Relative and absolute abundance of trilobites and rhynchonelliform brachiopods across the Lower/Middle Ordovician boundary, eastern Basin and Range

Seth Finnegan and Mary L. Droser

Abstract.—Relative abundance data are of primary importance in paleoecology, but it is not always obvious how they should be interpreted. Because relative abundance is expressed as a proportion of the total sample, change in the abundance of one group necessarily changes the relative abundance of *all* groups in the sample. There are two possible interpretations for a trend in the relative abundance of a taxon: an ''active'' scenario in which the trend reflects change in the population density of the group itself, or a ''passive'' scenario in which the change is driven by population changes in other taxa. To discriminate between these scenarios it is necessary to collect absolute abundance data (abundance expressed as a function of sample area or volume).

We examine both absolute and relative abundance trends through a major paleoecological transition: the shift from trilobite-dominated to brachiopod-dominated paleocommunities in shallow marine carbonates spanning the Lower/Middle Ordovician boundary in western Utah and eastern Nevada. We sampled 61 carbonate mudstone and wackestone beds from the upper Ibex Series (Lower Ordovician) and lower Whiterock Series (Middle Ordovician) at three sections that span the boundary. All samples come from the shallow subtidal Bathyurid trilobite biofacies. Samples were broken into small pieces, and all skeletal fragments >2 mm were identified to the finest possible taxonomic level. Consistent with previous work on this interval, the relative abundance of trilobites declines sharply across the boundary, while the relative abundance of brachiopods increases. Absolute abundance data indicate that the decline in trilobite abundance is genuine and not an artifact of normalization. The trend is not easily explained by sampling bias, facies distribution, taphonomic regime, or sedimentation style.

The dramatic shift in abundance contrasts with relatively minor changes in relative genus richness across the boundary. This is partly ascribable to differences in the relative abundance structure of trilobite faunas. Though comparable numbers of trilobite and brachiopod genera occur above and below the boundary, the trilobite fauna from the upper Ibex Series has lower evenness then the lower Whiterock Series fauna. Hence sampled trilobite richness is high in the lower Whiterock despite the small number of specimens. This highlights the importance of collecting abundance data. Although these data suggest that in at least some cases richness and abundance patterns are not closely coupled, more robust richness data are necessary to confirm this conclusion.

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Introduction

Delineating long-term changes in the structure of ecosystems is the principal goal of paleoecology. Doing so means integrating many kinds of data. These include the distribution of taxa among paleocommunities (taxonomic composition), the geographic and environmental distribution of taxa (biogeography), and the distribution of individuals and biomass among taxa (diversity-abundance structure). Abundance patterns are particularly difficult to reconstruct. Taxon counts are rarely available in the published literature, and a spectrum of taphonomic processes can potentially skew the abundance structure of fossil assemblages away from that of the biological communities from which they derive (Springer and Miller 1990; Parsons and Brett 1991; Kidwell and Bosence 1991; Kidwell and Flessa 1995; Martin 1999; Behrensmeyer et al. 2000). Recent work, however, suggests that for at least some groups fossil assemblages record a surprisingly faithful signal of original community abundance structure (Kidwell 2001, 2002). This finding has spurred greater interest in abundance data and their relationship to patterns of taxonomic diversity (Wing et al. 1993; Lupia et al. 1999; Powell and Kowalewski 2002; Novack-Gottshall and Miller 2003a,b; Peters 2004a,b), lineage evolution

(Kucera and Malmgren 1998), and environmental change (Pandolfi 1999).

Abundance can be measured in two distinctly different ways. Paleoecologists typically measure taxon abundance as a proportion of all individuals in the sample (relative abundance). The relative abundance structure of an assemblage is, ideally, a probability distribution describing the likelihood that an individual randomly sampled from the assemblage will belong to the target group. There are both practical and theoretical reasons for this approach. Relative abundance data can be fairly easily collected in the field or laboratory, and can be used to compare fossil assemblages from widely varying depositional environments. They are robust to variation in sample size, especially where ecologically dominant taxa are concerned. The apportioning of individuals among taxa (evenness, or its inverse, dominance) is essential information for calibrating diversity estimates (Sanders 1968) and may itself be an ecologically important aspect of community structure (Magurran 1988; Peters 2004a).

Abundance can also be measured as a function of the total area or volume sampled (density, or absolute abundance), rather than the number of individuals sampled. Absolute abundance data are routinely used by neontologists to define ecological gradients. However, paleontological absolute abundance data are harder to interpret than data from living assemblages. Fossil density distributions are usually spatially and volumetrically patchy at several scales, and this patchiness reflects taphonomic and depositional as well as ecological patterns (Cummins et al. 1986a; Kidwell 1986; Miller and Cummins 1990). For this reason, and because they are difficult and time consuming to obtain, paleontologists rarely collect absolute abundance data (but see Schneider 2001, for an example).

Nevertheless, there are compelling reasons for collecting these data in some situations. It is impossible to resolve the ecological meaning of abundance trends on the basis of relative abundance data alone (Jackson 1997). Normalizing to the number of individuals in the sample necessarily couples variables that may be entirely uncorrelated (Aitchison 1981,
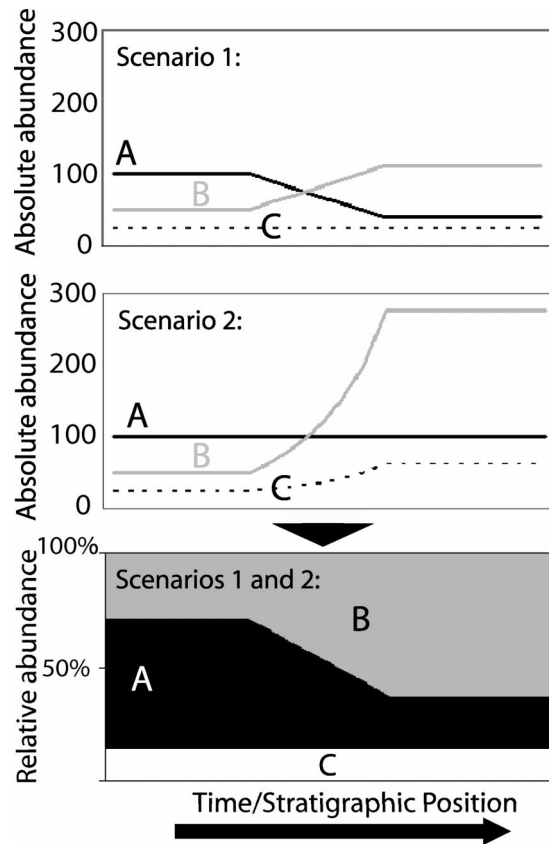

FIGURE 1. Two hypothetical sets of absolute abundance trajectories that produce identical relative abundance trends. In scenario 1, the decline in relative abundance of taxon A results from a true decrease in its absolute abundance. In scenario 2, the decline is an artifact of normalization and is driven by increases in the absolute abundance of taxa B and C.

1982). Discounting the nonbiological factors that affect fossil abundance, any change in the relative abundance of a taxon can be explained in two ways (Fig. 1). A change in its absolute abundance will obviously cause a corresponding change in its relative abundance. Alternatively, the shift may be driven by changes in the absolute abundance of *other* taxa in the assemblage, such that the absolute abundance of the taxon itself does not change, but its relative contribution to the sample necessarily does. This has been referred to as ''the problem of closed arrays'' (Grayson 1984). Discriminating between the two cases is of obvious significance: in the former case the shift in relative abundance has true ecological significance for the taxon under consideration; in the latter

case it is a spurious artifact of data normalization.

A dramatic transformation in the structure of benthic macroinvertebrate assemblages occurred during the Ordovician Period. Over the 46 million years of the period (Webby et al. 2004a), the preserved familial diversity of marine invertebrates nearly tripled (Sepkoski 1993), and many of the taxa that characterize marine ecosystems for the remainder of the Paleozoic first rose to ecological dominance (Sepkoski 1981; Bambach 1985; Droser et al. 1996; Peters 2004b; Webby et al. 2004a). Perhaps the most conspicuous increase in both diversity and abundance occurred among the rhynchonelliform brachiopods, especially the orthides and strophomenides (Williams and Harper 2000; Harper and MacNiocaill 2002; Harper et al. 2004). Though they are minor elements of most Cambrian benthic assemblages, rhynchonelliform brachiopods taxonomically and numerically dominate most post-Ordovician Paleozoic benthic assemblages. In contrast, trilobites dominate the majority of Cambrian assemblages but are less conspicuous in most post-Ordovician assemblages (Droser et al. 1996; Adrain et al. 2000; Peters 2004b).

Sepkoski and Sheehan (1983) and Sepkoski and Miller (1985) showed that by the Late Ordovician paleocommunities taxonomically dominated by trilobites are generally restricted to deep-water settings, whereas shallow-water paleocommunities are taxonomically dominated by orthide and other brachiopods. It has since been demonstrated by Westrop and Adrain (1998a) and Adrain et al. (2000) that there is no decrease in the average alpha (local) species richness of trilobite assemblages between the Late Cambrian and the mid Silurian. This implies that the decline of trilobite-dominated shallow-water assemblages is driven by taxonomic dilution of trilobite richness as the richness of other clades increases in onshore and midshelf settings.

It has been argued that the apparent decrease in trilobite *abundance* is also relative in nature, and results from physical dilution of trilobite material by the influx of material from new skeletonized taxa, especially calciate brachiopods (Westrop et al. 1995; Westrop

and Adrain 1998a,b; Adrain et al. 2000). Alternatively, the shift may be interpreted as reflecting a genuine decline in the absolute abundance of trilobite shell material that is roughly synchronous with an increase in the absolute abundance of brachiopod material (Droser et al. 1996; Miller et al. 1998; Li and Droser 1999). The first scenario provides support for a strong linkage between abundance and taxonomic diversity, whereas the second implies that, in some cases, the two may be partially decoupled.

The dominance transition is quite abrupt in places. In the classic carbonate strata of the Basin and Range (Utah, Nevada, and California), the faunal composition of shell beds shifts sharply from trilobite-dominated to brachiopod-dominated near the boundary between the Lower Ordovician Ibex Series (489–472 Ma) and the Middle Ordovician Whiterock Series (472–457.5 Ma) (Li and Droser 1999). The pattern is apparent in a variety of lithofacies and persists through the remainder of the Basin and Range Ordovician. However, the lack of published numerical abundance data and concerns about the ecological fidelity of shell beds mean that these data cannot by themselves resolve the nature of the shift in relative abundance.

The Ibex-Whiterock boundary interval appears to be a critical period during which many of the evolutionary events associated with Ordovician biodiversification took place, both regionally and globally (Droser et al. 1996). Events occurring at or near the boundary include the first Laurentian appearance of several new trilobite families (Fortey and Droser 1996, 1999), the global diversification of the Whiterock Evolutionary Fauna of trilobites (Adrain et al. 1998, 2004), regional and global diversifications of rhynchonelliform brachiopods (Harper and MacNiocaill 2002; Harper et al. 2004), and a sharp increase in the overall macrofaunal diversity of the global oceans (Miller and Foote 1996). Paleoecological trends associated with this interval are thus of considerable interest.

