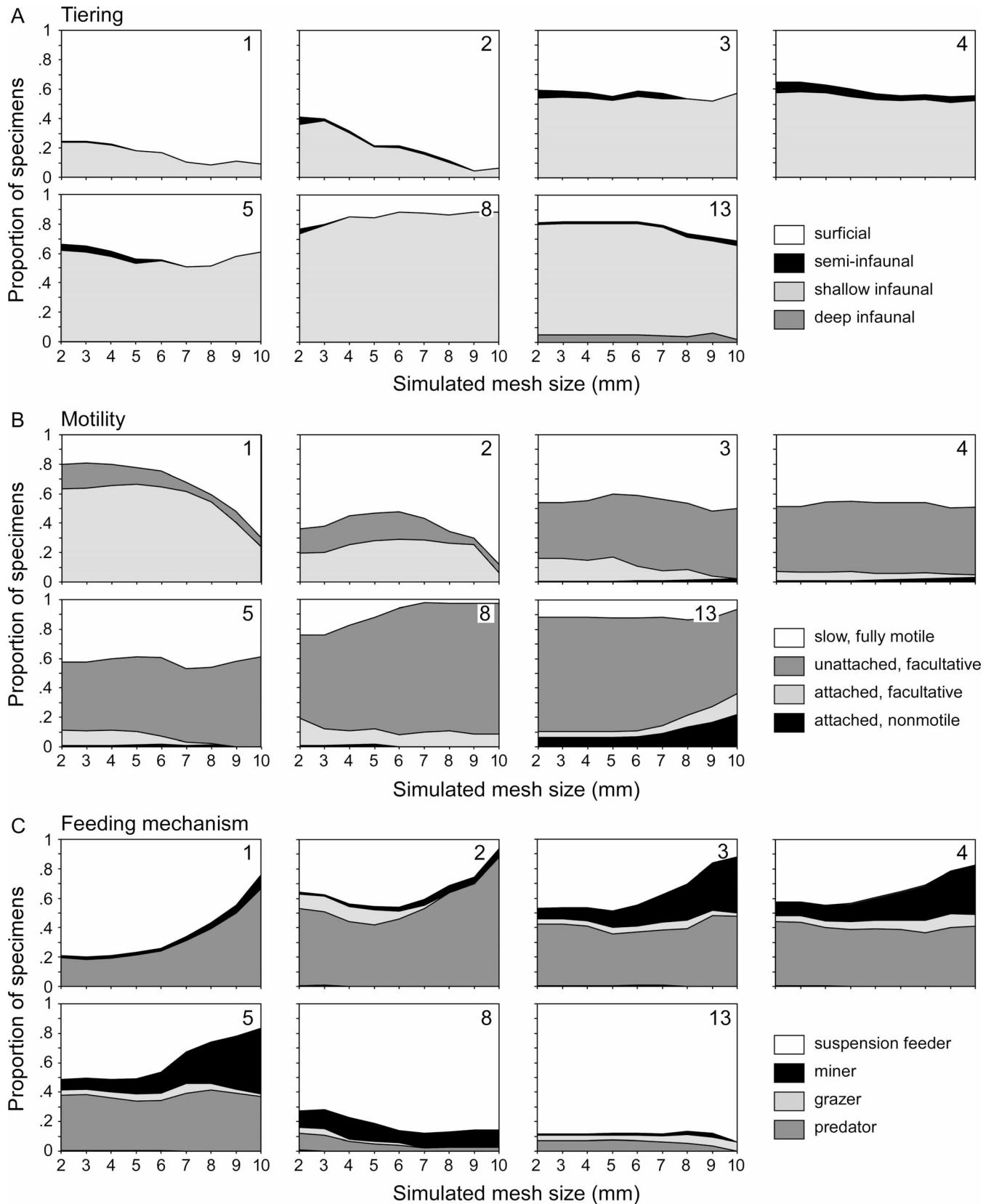


FIGURE 2—Estimated mesh-size effects on apparent proportional abundances of ecologic categories for seven individual bulk samples in set A. Proportions were calculated only when ≥ 30 specimens remained at a given mesh size. A) Tiering. B) Motility. C) Feeding mechanism. See Table 1 for sample information.

