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Pennsylvanian sea level cycles, nutrient availability and brachiopod paleoecology

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Abstract

As with modern organisms, the spatial and temporal distribution of fossil communities was controlled by both the physical setting in which the organisms lived and by the organisms' physiology and interactions. By studying the sedimentological and geochemical context of fossil communities, it is possible to assess the relative importance of the physical setting and the organisms' physiology. Comparison of Pennsylvanian brachiopod associations with changing sedimentological context (water depth/facies) and nutrient availability indicates that body size is a function of water depth and nutrient availability for most spire-bearing (athyridids and spiriferids) brachiopods but rarely for productid brachiopods. Spire-bearing brachiopods dominate the associations in high-nutrient settings, and productid brachiopods dominate the associations in low-nutrient settings. This difference suggests that physiological differences between brachiopod orders, such as lophophore filtering efficiency, play an important role in controlling their distribution.

Keywords: Pennsylvanian; Brachiopods; Sea level change; Nutrients; Weathering

1. Introduction

Fossil communities analyzed in the context of their sedimentological and geochemical setting can give fundamental information about paleoecological controls on their structure, composition, and spatial distribution. In benthic marine communities, the two most important factors are thought to be physico-chemical control (e.g., substrate composition/structure; water depth, oxygen availability; Boucot, 1981) or biological control (e.g., species interactions, availability of nourishment; Fürsich and Hurst, 1974). Traditionally, the physico-chemical factors substrate type and sedimentary facies were thought to be the primary controls on the distribution of benthic organisms, especially for filter-feeders, with biological controls playing a secondary role. However, for some benthic organisms such as brachiopods, food supply

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and nutrient availability may control their distribution (Fürsich and Hurst, 1974). Because nutrient availability is in part a function of terrestrial inputs (e.g., most phosphorous is derived from continental weathering), sea level changes could be important both as an intrinsic and extrinsic control. Here, we use Pennsylvanian brachiopod communities to determine whether their distribution is controlled by physico-chemical or biological factors, or some combination of processes.

2. Field Area

The Great Basin of Nevada and Utah exposes Pennsylvanian-aged carbonates deposited in shallow water carbonate ramps that show water depth-depositional facies cycles on a variety of scales (Fig. 1). These deposits resulted from sedimentation in the Ely Basin (e.g., Larson and Langenheim, 1979; Snyder et al., 1990) within the Miogeosynclina Province of the Western Cordillera (Miller et al., 1992). Research was conducted in Millard County, Utah and White Pine Country, Nevada at eight sites (Pérez-Huerta, 2004). Pennsylvanian rocks are exposed in the eastern part of Millard County in the Confusion Range, Foote Range, Conger Range, Burbank Hills, Mountain Home Range, and Pahyant Range (Hintze and Davis, 2003), and in the eastern part of White Pine County in the White Pine Range and at Buck Mountain (Hose and Blake, 1976). Combined geochemical analyses and study of brachiopod faunas were conducted in carbonate sequences at Illipah, Nevada, and near Skunk Springs, Utah (localities 1 and 2 in Fig. 1A).

3. Materials and methods

3.1. Fieldwork and stratigraphy

Stratigraphic sections were logged over multiple field seasons and correlations between sections were made using standard methods including biostratigraphy (details in Pérez-Huerta, 2004). Combined geochemical and paleoecological studies were conducted in upper Atokan–lower Desmoinesian (Baskhirian–early Moscovian) deposits in the section at Illipah (Nevada) and upper Desmoinesian (late Moscovian) deposits in the section at Skunk Springs (Utah)