Below, we examine both relative and absolute abundance trends in 61 samples collected from shallow subtidal carbonate strata spanning the Ibex/Whiterock boundary at three
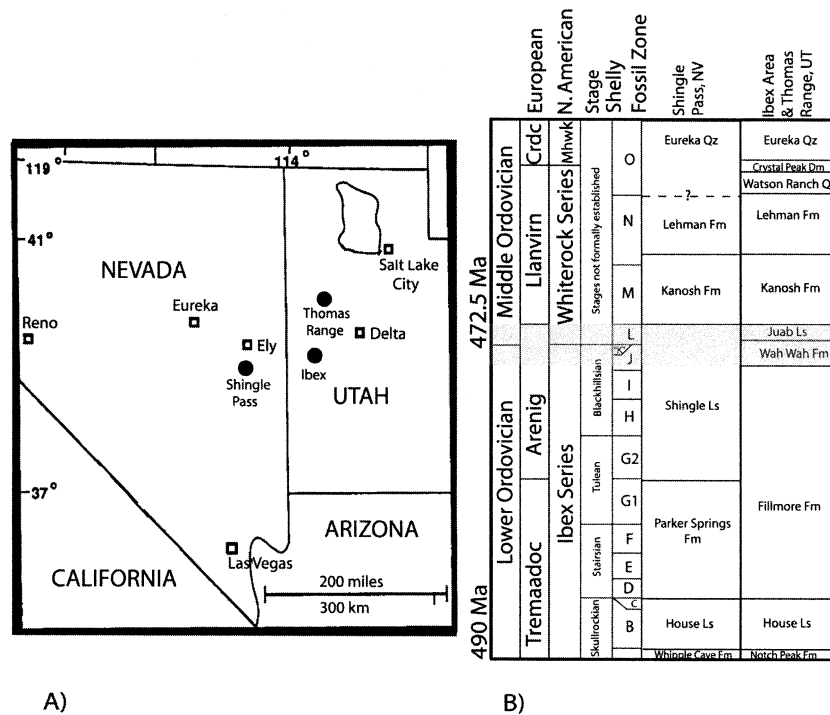
FIGURE 2. A, Map of the study region showing locations of the Ibex, Thomas Range, and Shingle Pass localities. B, Regional lithostratigraphy and regional, North American, and European biostratigraphic framework.

sections in western Utah and eastern Nevada. Because absolute abundance trends are potentially influenced by many factors other than population density, we develop a set of tests to evaluate their effect on our data.

Geological Setting

Regional Stratigraphy and Biostratigraphy.— The Basin and Range province (Fig. 2A) provides a nearly ideal setting for studying benthic paleoecology during the Ordovician Radiations. Lower and Middle Ordovician rocks occur in a broad belt across southern Idaho, western Utah, Nevada, and eastern California. Outcrops are commonly spectacularly exposed and richly fossiliferous. Early Ordovician Ibex Series strata were deposited on a broad, shallow, mixed carbonate-clastic ramp lying near the equator (Ross 1977; Ross et al. 1989). Middle Ordovician Whiterock Series strata record the development of a rimmed carbonate platform that continued to receive considerable clastic input (Ross et al. 1989). Overall, the region is characterized by general environmental stability throughout the late

Early and early Middle Ordovician (Fig. 2B, zones H–L) (Ross 1977; Ross et al. 1989; Ross et al. 1997). In contrast to many other regions of Laurentia, there is no major Lower/Middle Ordovician unconformity in the Basin and Range (Fortey and Droser 1996; Ross et al. 1997).

Upper Ibex and lower Whiterock strata consist of massive to thinly bedded grainstones, packstones, wackestones, and carbonate mudstones interbedded at the meter scale with shales (Hintze 1951, 1973; Ross et al. 1997). The primary study section is Hintze's (1951, 1953, 1973) section J near Ibex, Confusion Range, Millard County, Utah. This area was selected because it is the best exposure of the Pogonip Group in which similar and highly fossiliferous facies occur both below and above the Ibex/Whiterock boundary (Figs. 3, 4).

The upper Ibex Series is represented here by the Wah Wah Formation, which bears a fauna that has been assigned to zone J (*Pseudocybele nasuta* zone) of Ross (1951) and Hintze (1951). The lower half of the formation is profusely
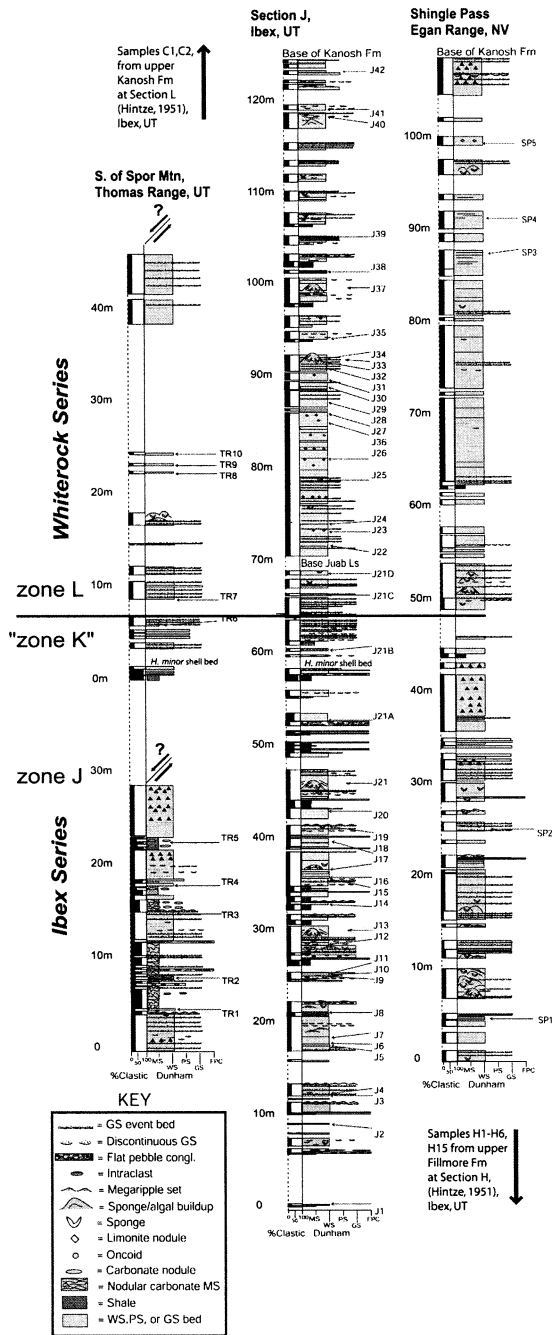
FIGURE 3. Measured sections at Ibex, Thomas Range, and Shingle Pass localities. Arrows indicate the position of sampled beds.
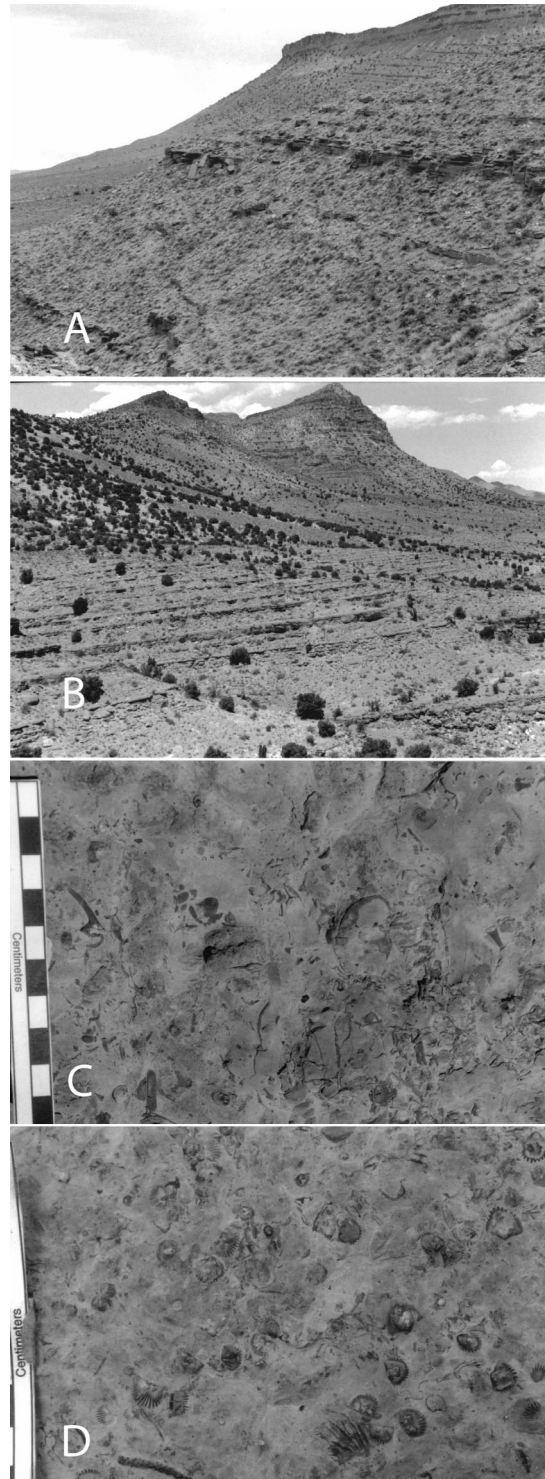
FIGURE 4. A, The Wah Wah Formation, looking south from section J (Hintze 1951, 1973) at Ibex, Utah. B, The Juab Limestone, looking north from section J. C, Wackestone bedding surface in the Wah Wah Formation at Ibex. D, Wackestone bedding surface in the Juab Limestone at Ibex.

fossiliferous, whereas intact fossils are sparser in the uppermost 30 meters. The series boundary is located slightly below the top of the Wah Wah Formation, the lowest identifiable Whiterock faunas occurring 6.4 m above the prom-

inent *Hesperonomiella minor* shell bed (Fortey and Droser 1996). Intervening strata were assigned to zone K (*Hesperonomiella minor* zone) by Hintze (1951) but the formal use of zone K has been dropped because it can only be recognized regionally (Hintze 1973). Zone K is now subsumed into zone J; in this paper we use it only as an informal division. The uppermost Wah Wah Formation and the very fossiliferous overlying Juab Limestone are assigned to the lowermost Whiterock zone, zone L (*Orthidiella* zone of Ross 1951 and Hintze 1951; *Psephosthenaspis* zone of Fortey and Droser 1996).

There is substantial faunal turnover between zones J and L—only five trilobite genera and one brachiopod genus are known to cross the boundary in the eastern Basin and Range (Fortey and Droser 1996; Ross et al. 1997). Despite the turnover, at the class level there is little difference in taxonomic composition between zone J and zone L strata. Both are taxonomically dominated by diverse trilobite faunas, with ancillary contributions from rhynchonelliform brachiopods, linguliform brachiopods, echinoderms, gastropods, cephalopods, and sponges.

Zone M (*Anomalorthis* zone) begins at the base of the Kanosh Formation. The lower Kanosh represents a sharp shift in depositional environment to a siliciclastic-dominated, poorly oxygenated system (McDowell 1987).

The entire section is excellently exposed, allowing for nearly complete sampling of carbonate facies. The macrofossil fauna found at section J has been described by Hintze (1951 1953), Jensen (1967), Braithwaite (1976), Fortey and Droser (1996) and Adrain et al. (2001) and so, when sufficiently preserved, presents few problems of identification at the genus level. Both the Wah Wah and Juab Formations contain faunas typical of the nearshore bathyurid trilobite biofacies (Fortey and Droser 1996; Adrain et al. 2004).

A correlative section is exposed in the southern Thomas Range in Juab County, approximately 90 km NNE of Ibex. Ibex/Whiterock boundary strata here were mapped as Garden City Formation (of Ross 1951) by Staatz and Carr (1964) but are closely similar to Ibex area strata in faunal and sedimento-

logical composition. The well-known *H. minor* shell bed of the Ibex area is also present here, providing a useful stratigraphic marker of the uppermost Ibex Series. Complex faulting and poor exposure makes it impossible to measure a continuous section through the boundary interval. Instead, we measured and collected two discrete sections. The first spans 29 m of interbedded shales and limestones bearing a zone J fauna. The second begins 2 m below the *H. minor* shell bed (zone K of Hintze 1951) and spans 46 m of poorly exposed limestone ledges bearing a zone L fauna.

Approximately 130 km WSW of Ibex, the Ibex/Whiterock series boundary occurs in the Shingle Limestone (Kellogg 1963; Sweet and Tolbert 1997) which is exposed immediately south of Shingle Pass in the southern Egan Range, Nevada. Though harder to sample than Ibex Thomas Range strata, the Shingle Limestone shares many features and most taxa in common with the Wah Wah and Juab and represents a generally similar depositional environment.