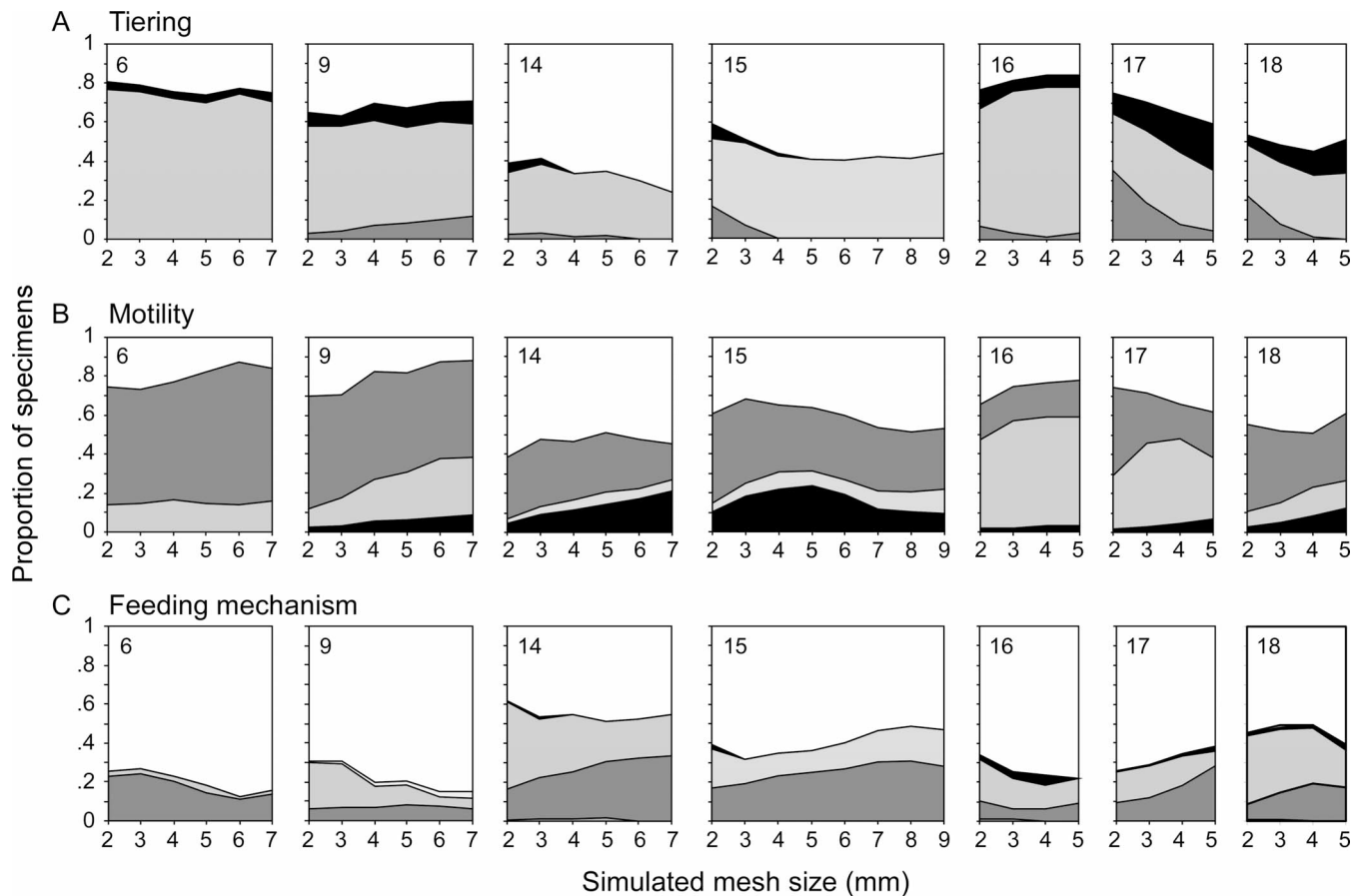


FIGURE 3—Estimated mesh-size effects on apparent proportional abundances of ecologic categories for seven additional individual bulk samples in set B. Proportions were only calculated when ≥ 30 specimens remained at a given mesh size. A) Tiering. B) Motility. C) Feeding mechanism. See Table 1 for sample information and Fig. 2 for keys to shading.

surprising that so little averaging within a single general facies removed so much bias, but from Figure 2 it is apparent that these samples are quite different in ecologic composition. Performing the same averaging analyses using greater numbers of samples but a smaller range of mesh sizes yielded similar results (not shown).