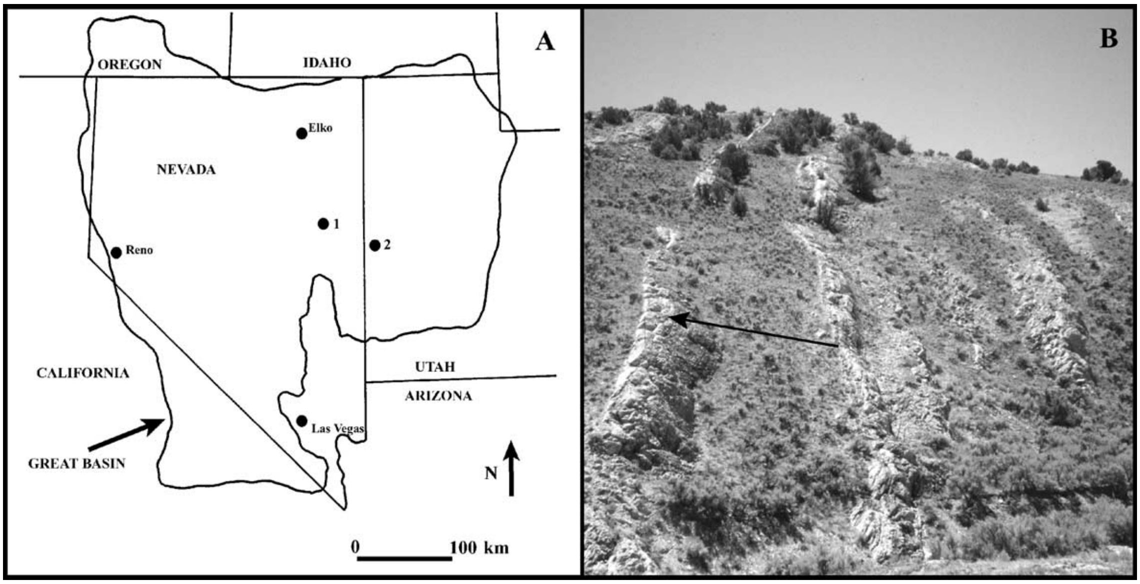

Fig. 1. Map and outcrop photo. A) Map of the Great Basin and the location of field sites in Illipah (locality 1; 39° 27′ 30″/115° 24′ 30″), White Pine County, Nevada and in Skunk Springs (locality 2; 39° 18′ 30″/113° 38′ 50″), Conger Range, in Millard County, Utah [additional field sites in Millar County: 1; southern Burbank Hills, 38° 44′ 10″/113° 55′ 20″; northern Mountain Home Range, 38° 42′ 30″/113° 56′ 10″ and White Pine County: Moorman Ridge, 39° 18′ 30″/115° 22′ 30″; Limestone Peak, 39° 11′ 40″/115° 18′ 30″; Buck Mountain top, 39° 33′ 45″/116° 39′ 30″; Buck Mountain flank, 39° 34′ 15″/116° 40′ 30″]. B) Outcrop photo showing depositional cycles.

(Fig. 2). Studies were conducted at sites with different paleogeographic settings to compare results from more proximal and distal localities within the Antler Foreland Basin (Snyder et al., 1990). Both localities were selected to determine possible diagenetic effects given their different ages of deposition and slightly dissimilar facies. Different carbonate facies were identified in the field including mudstone, wackestone, packstone, and grainstone and the sedimentary cycles were described as shallowing-upward subtidal sequences (sensu James, 1984; Fig. 1B). These shallowing-upward sedimentary cycles have been extensively described in the Pennsylvanian of the Great Basin and areas nearby (e.g., Arrow Canyon in southern Nevada) (e.g., Dott, 1958; Mollazal, 1961; Coogan, 1962; St. Aubin-Hietpas, 1983; Moffet and Langenheim, 1986; Morrow, 1989; Pérez-Huerta, 2004). Four sedimentary cycles of small scale (8–20 m in thickness) in Illipan section (SEL 1–4 in Fig. 2) and three of intermediate to large scale (26–45 m in thickness) in Skunk Springs section (Fig. 2) were used for geochemical analyses and for the collection of brachiopod specimens. Multiple slabs were collected from each facies within a cycle to make thin-sections, to look for palynomorphs, and for dissolution in acetic acid. Analyses of thin-sections reveal a very low content of clastic quartz and clay material, and an absence of concentrations of condensed Fe oxides and phosphatic aggregates (Pérez-Huerta, 2004). Palynomorphs were not found but grainstone and packstone limestones contained fragmentary