Lithofacies, Fauna, and Depositional Environments.—The Wah Wah Formation and Juab Limestone and correlative sections of the Shingle Limestone are primarily composed of parasequences from 2 to 8 m thick (Figs. 3, 4). The lower portions of parasequences usually consist of shales with nodular carbonate mudstones and wackestones. Upper portions consist of carbonate mudstones and wackestones with a substantial (10–30%) terrigenous clastic fraction. Parasequences are often capped by amalgamated, intraclastic skeletal grainstones. Common sedimentary structures include discontinuous grainstone event beds, coarsely developed cross-stratification, burrowed firmgrounds, planed-off hardgrounds, skeletal grainstone megaripple sets, and thin (2–20 cm) flat-pebble conglomerates. Sponge-algal mounds up to 3 m in diameter are common in the Wah Wah, Juab, and Shingle Formations (Johns 1994).

The fauna of all three formations consists primarily of bathyurid, pliomerid, and asaphid (in zone J) trilobites, orthide brachiopods, nautiloid cephalopods, disarticulated echinoderm material, gastropods, lithistid sponges, graptolites (in shales), and rare ostracods.

We agree with earlier interpretations that the Wah Wah, Juab and Shingle Formations represent deposition above storm wave base but below normal wave base on a shallowly dipping carbonate ramp to platform with significant clastic input (Ross et al. 1989).

Materials and Methods

Sample Selection.—Seventy-nine limestone beds ranging from 5 to 15 cm in thickness were sampled at section J (Hintze 1951) at Ibex (Fig. 3), Utah. Sampling was limited to carbonate mudstones and wackestones (Dunham 1962). Beyond this restriction, sampling was conducted explicitly without reference to fossil density—ease of sampling and maximum stratigraphic coverage were our primary criteria. After laboratory examination, 33 of these samples were rejected because they contained grainstone event beds or had shale partings (see below), leaving 46 samples (21 zone J, 2 ''zone K,'' and 23 zone L) of approximately 7 kg each. Replicate samples were collected from seven of these beds to assess lateral variability. An additional ten samples of approximately 3 kg each were collected from the Thomas Range section (five from zone J, one from ''zone K,'' and four from zone L), and five from the Shingle Limestone at Shingle Pass (two zone J and three zone L). To assess the temporal continuity of abundance trends, we took seven samples from shallow subtidal wackestones in the upper Fillmore Formation (*Calathium* calsisiltite at section H of Hintze 1951), which conformably underlies the Wah Wah Formation and bears zone H–I faunas. Two samples were taken from wackestones of the upper Kanosh Formation (base of the Camp Section of Hintze 1951), which is assigned to zone N. The Fillmore, ''zone K,'' and Kanosh samples are included in some figures to illustrate trends, but because of the small sample sizes they are not included in any statistical analyses.

Sampling focused on carbonate mudstones and wackestones, for three principal reasons:

1. Carbonate facies form resistant ledges and are easily sampled, whereas shales generally form covered benches, which are difficult and time consuming to sample consistently.
2. Sedimentation rate is a first-order control on the concentration of fossil material in any bed (Kidwell 1986). Because changes in absolute abundance may be driven by changes in sedimentation rate, it is inappropriate to compare absolute abundance patterns among disparate depositional environments. We hope to minimize this problem (but cannot eliminate it) by sampling only a limited range of bed types in the same lithofacies and biofacies. Samples with clear evidence of very rapid or very slow sedimentation (grainstone horizons, scoured bed contacts, firm or hardgrounds) were rejected.
3. Concerns about the taphonomic nature of shell concentrations (Westrop 1986; Kidwell 1986; Li and Droser 1999; McFarland et al. 1999; Adrain et al. 2000) complicate ecological interpretation of the previously discussed trend in shell bed composition through the Ordovician of the Basin and Range (Li and Droser 1999).

Shell beds also have an inherent limitation where absolute abundance patterns are concerned. The relationship between living density and absolute abundance is largely governed by the ratio of net skeletal production rate to net sedimentation rate. When this ratio is sufficiently low (mudstones and wackestones), changes in living density should cause proportional changes in absolute abundance. When the ratio is too high (packstones and grainstones), geometric packing limitations and lack of accommodation space damp the response of absolute abundance to living density, and there is no longer a meaningful distinction between absolute and relative abundance (Fig. 5). Thus shell beds are not a meaningful source of absolute abundance data in the strict sense (but see Kidwell and Brenchley 1994 on the possible relationship between marine skeletal biomass and the number and thickness of shell concentrations).

Because they are by definition matrix-supported and sparsely to moderately fossiliferous, we see no a priori reason to believe that absolute abundance in mudstones and wacke-
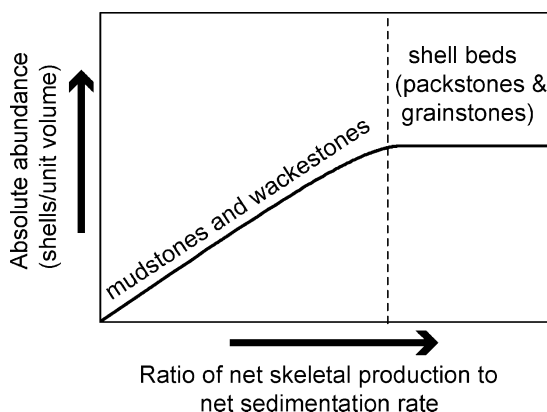
FIGURE 5. Schematic representation of relationship between net skeletal production, net sedimentation rate, and absolute abundance. When the ratio of net skeletal production to sediment accumulation is low, some linear or quasilinear relationship between net skeletal production and absolute abundance is expected. When the ratio is high, bioclast accommodation space is limited by packing geometry and there is no direct relationship between net skeletal production and the concentration of fossil material in the bed.

stones should not respond to changes in living density. Comparing single samples has little meaning—abundance is likely to vary over orders of magnitude (as it does in our data) for both taphonomic and ecological reasons. But comparing relatively large sets of samples from very similar beds should yield a meaningful signal.

Sample Processing.—Samples were broken apart with a sledgehammer and all visible fossil material >2 mm in long dimension was identified to the finest possible taxonomic level by using a hand lens and dissecting microscope. We chose this "crack-out" method for several reasons. Earlier work on Ibex and Whiterock faunas has been accomplished largely on the basis of silicified material, but there are clearly taxonomic biases associated with silicification. Beautifully silicified trilobites are abundant in the Ibex Series, but no other group is consistently, or even commonly, silicified. There is little if any silicification in zone L sections in the eastern Basin and Range, and silicified Whiterock faunas in the central Basin and Range generally do not preserve trilobites (Ross 1964). Comparisons between zones and among groups are therefore impossible with silicified material. Slab or thin-section counts allow more controlled

sampling but generally cannot be used to assess diversity below the class level. Although we do not claim that crack-out counts precisely measure all fossil material in a sample, we believe that they provide a reliable *estimator* of fossil density. Problems associated with this approach are discussed further below.

Generic assignments were made primarily on the basis of plates from Hintze (1953), Jensen (1967), and Fortey and Droser (1996), but even material identifiable only to class or ordinal level (i.e., "indet. trilobite fragment," "indet. orthide brachiopod") was counted. Taking this material into account also helps to minimize the effects of variation in quality of preservation among samples and taxa.

We calculated absolute abundance in each category by dividing the total number of shell fragments counted by the sample weight, so that abundance is measured in fragments/kg. Sample weight is assumed to be a good proxy for volume within the narrow range of lithologies represented here. Of course, the proper measure of sampling intensity is not volume but surface area examined. Because this is highly influenced by rock properties, especially the distribution of parting surfaces, we also tested for differences in total area examined between sample sets (see discussion).

In most analyses we made no attempt to quantify the number of individuals represented in a sample. We are not concerned with precisely reconstructing the original abundance structure of the biological community or communities from which samples derive (Gilinsky and Bennington 1994). Rather, we want to track changes in the abundance of different types of shell material. We assume that significant changes in the skeletal contribution of a given taxon broadly reflect changes in the standing biomass of that group. In diversity estimates, however, we used the following counting protocol: In calculating rarefaction curves for the *pooled* zone J and zone L data sets we counted both cranidia and pygidia for each genus but used only the larger of the two values as the minimum number of individuals. We did the same with brachiopod pedicle and brachial valves. To determine genus richness for *individual* samples, we counted any shell element identifiable to genus or clearly

distinguishable from other genera in the sample. This approach maximizes richness estimates for what are often quite small samples of identifiable skeletal material.

Statistics and Terminology.—We do not test formal abundance models, but we test for differences between zone J and zone L abundance (and other) distributions with two non-parametric comparison tests: the Mann-Whitney (M-W) *U*-test, which tests for equality of medians and is therefore sensitive to central tendency, and the Kolmogorov-Smirnov (K-S) test, which tests for equality of distributions and is more sensitive to skewness and kurtosis (Hammer et al. 2001) For M-W and K-S comparisons of absolute abundance data, which are not generally normally distributed, we transformed the data by taking the natural logarithm of the measured value plus one (adding one avoids the problem of taking ln[0]). In discussing data distributions, we use ''sample set'' to refer to a selection of samples. We use ''value'' to refer to the sample value in a given category (e.g., trilobite absolute abundance in sample J27), and ''value set'' to refer to the set of all values occurring in each zone (e.g., zone J trilobite absolute abundance value set). Values are treated as independent variables in comparing abundance distributions. ''Data set'' refers collectively to all values in all samples. For comparing abundance trends in zone J and zone L data sets, we use the ratio between the median zone J value and the median zone L value (J:L median ratio). Because medians are less influenced by statistical outliers than are averages, they provide a better estimator in data that are not normally distributed.

Results

Trends Across the L/M Ordovician Boundary.— Absolute abundance values are shown in stratigraphic order in Figure 6 (see Fig. 3 for lithostratigraphic context). Relative abundance values are not shown explicitly but can be inferred. In each section there is a marked decrease in the absolute abundance of trilobite material across the L/M Ordovician (zone J/ zone L) boundary. The abundance of brachiopod material generally increases across the boundary, though there are several very bra-
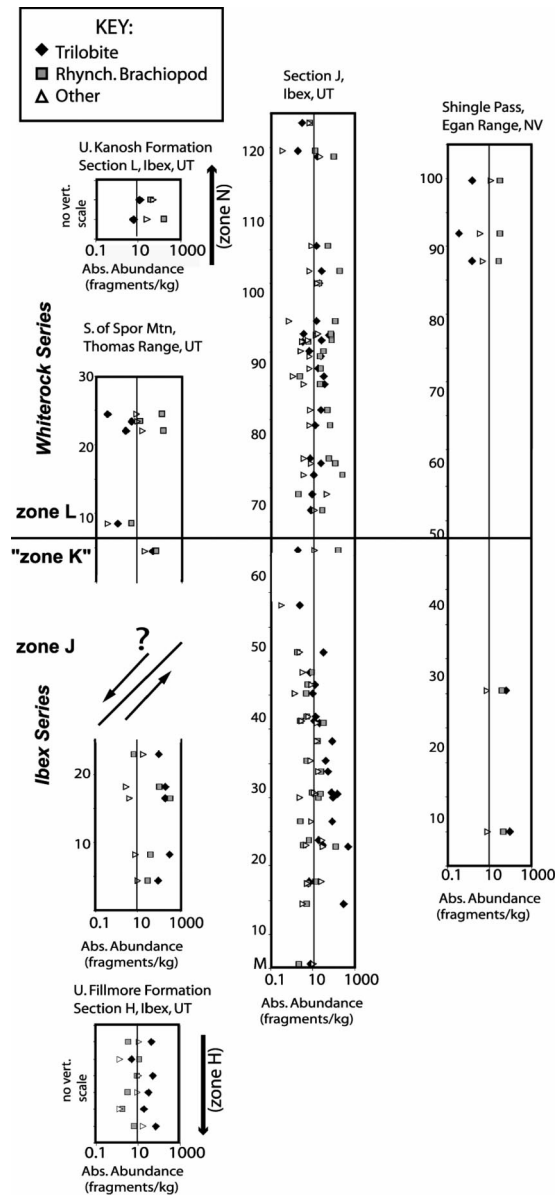
FIGURE 6. Abundance trends of trilobite, brachiopod, and other fossil material in each sampled section. Samples from Ibex, Thomas Range, and Shingle Pass sections are shown in stratigraphic position. Samples from the upper Fillmore and upper Kanosh Formations are in stratigraphic order but are not shown in stratigraphic position. Note that the x-axis is logarithmic.

chiopod-rich zone J samples. Zone J samples from the Thomas Range are especially rich in both trilobite and brachiopod material; in fact three of the five most fossiliferous samples in the entire sample set come from this section. As discussed below, there are good reasons

for excluding these samples from analyses of trends. There is no obvious trend in the abundance or taxonomic composition of other skeletal material—in both zone J and zone L this category is composed primarily of echinoderms, with minor contributions from gastropods, cephalopods, linguliform brachiopods, and ostracods.