Figure 5C shows the average of all the samples for which all size classes were available, including both sandy and clayey facies. There were only two samples available from the clayey facies, and although they derived from different localities over 200 km apart, they were very similar in their responses to sieving. Therefore, averaging them in with the sandy facies actually increased the effects of sieving on ecologic proportions, but this is presumably a small sample-size problem.

The tiering, motility, and feeding categories were also combined to form more refined ecologic categories, referred to as modes of life (Bambach et al., 2007; Bush et al., 2007). For example, many bivalves in the data set were classified as either shallow infaunal, unattached facultatively motile suspension feeders or surficial, attached facultatively motile suspension feeders, and many gastropods were classified as surficial, slow motile predators. The relative abundances of these modes of life are shown in the bottom row of Figure 5; the three modes of life mentioned above are labeled *i*, *ii*, and *iii*, respectively. These modes of life could be summed in various ways to form the tiering, motility, and feeding categories. Again, the spatial averaging shown in Figures 5B and 5C reduced the variability in apparent ecologic composition related to mesh-size variations. While many modes of life varied in relative abundance as mesh size changed, the most abundant modes at least remained present across the full range of mesh sizes tested.

Biomass

The effects of the mesh-size bias were also calculated using estimates of biomass (Staff et al., 1985; McKinney et al., 1998; Finnegan and Droser, 2005b; Payne et al., 2006; Payne and Finnegan, 2006) instead of abundance counts (Fig. 5D). Biomass was assumed to be proportional to volume, which was estimated as being proportional to the cube of the maximum dimension of each specimen. In general, shell volume is an imperfect proxy for biomass because different higher taxa have different ratios of biomass to shell volume (e.g., mollusks vs. brachiopods). This is not such a problem for a mollusk-only data set, but the method is still not entirely realistic because it assumes that the bivalves and gastropods in the data set did not vary in shape. A better estimate could have been calculated for bivalves, for which both anterior-posterior and dorsal-ventral lengths were measured, but this would preferentially lower the apparent biomass of bivalves relative to gastropods. Although rough, this protocol was considered useful because the error introduced is less than the signal recovered. A 2 mm specimen and a 20 mm specimen differ from one another in calculated volume by a factor of 1000, whereas variations in volume resulting from differences in shape are in general going to be 1–2 orders of magnitude less important.

The mesh-size bias was further attenuated by using biomass instead of abundance; the relative biomass values of the ecologic categories changed relatively little as mesh size changed in the averaged data (Fig. 5D). This result is a logical geometric consequence of using biomass; because biomass is related to length cubed, the contribution of small specimens to the observed proportions of the ecologic groups was greatly reduced, and their loss via sieving had less effect. Whether or not the heavy weighting

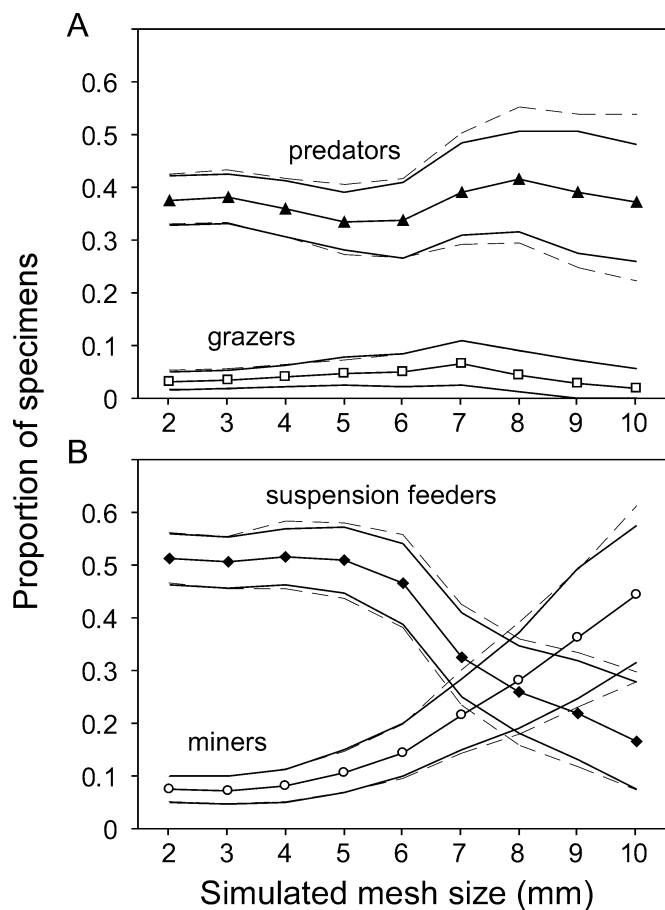


FIGURE 4—Proportional abundances of feeding groups for sample 5, with 95% confidence intervals calculated using naïve bootstraps based on two sets of assumptions (see text for further explanation). Data are split onto two plots for clarity. A) Predators and grazers. B) Suspension feeders and miners.

of large specimens and the virtual neglect of very small specimens is otherwise beneficial to a particular analysis must be determined, however. Although these specific results should not be interpreted too strongly because biomass was estimated roughly, the fact that biomass reduces the influence of small specimens should make it resilient to mesh-size biases in other cases as well.

Richness

Richness, the number of taxonomic (or ecologic) units in a single collection, is of great interest in studies of alpha diversity history (e.g., Bambach, 1977, 1983; Westrop and Adrain, 1998; Kidwell, 2002a; Powell and Kowalewski, 2002; Bush et al., 2004; Bush and Bambach, 2004a, 2004b; Peters, 2004; Finnegan and Droser, 2005a; Kowalewski et al., 2006). In sieved samples, the total richness of a finite assemblage must decrease as mesh size coarsens because specimens are being removed, and eventually taxa and modes of life will be lost. If the samples are rarefied (Hurlbert, 1971; Raup, 1975) to a constant number of specimens after sieving, however, the number of taxa or modes of life need not decrease as mesh size increases. For example, if sieving removes a small, hyperabundant taxon, the rarefied richness can actually increase with mesh size (e.g., Kowalewski et al., 2006, fig. 10).

Kowalewski and Hoffmeister (2003) examined the effects of mesh size on the richness of these samples pooled by bioprovince, finding that species richness dropped by an average of 19% between sieve sizes of 2 mm and 10 mm when data from the two bioprovinces were rarefied to 200 specimens. Similarly, when rarefied to 100 specimens, the number of

genera and modes of life each dropped by an average of 16%–17% (9% and 24%; 16% and 16%, respectively).

Figure 7 extends this analysis to individual bulk samples, with richness shown as both the number of genera and modes of life, rarefied in each case to 100 specimens. Curves are only shown for samples that had 100 specimens remaining at a mesh size of 5 mm. Both measures of richness were fairly stable for these samples up to a mesh size of about 5–6 mm, which is perhaps not surprising, given that these particular samples all had broad size-frequency distributions that included significant proportions of larger specimens (average median value = 6.1 mm; see Table 1). Considering coarser meshes, the richness of several samples began to change either upward or downward. From a mesh size of 2 mm to the maximum mesh size shown for each sample, some samples decreased in richness while others increased overall; on average, the number of modes of life dropped by 2.3%, and the number of genera dropped by 1.1%. This is a small amount relative to the width of the confidence intervals around the data points (Fig. 7). This is also a minor amount compared to the apparent effects of mesh size at the province level, but some of this results from a narrower range of mesh sizes. Between mesh sizes of 2 mm and 7 mm, the range of mesh sizes available for many of the individual samples in Figures 7A and 7B, the regional data only dropped in richness by an average of 9% (number of modes of life or genera) or 3% (number of species).

DISCUSSION AND CONCLUSIONS

The effects of mesh size on the ecologic composition of these molluscan samples from the Miocene of Europe are at once cautionary and heartening. Comparisons of the properties of individual samples should be made with care because changes in the mesh size with which a sample was processed (or the degree to which other processes affected the size-distribution of fossils) can have noticeable effects on its apparent ecologic composition. Therefore, two samples from identical paleocommunities could appear ecologically distinct if they were processed differently. For example, sample 1 would appear to be dominated by attached, facultatively motile forms if sieved with 1–7 mm meshes, but it would appear to be dominated by slow, fully motile forms if sieved with a 10 mm mesh (Fig. 2B). As shown by Kowalewski and Hoffmeister (2003) for other ecologic parameters, comparisons of two or more samples may yield different results depending on the mesh size used, even if that mesh size is constant among samples. These problems are not universal, however; the proportions of some ecologic types in some samples were not greatly affected by heterogeneous sieving.