Samples from zone H in the upper Fillmore Formation and zone N in the upper Kanosh Formation, though too few in the latter case to be robust, demonstrate that the dominance transition occurs primarily at the Ibex/Whiterock boundary: zone H samples are trilobite dominated, and zone N samples are brachiopod dominated. The pattern is consistent with Li and Droser's (1999) data on the taxonomic composition of shell beds through this interval. The shift in dominance actually appears to occur in uppermost Ibex strata: where it can be recognized near the top of the Wah Wah formation at Ibex and in the Thomas Range, two of three samples from "zone K" (the now abandoned *Hesperonomiella minor* zone) are dominated by brachiopods. The increase in abundance of other shell material in zone N samples is due to the appearance of leperditiid ostracods, which occur in great numbers in zone M and N strata.

Lateral Variation.—To assess lateral variability, seven laterally traceable beds (four zone J and three zone L) were selected for replicate sampling at Ibex section J. Replicate samples were taken from between ten and 100 meters away from the original sample site. Though precise correlation is difficult because of the gradational nature of bed contacts, there is generally good agreement between sample pairs in the absolute and relative abundance of major groups (Fig. 7), indicating that the faunal composition of beds is broadly homogenous at the class level.

Magnitude and Significance of Abundance Trends.—The distribution of absolute abundance values in zones J and L is shown in Figure 8, and relative abundance values are shown in Figure 9. We performed M-W and K-S tests on seven categories of data values: absolute trilobite, brachiopod, other, and total abundance, and relative trilobite, brachiopod, and other abundance. Each set of tests was run on three
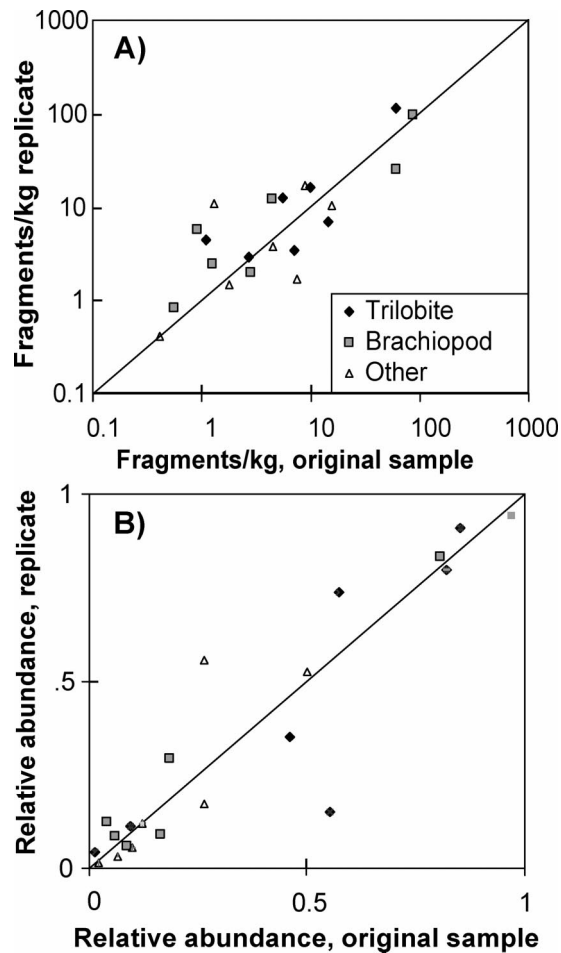
FIGURE 7. Correlation between original and lateral replicate samples in the absolute (A) and relative (B) abundance of trilobite, brachiopod, and other shell material. Lines are lines of perfect correlation, not linear regression trendlines.

different sample sets that represent increasingly conservative culls. The first ("All") includes all samples from each of the three sampled sections. The second ("Culled") is based on visual inspection of the distribution of combined (total) abundance values (Fig 10). Four samples are anomalously large. Three of these are from the Thomas Range section, and one is from section J at Ibex. The abundance of fossil material in these samples, as well as their stratigraphic context (at the contact with, or occurring within, carbonate-rich shales) suggests that they reflect a fundamentally different, probably more storm-influenced depositional process (see "Variation in Sedimentation Rate" below). We therefore culled these samples, as well as the
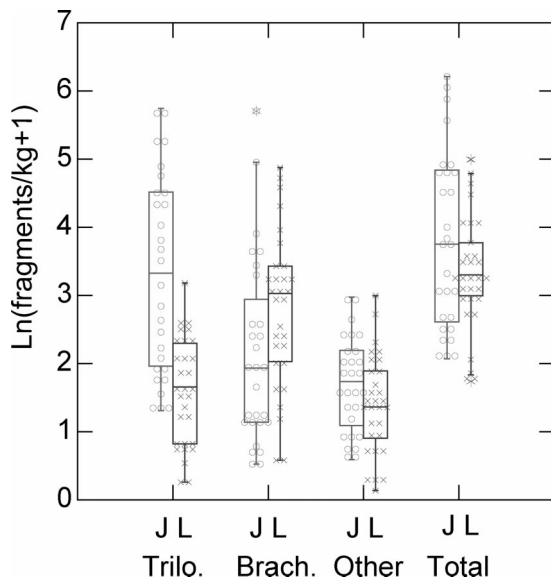
FIGURE 8. Box plots of absolute abundance value distributions for trilobite, brachiopod, all other, and total fossil material in zone J and zone L data sets. Horizontal line marks the median value; boxes contain the second and third quartiles. Whiskers extend to the range of values within 1.5 times the interquartile range of the first and third quartiles. Outliers beyond this range are marked with an asterisk. Zone J $n = 28$, zone L $n = 30$ for all categories.

FIGURE 9. Box plots of relative abundance value distributions for trilobite, brachiopod, and all other fossil material in zone J and zone L data sets. See Figure 8 for details. Outliers more than three times the interquartile range from the first and third quartiles are marked by open circles. Zone J $n = 28$, zone L $n = 30$ for all categories.

remaining two, also quite fossiliferous, Thomas Range zone J samples. The final sample set (Culled, Ibex-only) compares only samples from the lower part of the Wah Wah Formation (minus the outlying J5) and Juab Limestone at section J in the Ibex area. This eliminates potential geographic variation by restricting the analysis to the only section for which we have a statistically robust number of samples. Both zone J and zone L samples from the upper portion of the Wah Wah (J16–J21D) are excluded because of the anomalously low abundance of all fossils in this interval (Fig. 6). Though this sample set contains only 14 zone J and 21 zone L samples, it is the best constrained of the three.

Both M-W and K-S tests confirm significant differences in the absolute abundance of trilobites and brachiopods between zones J and L in all three sample sets (Table 1). Neither test finds significant difference in the absolute abundance of other fossil material except in the Ibex-only data set (where the magnitude of the difference is minor). There are no sig-

nificant differences in the total abundance of fossil material in any of the sample sets.

The magnitude of differences in median values varies considerably between data sets. The ratio of median zone J trilobite abundance to median zone L abundance ranges from 2.8:1 in the Ibex-only and culled sample sets to 6.4:1 in the complete sample set. The J:L median ratio for brachiopods ranges from 1:3.2 in
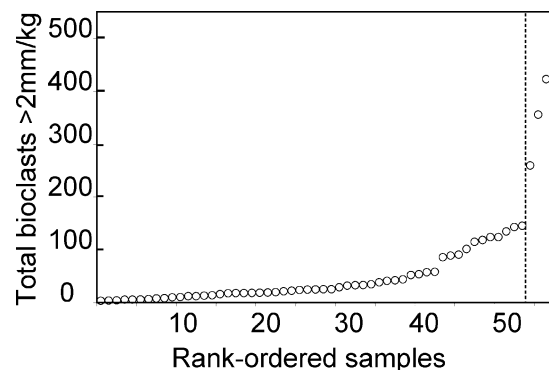
FIGURE 10. Total fossil abundance values of all zone J and zone L samples in rank order. The trend is generally log-normal except for four samples (J5, TR2–TR4), which are anomalously fossiliferous.

TABLE 1. Results of comparison tests between zone J and zone L abundance distributions, and median values in each category. M-W = Mann-Whitney *U*-test. K-S = Kolmogorov-Smirnov test. All absolute abundance comparisons used log-transformed data. *p*-values significant at α = 0.05 are italicized. See text for explanation of sample sets. δ % Pred. is the predicted change in relative abundance based on the observed change in absolute abundance if there is perfect correspondence between absolute and relative abundance changes. δ % Obs. is the actual relative abundance change observed in the sample set. Pred.–Obs. is the misfit between predicted and observed relative abundance trends.

Sample set	*n* (J,L)	M-W *p*-value	K-S *p*-value	Zone J median	Zone L median	Ratio (J:L)	Pred. δ %	Obs. δ %	Pred.–Obs.
Abs. trilobite abund.					**Fragments/kg**				
All	28,30	*<0.0001*	*<0.0001*	27.338	4.243	6.4:1	−0.816	−0.506	+0.310
Culled	22,30	*0.001*	*0.005*	11.814	4.243	2.8:1	−0.347	−0.474	−0.127
Ibex	14,21	*0.005*	*0.005*	19.204	6.938	2.8:1	−0.374	−0.561	−0.187
Rel. trilobite abund.					**Proportion of sample**				
All	28,30	*<0.0001*	*<0.0001*	0.675	0.169	4.0:1			
Culled	22,30	*<0.0001*	*<0.0001*	0.643	0.169	3.8:1			
Ibex	14,21	*0.0004*	*0.002*	0.739	0.178	4.2:1			
Abs. brachiopod abund.					**Fragments/kg**				
All	28,30	*0.032*	*0.027*	5.906	19.637	1:3.3	+0.430	+0.531	−0.101
Culled	22,30	*0.001*	*0.003*	2.529	19.637	1:7.8	+0.909	+0.553	+0.356
Ibex	14,21	*0.017*	*0.035*	4.089	19.067	1:4.7	+0.468	+0.571	−0.103
Rel. brachiopod abund.					**Proportion of sample**				
All	28,30	*<0.0001*	*<0.0001*	0.171	0.702	1:4.1			
Culled	22,30	*<0.0001*	*<0.0001*	0.149	0.702	1:4.7			
Ibex	14,21	*<0.0001*	*<0.0001*	0.122	0.693	1:5.7			
Abs. other abund.					**Fragments/kg**				
All	28,30	0.102	0.184	4.714	2.908	1.6:1	−0.032	−0.025	+0.007
Culled	22,30	0.431	0.770	3.871	2.908	1.3:1	−0.042	−0.047	−0.005
Ibex	14,21	*0.009*	*0.025*	*5.139*	2.731	1.9:1	−0.065	−0.057	+0.008
Rel. other abund.					**Proportion of sample**				
All	28,30	0.738	0.878	0.121	0.096	1.3:1			
Culled	22,30	0.198	0.293	0.143	0.096	1.5:1			
Ibex	14,21	0.116	0.231	0.143	0.086	1.7:1			
Abs. total abund.					**Fragments/kg**				
All	28,30	0.259	0.137	41.633	26.107	1.6:1			
Culled	22,30	0.803	0.392	20.565	26.107	1:1.3			
Ibex	14,21	0.149	0.366	33.202	26.400	1.3:1			

the complete sample set to 1:7.8 in the culled sample set.