The severity of the mesh-size bias (that is, the degree to which ecologic proportions or other parameters vary with mesh size) depends in part on the size-frequency distribution of a particular sample. Samples dominated by small specimens have more potential to be volatile in ecologic composition, as sieves vary among fine meshes, than those dominated by large individuals. This result is, of course, intuitive; once much of a sample has been removed by sieving, only the upper tail of the size distribution remains, and this tail is often not ecologically representative of the entire sample. The samples in set A, shown in Figures 1A, 1C, and 2, have larger specimens, and, on average, they do not lose half of their specimens until sieved with a 6 mm mesh. These samples also tend to have stable proportions of ecologic categories below about 6 mm mesh size. In contrast, the samples in set B, shown in Figures 1B, 1D, and 3, are dominated by smaller specimens—the average sample loses half of its specimens larger than 2 mm between the 3 mm and 4 mm sieves. The apparent ecologic proportions of these samples are much more volatile at mesh sizes <6 mm (Fig. 3).

Given these data, what size mesh should be used when one intends to calculate relative abundances and ecologic proportions? Kidwell (2001, 2002b) found molluscan death assemblages sieved with mesh sizes >1 mm had better taxonomic fidelity to the original living community than those sieved with finer meshes because finer meshes picked up large

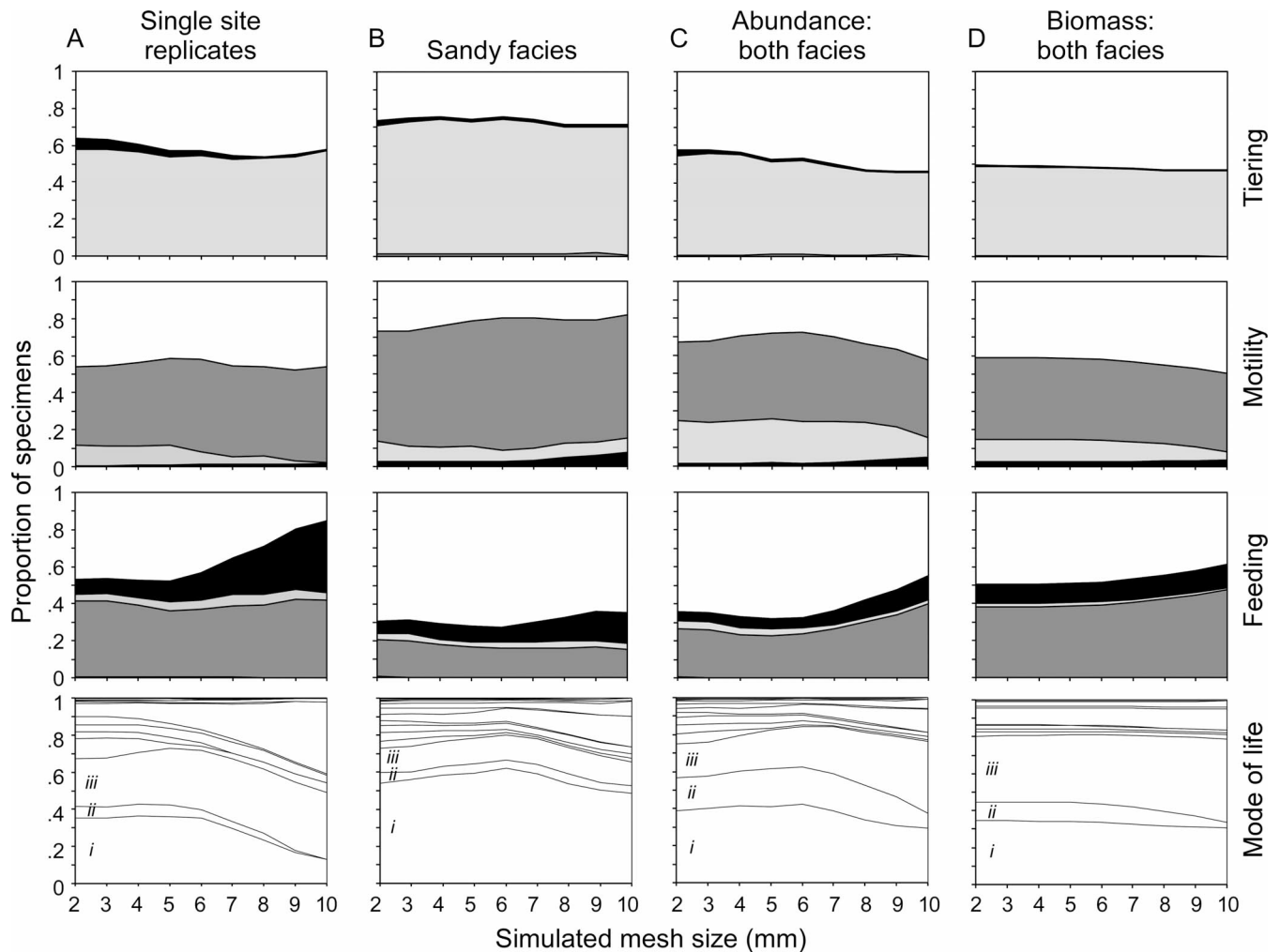


FIGURE 5—Estimated mesh-size effects on ecologic composition averaged over various combinations of the seven samples with ≥ 30 specimens remaining at mesh size of 10 mm (set A; see Figs. 1A, 1C, 2). A) Single site replicates (samples 3–5) combined. B) Samples from sandy facies combined (3, 4, 5, 8, 13). Samples 3–5 were averaged first because they represent the same location. C) All Fig. 2 samples combined, with 3–5 averaged first. D) All Fig. 2 samples combined using estimates of biomass instead of relative abundance. See Fig. 2 for keys to shading and text for further explanation.