Unsurprisingly, the relative abundance signal is much more stable than the absolute abundance signal. M-W and K-S tests return highly significant differences in the relative abundance of both trilobites and brachiopods in each sample set. There is no meaningful variation in relative abundance trends among the three sample sets; the magnitude and significance of differences between zone J and zone L samples are robust to all but the most extreme data culls. This implies that relative abundance data are buffered against the sampling, taphonomic, and depositional factors that affect absolute abundance data and may partially obscure ecological trends.

Absolute Abundance Change versus Data Normalization: Relative Effects.—If changes in the absolute abundance of one group are perfectly balanced by changes in the absolute abundance of other groups in the sample, absolute and relative abundance trends are identical. Therefore, the impact of data normalization on
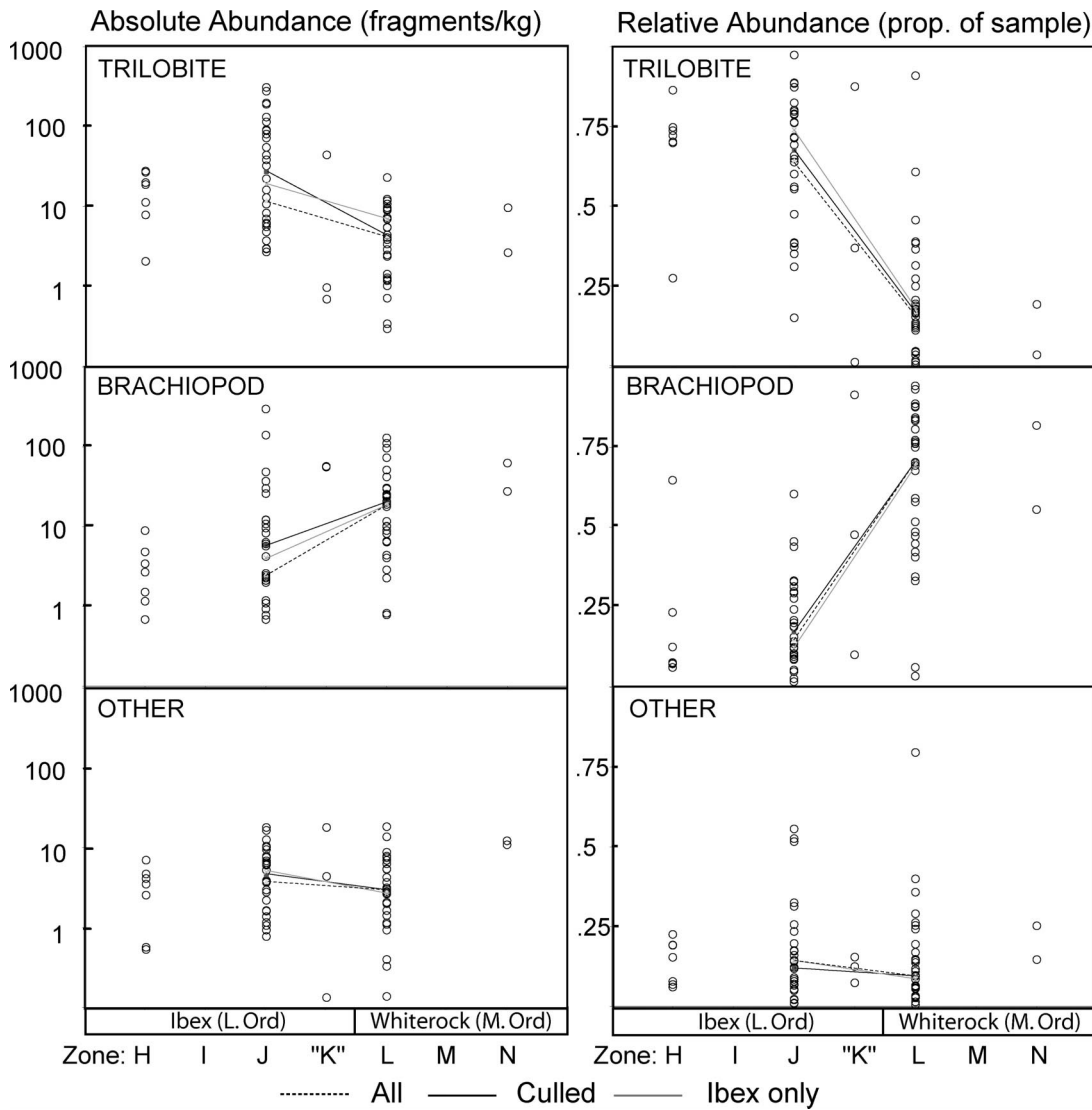
FIGURE 11. Trends in median absolute and relative abundance of trilobites, brachiopods, and other fossil material. Lines connect zone J and zone L medians for each of the three sample sets considered (all, culled, and Ibex-only). Medians are not plotted for zone H, ''zone K,'' or zone N. No samples were taken from zones I and M. Note that y-axis is logarithmic on absolute abundance plots.

relative abundance trends can be measured by the misfit between proportional change in absolute abundance and in relative abundance. For trilobites, brachiopods, and other material these trends are generally quite similar (Table 1, Fig. 11). The amount of relative abundance change that is accounted for by change in *absolute* abundance of the group in question can be estimated by multiplying the amount and direction of relative abundance change between zones J and L (i.e., −51%) by the me-

dian absolute abundance ratio divided by the median relative abundance ratio. The difference between this predicted change in relative abundance and the observed change is thus ''normalization error'' that results from changes in the absolute abundance of other groups in the data set.

When all samples are considered, the change in relative abundance of trilobites understates the change in absolute abundance by +31%. That is, if there were perfect agreement

in proportional change between absolute and relative abundance trends, a −82% shift in relative abundance would be predicted, but the observed shift is −51%. In contrast, relative abundance *overstates* the change in trilobite absolute abundance by −13% in the culled sample set and by −19% in the Ibex-only sample set. Because it is based on the best-constrained sample set, we regard the Ibex-only estimate as the most reasonable. Thus, dilution seems to account for about one-third (1 − [−37%/−56%]) of the decrease in the relative abundance of trilobites.

Relative abundance data overstate the change in the absolute abundance of brachiopods by +10% in the full data set. They understate it by −36% in the culled data set and overstate it by +10% in the Ibex-only sample set. Again using the Ibex-only sample set as a best estimate, absolute abundance change accounts for more than 100% of the observed change in relative abundance—relative abundance data understate the proportional change by one-fifth (1 − [46%/57%]).

Hence, though normalization effects clearly play a minor role, these data do not support the hypothesis that the decrease in the relative abundance of trilobites is driven *primarily* by dilution. Rather, they support a ''literal'' reading of the shift in which the abundance of trilobite material increases as the abundance of trilobite material decreases, with no net increase in the combined abundance of skeletal material. But such a trend does not necessarily reflect ecological change: there are sampling, taphonomic, and depositional factors that can strongly influence absolute abundance trends. Below we consider the potential impact of these factors on the data.

Discussion

Sources of Error

The type and amount of skeletal material in the sedimentary record is controlled by the complex interaction of many factors, only some of which (population density, generation time) are of direct ecological interest. Absolute abundance may also be strongly influenced by the mode and rate of shell destruction, physical and biological reworking, and burial. In addition, there are potential biases associated with sample collection, processing, and counting. To confirm the ecological reality of an absolute abundance trend, the alternative possibility that the trend is driven by variation in one or more or these factors must be ruled out. Here we consider the effects of sampling intensity, facies distribution, taphonomic regime, and sedimentation style.

Sampling Intensity.—Though we express absolute abundance as a function of total sample weight, the proper measure of sampling intensity is volume or area. Because all samples come from the same lithology, sample weight should be a good proxy for volume. We view volume as an appropriate measure because most fossils in our samples are dispersed throughout the matrix—we did not sample beds with obvious fossil concentrations. However, because fossils can be seen only on surfaces, the best measure of sampling intensity is total surface area examined. We attempted to roughly standardize the degree of sample fragmentation, but this is difficult to do precisely. Fragmentation is highly influenced by the distribution of parting surfaces, and though we avoided beds with well-developed parting surfaces, nearly all limestone beds in both formations have numerous thin (<1 mm) shaly parting surfaces. To test for differences in total surface area examined, we subsampled 25 rock fragments each from 14 samples (seven zone J and seven zone L) randomly selected from the Ibex sample set. We measured the longest dimension (as a proxy for bedding plane area) and the thickness (perpendicular to bedding) of each of the 350 subsampled fragments.

Box plots of these dimensions are shown in Figure 12. Both M-W and K-S tests reject the hypothesis of significant differences in fragment longest dimension between zone J and zone L data sets, or in total area (length times thickness). There is a small but moderately significant difference in fragment thickness between zone J (median = 1.9) and zone L (median = 1.6) subsamples. It is thus possible that zone L samples are slightly more finely divided than zone J samples. This would result in approximately 19% greater total surface area examined for zone L samples. This
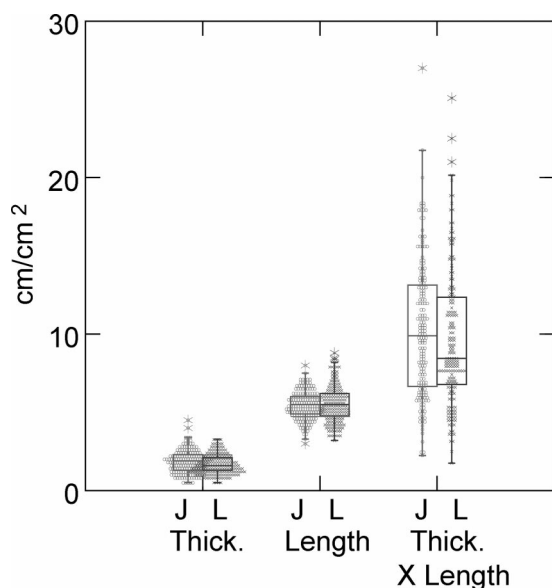
FIGURE 12. Box plots of longest dimension, thickness, and thickness times longest dimension for rock fragments randomly subsampled from 14 Ibex samples (seven zone J and seven zone L; 25 fragments from each). See Figure 8 for details. Zone J $n = 175$, zone L $n = 175$ for all categories. X-axis is cm for thickness and length, cm² for thickness × length. Samples used: J2, J4, J8, J13, J14, J15, J19, J23, J29, J32, J33, J40, J41, J43.

is a minor difference, but it can easily be corrected for by multiplying zone J median absolute abundance values in the ''Ibex only'' samples set by 1.19. In the adjusted sample set the ratio of median zone J absolute abundance to median zone L abundance is 3.3:1 for trilobites and 1:3.9 for brachiopods. This implies that the amount of relative abundance change accounted for by normalization effects is closer to −12% for trilobites and +18% for brachiopods. This adjustment has little effect on the significance of statistical comparisons.

Facies Change.—Distinguishing true temporal trends within a single environment from apparent trends produced by facies juxtaposition is a perennial problem in paleoecology. Lateral migration of depositional environments and their associated faunas can create spurious patterns of ecological change when there has been no change in the underlying ecological gradient (Miller 1997). There are indeed some differences between the Wah Wah Formation and Juab Limestone. Juab parasequences are somewhat thinner than those in the Wah Wah. Grainstone event beds and flat

pebble conglomerates are also generally thinner than in the Wah Wah, and megaripple sets rarer.

We interpret these differences to indicate a slightly more distal depositional environment for the Juab but do not consider this a serious problem for several reasons. Both Ibex and Whiterock strata are broadly exposed, but we know of no Ibex units that are brachiopod dominated or Whiterock units that are trilobite dominated. Distal correlatives of the Wah Wah and Juab Formations in central Nevada (Ninemile and Antelope Valley Formations) are dominated by trilobites and brachiopods, respectively (Li and Droser 1999; Finnegan unpublished data). The two formations represent the same trilobite biofacies (Fortey and Droser 1996; Adrain et al. 2004) and fall within the same environmental bin in the scheme used by previous studies of Ordovician paleoecological trends (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Westrop and Adrain 1998; Adrain et al. 2000).

Taphonomic Regime.—The abundance of fossil material in the death assemblage is controlled by the ratio of skeletal production rate to destruction rate. Both intrinsic (skeletal mineralogy, morphology, microstructure and thickness) and extrinsic (ocean and porewater chemistry, physical and biological reworking) factors influence skeletal destruction rates (Chave 1964; Hollman 1968; Schäfer 1972; Flessa and Brown 1983; Walter 1985; Norris 1986; Cummins et al. 1986b, Glover and Kidwell 1993; Best and Kidwell 2000a,b).

Certainly there are important intrinsic differences between trilobites and brachiopods, and it is likely that many trilobite sclerites were more easily fragmented and destroyed than relatively robust brachiopod sclerites (Speyer 1991; Westrop et al. 1995; Copper 1997). Although this is a problem for directly comparing the abundance of the two groups, it is not a factor in trying to track abundance trends *within* each group.

What data are available from modern tropical soft-bottom carbonate and mixed carbonate-clastic environments suggest it is unlikely that there was substantial variation in shell destruction rates in the narrow range of carbonate environments represented by these

samples (Best and Kidwell 2000a; Callender et al. 2002). Among mollusk shell arrays deployed on a forereef slope of the Bahamas platform, Callender et al. (2002) found little consistent depth-related variation in rates of shell damage. The depth gradient examined in Callender et al.'s study is certainly far greater than that represented by the Wah Wah and Juab Formations.

One proxy for shell destruction rate is the proportion of all skeletal fragments that are identifiable to genus. We calculated this proportion for all samples. The median proportion of trilobite fragments identifiable in all samples is 0.074; for brachiopods it is 0.37. Hence, to avoid skewing medians by including small samples without a reasonable probability of containing identifiable material, we include only samples with at least 15 trilobite fragments (1/0.074 = 13.5) or five brachiopod fragments (1./0.37 = 2.7). We also excluded the anomalously well-preserved material in samples TR1–TR5 and J5. Because proportions based on such small numbers are volatile, we also calculated the proportion of identifiable skeletal fragments in the pooled set of all samples from each zone.

The frequency distributions of these data suggest that modal shell destruction rates were roughly comparable in zone J and zone L depositional environments (Fig. 13). The median proportion of trilobite fragments identifiable to genus is slightly higher in zone L than in zone J, but the difference is not significant and it is not apparent in the pooled sample sets: 12.4% (698/5650) of all trilobite fragments in zone J are identifiable, versus 11.4% (136/1191) in zone L. The median proportion of brachiopod fragments identifiable is moderately but significantly higher in zone L (45%) than in zone J (29%), and this difference is apparent in the pooled data (zone J: 34% [407/1197], zone L: 45% [2435/5401]). This probably reflects a difference in the morphology of dominant genera: *Hesperonomia*, the most abundant brachiopod in Ibex Series samples, is larger and flatter than the Whiterock dominant, *Paralenorthis*. Identification is based primarily on features in the umbo region of the shell, which is of comparable size in both genera, but *Hesperonomia* can poten-
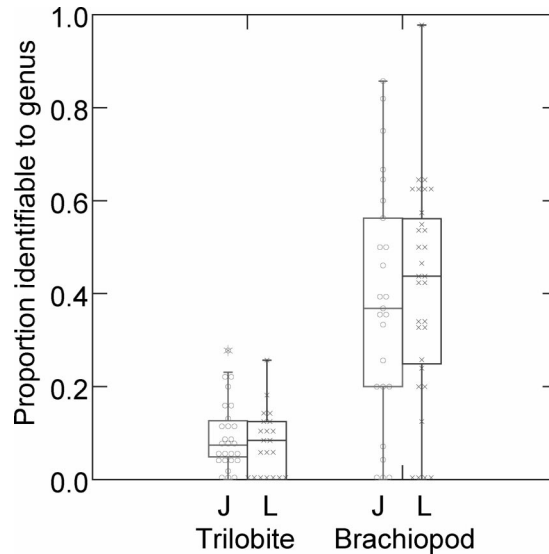
FIGURE 13. Box plots of the proportion of skeletal fragments identifiable to genus for all samples with at least 15 trilobite or 5 brachiopod fragments. See Figure 8 for details. Trilobites: Zone J $n = 27$, zone L $n = 21$. Brachiopods: Zone J $n = 25$, zone L $n = 28$.

tially produce more unidentifiable fragments from the outer part of the shell than can *Paralenorthis*.

A closely related source of possible error is the size distribution of skeletal fragments. Because we counted fragments of all sizes equally, a difference in the degree of skeletal fragmentation between zones could give the appearance of a trend in absolute abundance when there is none. As an additional test for differences in degree of fragmentation, we measured the longest dimension of all trilobite and brachiopod fragments in the same seven zone J and seven zone L samples that we subsampled for rock fragment dimensions. There is no indication of a difference in fragment size distribution (Fig. 14). The upper range of size values is slightly higher in zone J than in zone L for both groups, reflecting size differences between dominant taxa: *Hesperonomia* is somewhat larger than *Paralenorthis*, and the dominant zone J trilobite, *Lachnostoma*, attains larger size than the zone L dominant, *Psephosthenaspis*. In neither case are the size distributions significantly different. We conclude that differences in skeletal destruction and/or fragmentation alone cannot account for the observed abundance trends.
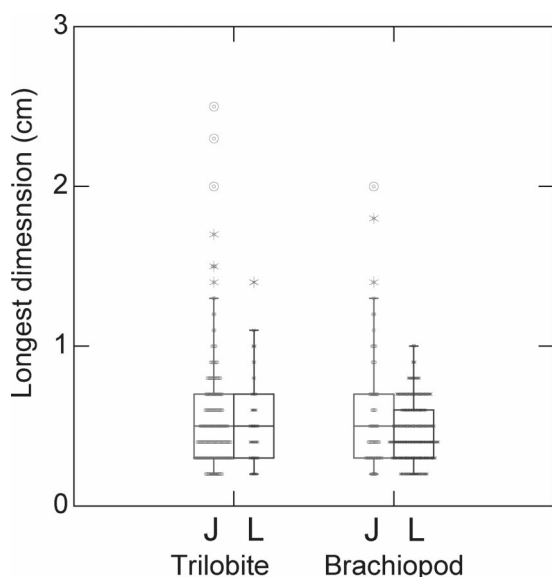
FIGURE 14. Box plots of the length (longest visible dimension) of skeletal fragments randomly subsampled from 14 Ibex samples (seven zone J and seven zone L). Details as in Figure 8. Outliers more than 3 times the interquartile range from the first and third quartiles are marked by open circles. Trilobites: Zone J $n = 183$, zone L $n = 66$. Brachiopods: Zone J $n = 47$, zone L $n = 225$. Samples used: J2, J4, J8, J13, J14, J15, J19, J23, J29, J32, J33, J40, J41, J43.

Variation in Sedimentation Rate.—Varying sedimentation rate has an obvious effect on absolute abundance—skeletal material is concentrated in sediments when deposition is slow, and diluted when it is rapid (Kidwell 1986). A substantial difference in net deposition rate between zones J and L would clearly be a source of error in comparing absolute abundance trends. The 60–70% decrease in trilobite abundance can be explained by sedimentary dilution only if the sedimentation rates represented by the Juab are two to four times higher than those represented by the Wah Wah. There is no indication that this is the case. The thickness of parasequences and the abundance and thickness of storm-related event beds implies, if anything, lower net sediment accumulation rates in the Juab than in the Wah Wah.

One test for the influence of sedimentation style on absolute abundance patterns is the covariance of taxa in the assemblage. If mode and rate of sedimentation are the primary controls on the abundance of skeletal material in any given bed, taxa are expected to covary positively in the sample set as a whole. This is because the assumed patchiness of original species distributions is homogenized as spatial and temporal averaging increase (Cummins et al. 1986a; Miller and Cummins 1990). Few of our samples contain enough material to assess covariance at the genus level, but the same pattern is expected at higher taxonomic levels, especially when faunas are highly dominated by a few taxa. This is the case in both zone J and zone L (see Appendix in online supplementary material at).

Figures 15A and 15B plot the log-transformed abundance of trilobite material against that of brachiopod material in all zone J and zone L samples. Axes are reversed between figures to facilitate comparison of covariance between the dominant and ancillary group in each sample set. When all samples are considered there is moderate positive covariance between trilobites and brachiopods in zone J, but it is clear that this is driven primarily by samples TR1–TR5 and J5. As previously discussed, these samples are probably more storm influenced and spatio-temporally averaged than others. When the Ibex-only culled data set is examined, both zone J and zone L show only weak and insignificant positive covariance. Covariance plots of trilobites and brachiopods against other material are not shown, but they also show no significant positive trend. Hence, absolute abundance values do not appear to be primarily under depositional control in either zone J or zone L.

Ecological Change.—That there is an increase in the abundance of orthides at the base of the Whiterock Series is uncontroversial (Harper et al. 2004), but the post-Ibexian abundance of trilobites has been the subject of considerable debate (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Westrop et al. 1995; Westrop and Adrain 1998a,b, Miller et al. 1998; Li and Droser 1999; Adrain et al. 2000). Although our results pertain to the issue, they should not be generalized beyond the narrow geographic, environmental, and temporal range of the data. Because the difference in abundance of trilobite material between zones J and L is not well explained by any of the other factors we have considered, we conclude that a decrease
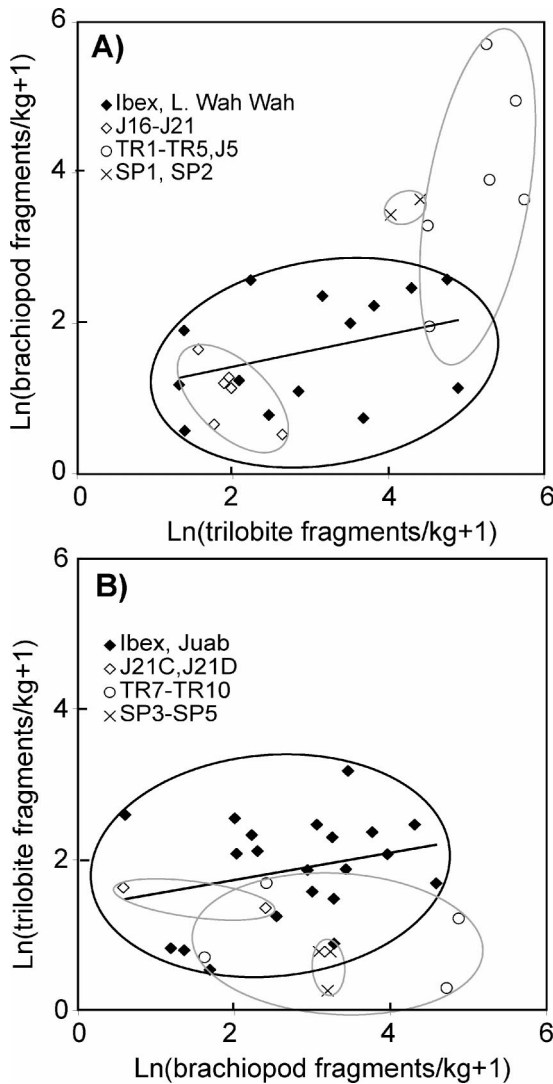
FIGURE 15. Cross-plots of log-transformed absolute abundance of trilobite and brachiopod material for all zone J (A) and zone L (B) samples. Axes are reversed between A and B to facilitate comparison of covariance between dominant and secondary taxa in each case. A weak positive covariance in zone J is driven primarily by the very brachiopod-rich samples J5 and TR1–TR5, which probably represent storm sedimentation. Trend-lines are for the ''Ibex-only'' sample set. Cross-plots of trilobites and brachiopods with other fossil material show similarly weak covariance patterns.

in population density is the most parsimonious explanation. Nevertheless, alternative explanations should also be considered. For instance, it is possible (although unlikely) that the decrease in abundance of trilobite material reflects differences in the growth rate and molt frequency of dominant taxa. This is be-

yond the scope of our study, though it is theoretically resolvable with well-preserved growth series.