numbers of juveniles that occur as irregular spatfalls. Therefore, mesh sizes < 2 mm are probably best avoided. Beyond this, the goal of calculating proportions is to characterize the entire fauna, so finer meshes, or coarser meshes that yield similar results, should be preferred. One should certainly not use a sieve that is so coarse that it excludes the majority of the size-frequency distribution (the majority of the distribution, that is, considering specimens ≥ 2 mm) because this larger half of the population may be ecologically distinct from the sample as a whole.

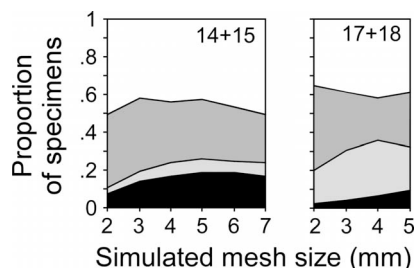


FIGURE 6—More examples of estimated mesh-size effects on ecologic composition averaged over pairs of samples from the same outcrop and lithostratigraphic unit. Both examples show motility groups; see Fig. 2B for key to shading. A) Sample pair 14–15. B) Sample pair 17–18.

For most samples in Figure 2, a mesh ≤ 6 mm would probably be sufficient, but for the samples shown in Figure 3, this could remove most of the specimens in the sample and do an imperfect job of characterizing the ecology of the populations. In general, therefore, late Cenozoic molluscan assemblages should probably be sieved with finer meshes, say, ≤ 4 mm. For calculating ecologic proportions, one could choose from mesh sizes between 2 mm and 4 mm depending on the trade-off between the mesh-size bias on one hand and the problem of assigning adult life habits to juveniles on the other. Alternatively, one could take a more refined approach to dealing with juvenile life habits.

For characterizing taphonomic signatures of molluscan assemblages, Kidwell et al. (2001) have significantly different recommendations regarding sieving. They advocate the separation of shells into size classes rather than the use of a single mesh-size cutoff. This should facilitate standardized comparisons between samples because size-frequency distributions vary considerably among samples and the frequency of taphonomic damage is often lower for smaller size classes. They also recommend using larger size fractions to maximize the detection of taphonomic damage. The ecologic proportions in the samples in Figures 2–3 do not all respond in a similar manner to changes in mesh size, so similar recommendations about size fractions are not relevant here.