The temptation to speculate about ecological changes associated with the diversification of the Whiterock Evolutionary Fauna of trilobites (Adrain 1998) should be resisted. Although its members occur in the uppermost Ibexian and lowermost Whiterockian, both the Wah Wah and the Juab are taxonomically and numerically dominated by members of the Ibex Evolutionary Fauna (Adrain et al. 2004).

Relationship between Local Richness and Abundance Trends

Species or genus richness is commonly used as a measure of paleocommunity dominance, with the implicit assumption that local abundance and richness patterns are closely linked. But there is growing evidence that this assumption is not always valid. Although there is some necessary covariance between the two, abundance trends are not always predictable on the basis of taxonomic richness data. Recent studies of a wide variety of groups have found both good correspondence (Novack-Gottshall and Miller 2003b for gastropods and bivalves) and poor correspondence (Wing et al. 1993; Lupia et al. 1999 for angiosperms, gymnosperms, and free-sporing plants; McKinney et al. 1998 for cyclostome and cheilostome bryozoans) between local richness and abundance patterns. Because publication of abundance data is still a relative rarity except in the micropaleontological and palynological literatures, the overall degree of correlation between relative richness and relative abundance patterns in the fossil record remains an open question.

Because they were collected as bulk samples, many of our collections provide only minimum richness estimates. Most material was identifiable only to class level, and we did not attempt identification below the genus level. In keeping with established paleoecological convention, we assume that genus richness is a good proxy for species richness. Among trilobites, at least, congeneric species rarely co-occur in the same sample (Westrop and Adrain 1998).
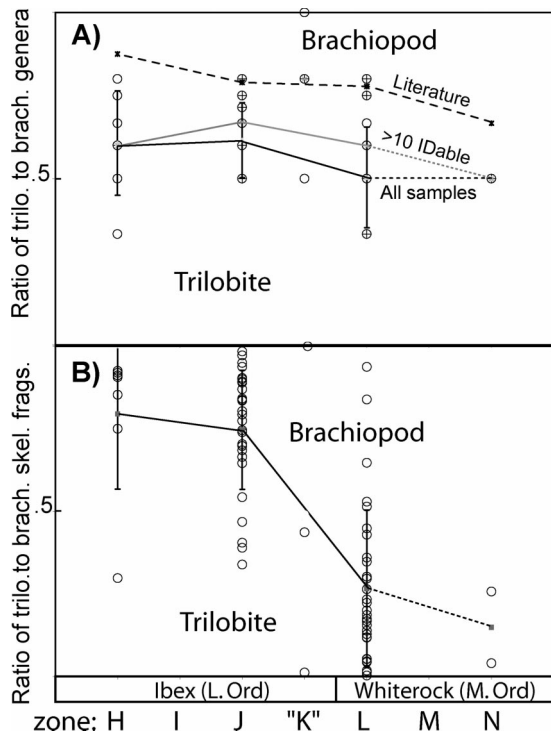
FIGURE 16.   Trends in the average trilobite-to-brachiopod ratio for sampled genera (A) and skeletal fragments (B). Relative richness trends are plotted for all samples, for only those samples with at least five identifiable trilobite and five identifiable brachiopod fragments (>10 identifiable) and, and for a compilation of regional genus occurrences (Literature). Bars show 1 SD for averages of all samples in both A and B. Lines connect average values; dashed portions of the ''All samples'' and ''>10 IDable'' lines indicate low confidence due to very small sample sizes. Some points represent multiple samples.

We determined average relative richness for all samples, for the subset of samples with at least five identifiable trilobite and five identifiable brachiopod sclerites, and for the pooled sample set in each zone. Our data show only minor changes in the local relative (and absolute) richness of trilobites and brachiopods through the L/M Ordovician boundary (Fig. 16A). The relative local richness trend is generally similar to the regional trend (compiled from Hintze 1951; Jensen 1967; Fortey and Droser 1996; Ross et al. 1997; Adrain et al. 2001), though the relative richness of trilobites is consistently higher at the regional level. Regional data should not be overinterpreted, because the trilobite fauna of zone L, though not silicified, has been the subject of recent atten-

tion (Fortey and Droser 1996). With the exception of the dimeropygids (Adrain et al. 2001), upper Ibexian faunas have not. Continuing work on Ibexian faunas will certainly increase the number of reported species and may significantly increase the number of genera.

As they currently stand, however, neither local nor regional richness patterns predict the sharp shift in relative abundance between the Ibex and Whiterock Series (Fig. 16B). Relative local richness values of trilobites and brachiopods in zone J are close to the averages reported by Peters (2004b) for the trilobite-dominated Cambrian Evolutionary Fauna and the brachiopod-dominated Paleozoic Evolutionary Fauna in the North American Arenig. Zone L values are slightly different, but still closer to the Arenig averages than those reported by Peters for the Late Ordovician. In contrast, though our late Ibexian samples have relative abundance values similar to his Arenig average, the relative abundance structure of our zone L samples is much closer to the average Caradoc value. While striking, this difference should not be overinterpreted, given the wide range of relative abundance values in Peters's Arenig sample set.

Richness is strongly influenced by both sampling intensity and the equitability (evenness) of species abundance distributions (Sanders 1968; Hurlbert 1971; Magurran 1988; Hayek and Buzas 1997; Powell and Kowalewski 2002; Olszewski 2004; Peters 2004a). Hence, richness data should not be interpreted without abundance data. Rarefaction curves (Sanders 1968; Hurlbert 1971) provide information on both richness and evenness—the slope of the steepest part of the rising limb of the curve is equal to Hurlbert's (1971) ''Probability of Interspecific Encounter'' (PIE) evenness metric (Olszewski 2004).

We produced rarefaction curves (using the method described in Hurlbert 1971) for the pooled zone J and zone L samples of trilobite and brachiopod individuals identifiable to genus (trilobites: zone J = 669, zone L = 100; brachiopods: zone J = 373, zone L = 639). These curves suggest that the disparity between richness and abundance trends in these data is driven primarily by a difference in evenness between zone J and zone L trilobite faunas
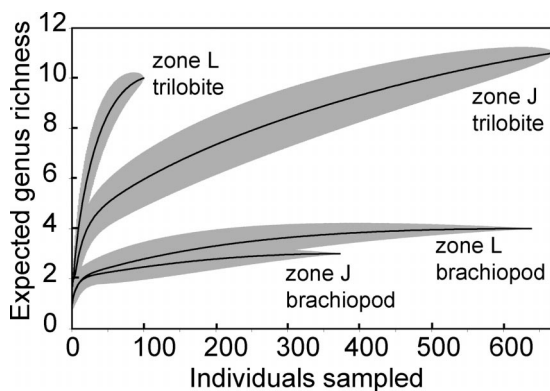
FIGURE 17. Rarefaction curves for trilobites and brachiopods in the pooled zone J and zone L sample sets. Shaded areas are 95% confidence intervals. Evenness (as measured by the Probability of Interspecific Encounter [PIE]), and expected richness at a sample size of 90 individuals ($Es_{(90)}$), for each sample as follows: zone J trilobites: PIE = 0.45, $Es_{(90)}$ = 5.8, zone L trilobites: PIE = 0.65, $Es_{(90)}$ = 9.9, zone J brachiopods: PIE = 0.23, $Es_{(90)}$ = 2.4, zone L brachiopods: PIE = 0.22, $Es_{(90)}$ = 2.7.

(Fig. 17). Although similar numbers of trilobite and brachiopod genera are recorded in the pooled samples, the higher evenness of the zone L sample means that at moderate sample sizes rarefied trilobite richness is considerably higher in zone L than it is in zone J. Brachiopods show comparatively little difference in evenness or sampled richness.

The evenness difference does not necessarily reflect true differences in abundance structure. At the genus level, estimates of richness and relative abundance based on crack-out counts should be viewed with suspicion. Skeletal elements that are flat and smooth are more likely to be identifiably exposed on fracture surfaces than those with high relief or ornate surfaces. Though the rank-ordering of genera in our pooled zone J sample is generally consistent with the qualitative abundance estimates reported by Hintze (1951) for silicified samples, there are some significant differences. Most notably the genus *Dimeropygiella*, which is common in several of his samples (and samples referenced in Adrain et al. 2001), is represented in our samples only by a single pygidium in a grainstone bed (not included in these analyses). The carapace of this genus is pustulose and unlikely to be well exposed on fracture surfaces; this may help to explain the disparity. The smooth and rela-

tively flat asaphid *Lachnostoma* dominates both our samples and Hintze's (1951) silicified samples, but crack-out effects may overstate its dominance in our data. Combined with underrepresentation of *Dimeropygiella*, this may explain the low evenness of the zone J trilobite fauna.

In summary, these data provide some evidence that richness and abundance trends are not closely coupled through the Ibex/Whiterock boundary, but the evidence is not unequivocal. Ongoing sampling of faunas exposed on bedding surfaces in both zone J and zone L should ultimately provide more reliable estimates of genus-level richness and relative abundance trends.

Conclusion

Absolute and relative abundance are often used interchangeably but should not be confused. Data normalization couples independent variables, making it impossible to evaluate the ecological meaning of major shifts in relative abundance structure. Because such shifts are the subject of much paleontological research, absolute and relative abundance should be kept distinct and their implications separately considered.

The data presented here confirm a dramatic shift in relative abundance in shallow subtidal carbonate facies spanning the Lower/Middle Ordovician boundary in the eastern Basin and Range. Samples from the upper Ibex series are trilobite dominated, whereas lower Whiterock Series samples are dominated by orthide brachiopods. The diminished relative abundance of trilobites is in part a function of increased brachiopod abundance and data normalization, but is primarily due to a roughly 60–70% decrease in the absolute abundance of trilobite material. There are only minor changes in the abundance of other groups, and no significant change in the abundance of skeletal material generally. These data do not support the hypotheses that the difference in trilobite absolute abundance results from variation in sampling intensity, taphonomic regime, or depositional environment. This strongly suggests that the trend in shell bed composition described by Li and Droser (1999) is driven pri-

marily by ecological, rather than taphonomic, factors.

The abundance trends stand in striking contrast to taxonomic diversity trends. Though there are shifts in faunal composition at the familial and ordinal levels, there is little discernable difference between upper Ibex and lower Whiterock samples in within-class genus richness. The disconnect between abundance and richness trends is partly explained by the higher evenness of the lower Whiterock trilobite fauna, but the evenness difference is probably heavily influenced by sampling issues. Though more robust richness data are needed, this work tentatively supports recent studies showing that, at least at the local scale, abundance and richness patterns may be decoupled. This may be especially true during major transitions in faunal dominance. For this reason, taxonomic data alone cannot serve as a proxy for ecological structure. Recognition of the ecological dynamics that accompany such turnovers must incorporate numerical abundance data.