Although the effects of mesh size on ecologic composition can be quite severe for some individual samples, they are less dramatic for faunas

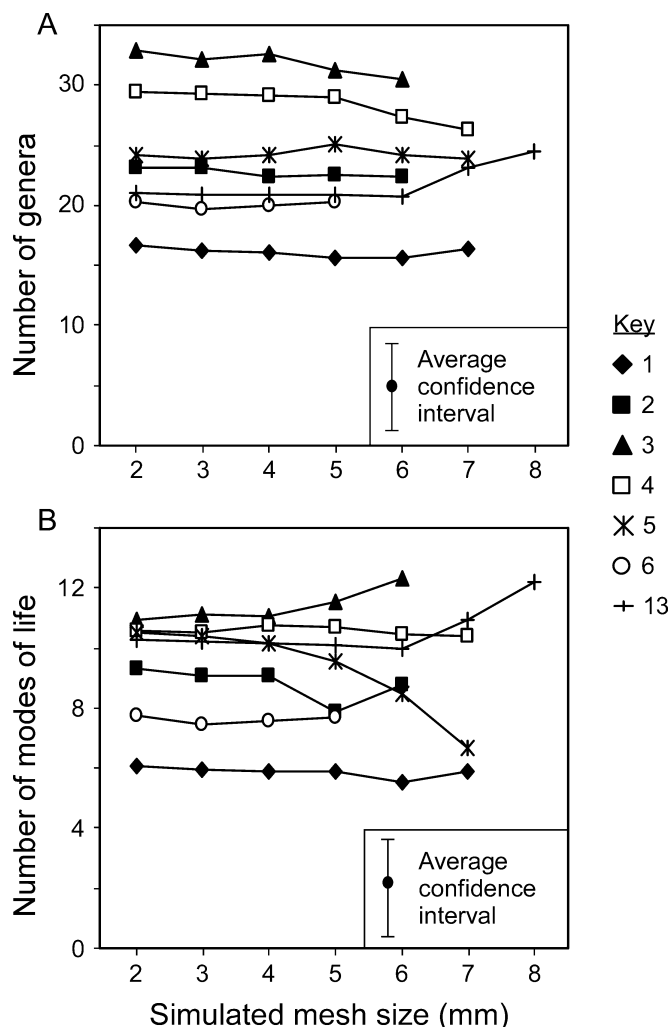


FIGURE 7—Effects of mesh-size bias on two rarefied richness measures. A) Number of genera in individual samples. B) Number of modes of life in individual samples. Curves are only shown for samples with 100 specimens remaining at mesh size of 5 mm; if 100 specimens were not available for a given sample and mesh size, no data point is shown.

averaged among samples (Fig. 5). This smoothing results simply from averaging those samples that vary greatly in composition as mesh size changes with those that do not with those that change in different ways. This is a natural consequence of averaging, so it should often be useful. This smoothing can occur at the bed or outcrop level, but only if replicate samples pick up patchiness. Averaging at the regional scale can further reduce the effects of mesh-size biases (Figs. 5B, 5C), and the use of biomass estimates were quite effective at damping the effects of the bias at the expense of virtually eliminating the influence of very small specimens on the results (Fig. 5D). Other data sets might react differently to averaging. If ecologic composition varied in a consistent way among samples as mesh size changed, then averaging would be less effective at smoothing out size-filtering biases. At the very least, however, averaging many samples to get a regional view of ecospace use should not intensify size-filtering biases.

These results from averaged samples are encouraging because broad-scale comparisons of secular trends in ecologic parameters must often rely on heterogeneously collected data. For example, Bush et al. (2007) compared the ecologic composition of a database of mid-Paleozoic and late Cenozoic fossil assemblages collected from the literature using the same ecologic groupings that were used here. The Cenozoic samples were sieved by different workers, and the Paleozoic samples were collected

using various methods from lithified rocks, which impose size filters of unknown intensity. They found large differences in ecologic composition between the two data sets, and it is encouraging to know that spatial and environmental averaging can help ameliorate the heterogeneities in size filtering that are inherent in a literature survey (Bush et al. also dealt with other heterogeneities using other tests). It should be noted, however, that others have suggested that size filtering associated with lithification may have stronger effects on measured diversity than those observed here (e.g., Hendy, 2005; Kowalewski et al., 2006).

Several studies have now shown that the apparent taxonomic and ecologic composition and diversity of fossil samples are affected by heterogeneities in size filtering. It is encouraging, however, that some of these studies have also suggested that the effects of these biases can be reduced by choosing a particular mesh size or spatial scale for the analysis. Further work should establish the generality of these conclusions and suggest further strategies for collecting and comparing fossil assemblages.

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