Acknowledgments

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Sample no.	J1	J2	J3	J4	J4R	J5	J6	J7
Formation	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J
Zone	J	J	J	J	J	J	J	J
Weight (kg)	7.7	7	7	6.8	7.7	7	84	7.7
Lachnostoma		204			1	140	8	
Pseudocybele		5	1	1		2		
Goniotelus						16	1	1
Ptyocephalus	2					20	1	
Cybelopsis								
Benthamaspis?								
Isoteloides		4						
Prebynileus								
Trigonocerca								
Carolinites		2						
Pseudomera						5	1	
Psephosthenaspis								
Ectenonotus								
Goniotelina								
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.	21							
trilo. frags.	2	716	18	19	20	1		53
Hesperonomia		10	9	10		1217	79	7
Diparalasma						155	4	
Hesperonomiella						3	1	
Anomalorthis								
Paralenorthis								
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	4	5	7	29	7	1		
echinoderm	29	2	16	74	10	185	5	12
Lingul. brach.						91	14	81
Naut. cephalopod		2						
gastropod	2	6						
ostracod						1		
sponge								

Appendix. Continued.

Sample no.	J7R	J8	J9	J10	J11	J11R	J12	J13
Formation	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J
Zone	J	J	J	J	J	J	J	J
Weight (kg)	3.2	6.4	6.4	5.9	2	7.7	7.3	7.5
Lachnostoma		36	26	15	9	26	8	4
Pseudocybele	1	7		2				
Goniotelus		2					2	5
Ptyocephalus		4	1			3		
Cybelopsis								
Benthamaspis?								
Isoteloides								
Prebynileus	1							
Trigonocerca								
Carolinites								
Pseudomera								
Psephosthenaspis								
Ectenonotus								
Goniotelina								
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.			4	6				
trilo. frags.	44	196	250	405	226	441	152	112
Hesperonomia	2	6	11		5		3	4
Diparalasma								2
Hesperonomiella								
Anomalorthis								
Paralenorthis								
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	2	1	42	64	20	34	6	
echinoderm	49	20	4	39	31	67	55	9
Lingul. brach.		2	2					22
Naut. cephalopod	1	2		1	1		1	
gastropod		1	1	2	3	2	1	1
ostracod								
sponge								5

Appendix.   Continued.

Sample no.	J13R	J14	J15	J16	J17	J18	J19	J20
Formation	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J
Zone	J	J	J	J	J	J	J	J
Weight (kg)	7.5	7.5	7.5	7.5	6.6	5	6.8	5.9
Lachnostoma	1	5						
Pseudocybele		4						
Goniotelus	3				3			
Ptyocephalus	1		2	1			2	
Cybelopsis				1				
Benthamaspis?								
Isoteloides								
Prebynileus			1					
Trigonocerca								
Carolinites				1				
Pseudomera								
Psephosthenaspis								
Ectenonotus								
Goniotelina								
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.								
trilo. frags.	69	234	59	33	38	30	36	22
Hesperonomia		20	46	2	1			5
Diparalasma		2						
Hesperonomiella								
Anomalorthis								
Paralenorthis								
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	21	26	45	5	13	13	16	20
echinoderm	32	47	46	9	18		25	10
Lingul. brach.								
Naut. cephalopod							4	
gastropod		1	1		1	4		
ostracod								
sponge	2							

Sample no.	J21	J21A	J21B	J21C	J21D	J22	J22R	J23
Formation	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Wah Wah Fm.	Juab Ls.	Juab Ls.	Juab Ls
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J
Zone	J	"K"	"K"	L	L	L	L	L
Weight (kg)	7.3	7.3	7.3	7.3	6.4	6.8	7.3	7
Lachnostoma								
Pseudocybele								
Goniotelus								
Ptyocephalus								
Cybelopsis								
Benthamaspis?								
Isoteloides	1							
Prebynileus								
Trigonocerca								
Carolinites						1		
Pseudomera								1
Psephosthenaspis								3
Ectenonotus								
Goniotelina						2		
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.	4							
trilo. frags.	89	7	5	21	26	27	8	64
Hesperonomia	1							
Diparalasma								
Hesperonomiella			248					
Anomalorthis								2
Paralenorthis				44	1	351	98	191
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	4		159	27	4	309	532	104
echinoderm	4		33	32	121	10	13	22
Lingul. brach.		1						
Naut. cephalopod	2							
gastropod	1							
ostracod								
sponge								

Appendix. Continued.

Sample no.	J24	J24R	J26	J27	J28	J29	J29R	J30
Formation	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J
Zone	L	L	L	L	L	L	L	L
Weight (kg)	5.9	3	8.9	6.1	8.4	7.3	7.3	6.6
Lachnostoma								
Pseudocybele								
Goniotelus								
Ptyocephalus								
Cybelopsis								
Benthamaspis?								
Isoteloides								
Prebynileus								
Trigonocerca								
Carolinites								
Pseudomera				1	3	7		1
Psephosthenaspis				1	13	13	9	
Ectenonotus								
Goniotelina					1			
Punka				2				
Kanoshia						1		1
Uromystrum					1			
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.						2		6
trilo. frags.	20	21	34	62	81	65	31	42
Hesperonomia								
Diparalasma								
Hesperonomiella								
Anomalorthis			11					11
Paralenorthis	95	73	47	78	31	2		19
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	55	106	111	46	23	4	4	29
echinoderm	10	22	18	15	9	2	3	14
Lingul. brach.					1	1		1
Naut. cephalopod			1	2				
gastropod				3				3
ostracod								
sponge								

Sample no.	J31	J32	J33	J34	J35	J36	J37	J38
Formation	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J
Zone	L	L	L	L	L	L	L	L
Weight (kg)	6.8	7.3	7	7.7	6.6	7	5.9	7.7
Lachnostoma								
Pseudocybele								
Goniotelus								
Ptyocephalus								
Cybelopsis								
Benthamaspis?								
Isoteloides								
Prebynileus								
Trigonocerca								
Carolinites			1		1			
Pseudomera	2				3	1	1	1
Psephosthenaspis	5	2		7	13		4	6
Ectenonotus							1	
Goniotelina								
Punka					4			
Kanoshia					1			
Uromystrum					1			
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.	4				5	1		
trilo. frags.	54	16	9	62	125	8	35	47
Hesperonomia								
Diparalasma								
Hesperonomiella								
Anomalorthis	5			12	17	13		
Paralenorthis	30	36	2	34	77	163	133	28
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	21	49	14	146	108	4	171	23
echinoderm	18	6	5	16	28	44	1	34
Lingul. brach.		1			2			1
Naut. cephalopod			1		2			4
gastropod	1		2		5	2	1	4
ostracod								
sponge								1

Appendix. Continued.

Sample no.	J39	J40	J41	J42	J43	TR1	TR2	TR3
Formation	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	Juab Ls.	''Garden City'' Fm.	''Garden City'' Fm.	''Garden City'' Fm.
Locality	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Ibex, J	Thomas R.	Thomas R.	Thomas R.
Zone	L	L	L	L	L	J	J	J
Weight (kg)	6.6	7.7	8.2	7	6.6	3	3	3
Lachnostoma						17	105	124
Pseudocybele						4	23	
Goniotelus						1	2	
Ptyocephalus								1
Cybelopsis								
Benthamaspis?								
Isoteloides								
Prebynileus								
Trigonocerca								
Carolinites							4	
Pseudomera								
Psephosthenaspis	1							
Ectenonotus								
Goniotelina								
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.	6						13	
trilo. frags.	65	42	45	5	8	242	773	440
Hesperonomia						3	57	725
Diparalasma						24	14	
Hesperonomiella								
Anomalorthis	40	3	12		2			
Paralenorthis	140	86	71	8	4			
Orthidiella?								
Tritoechia								
brach. indet. gen.								
brach. frags.	304	49	161	23	13	50	39	160
echinoderm	19	24	59		14	29	1	8
Lingul. brach.							2	4
Naut. cephalopod					3		7	
gastropod				1	1		13	
ostracod								
sponge								

Sample no.	TR4	TR5	TR6	TR7	TR8	TR9	TR10	SP1
Formation	"Garden City" Fm.	"Garden City" Fm.	"Garden City" Fm.	"Garden City" Fm.	"Garden City" Fm.	"Garden City" Fm.	"Garden City" Fm.	Shingle Fm.
Locality	Thomas R.	Thomas R.	Thomas R.	Thomas R.	Thomas R.	Thomas R.	Thomas R.	S. Egan R.
Zone	J	J	"K"	L	L	L	L	J
Weight (kg)	2	3	3	3	3	3	3	3.4
Lachnostoma	73							
Pseudocybele	16							
Goniotelus								53
Ptyocephalus	1	75						17
Cybelopsis								
Benthamaspis?								
Isoteloides								
Prebynileus								
Trigonocerca								1
Carolinites			2					
Pseudomera					1			
Psephosthenaspis			6					
Ectenonotus								
Goniotelina			2					
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?								
trilo. indet. gen.	1		3					
trilo. frags.	480	195	118	3	6	13	1	205
Hesperonomia	216	7						33
Diparalasma								7
Hesperonomiella			49					
Anomalorthis					3			
Paralenorthis					121		147	
Orthidiella?						13		
Tritoechia								
brach. indet. gen.								
brach. frags.	72	11	120	12	260	17	182	87
echinoderm	1		55	1	40	23	23	23
Lingul. brach.	5	36						
Naut. cephalopod		5						
gastropod	2	14			2	1		
ostracod								
sponge								

Sample no.	SP2	SP3	SP4	SP5	F1	F2	F3	F4
Formation	Shingle Fm.	Shingle Fm.	Shingle Fm.	Shingle Fm.	Fillmore Fm.	Fillmore Fm.	Fillmore Fm.	Fillmore Fm.
Locality	S. Egan R.	S. Egan R.	S. Egan R.	S. Egan R.	Ibex, H	Ibex, H	Ibex, H	Ibex, H
Zone	J	L	L	L	H	H	H	H
Weight (kg)	3.4	3.4	3.4	3.4	6.8	7	7.3	7.7
Lachnostoma	16							
Pseudocybele	3							
Goniotelus								
Ptyocephalus					2	1		
Cybelopsis								
Benthamaspis?								
Isoteloides								
Prebynileus						1		
Trigonocerca					1	3		
Carolinites	1							
Pseudomera								
Psephosthenaspis								
Ectenonotus								
Goniotelina								
Punka								
Kanoshia								
Uromystrum								
Pseudoolenoides								
Asaphellus?					1			
trilo. indet. gen.					2		8	10
trilo. frags.	168	4	1	4	177	191	49	77
Hesperonomia	4				1	5		
Diparalasma	50					1	1	
Hesperonomiella								
Anomalorthis		11	49					
Paralenorthis		45		67				
Orthidiella?	2							
Tritoechia								
brach. indet. gen.			7					2
brach. frags.	47	15	24	16	60	13	4	7
echinoderm	22	13	10	30	17	51	3	28
Lingul. brach.							1	
Naut. cephalopod								
gastropod				1	1			
ostracod								
sponge						1		

Sample no.	F5	F6	F15	K1	K1
Formation	Fillmore Fm.	Fillmore Fm.	Fillmore Fm.	Kanosh Fm.	Kanosh Fm.
Locality	Ibex, H	Ibex, H	Ibex, H	Ibex, L	Ibex, L
Zone	H	H	H	N	N
Weight (kg)	7.3	6.8	6.6	6.8	3.6
Lachnostoma					
Pseudocybele					
Goniotelus					
Ptyocephalus					
Cybelopsis					
Benthamaspis?					
Isoteloides					
Prebynileus					
Trigonocerca					
Carolinites					
Pseudomera					
Psephosthenaspis					
Ectenonotus					
Goniotelina					
Punka					
Kanoshia					
Uromystrum					
Pseudoolenoides				2	
Asaphellus?					
trilo. indet. gen.			15		6
trilo. frags.	145	14	109	18	29
Hesperonomia					
Diparalasma					
Hesperonomiella					
Anomalorthis					
Paralenorthis					
Orthidiella?					
Tritoechia					
brach. indet. gen.	8	12	6	87	30
brach. frags.	17	21	4	342	71
echinoderm	31	2	30	68	
Lingul. brach.					
Naut. cephalopod		1			
gastropod		1	2	5	
ostracod				4	46
sponge					