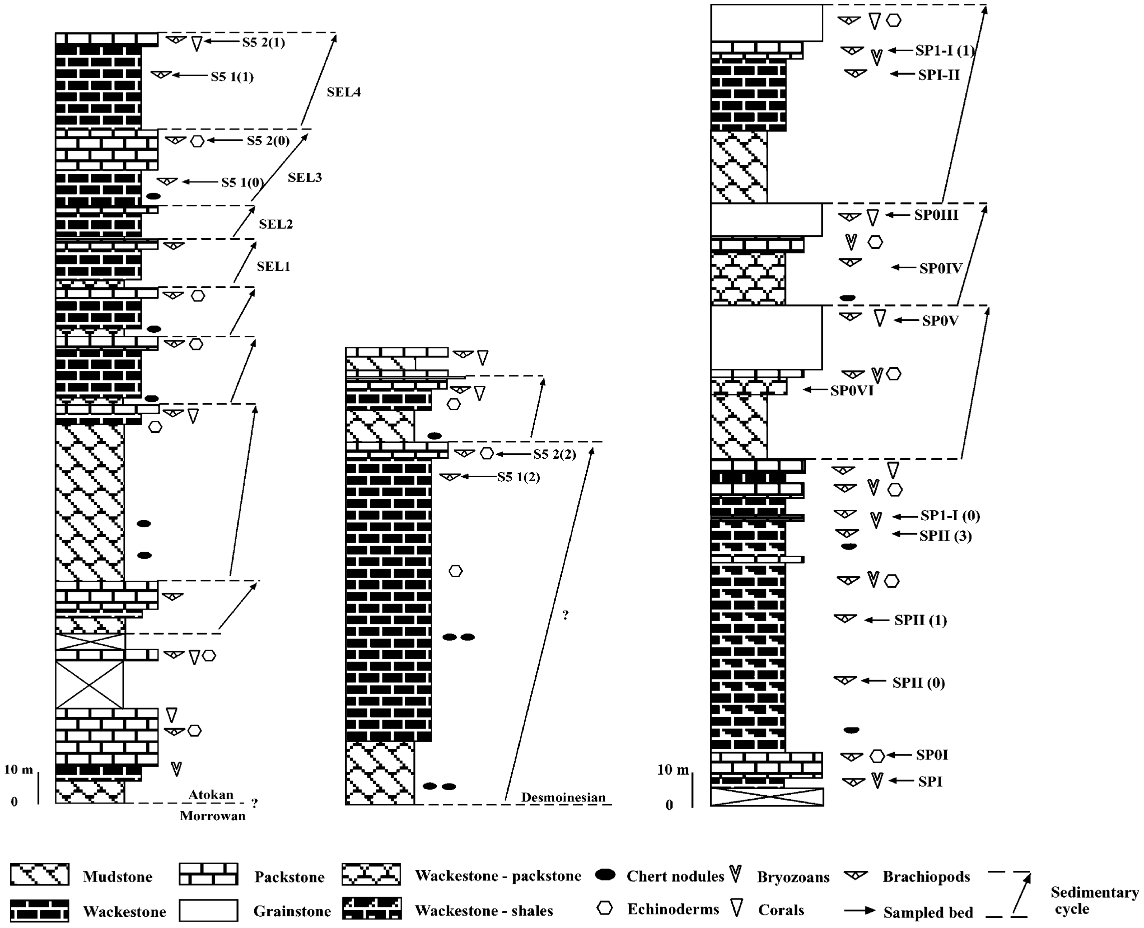

Fig. 2. Stratigraphic columns of upper Atokan–lower Desmoinesian deposits in the Illipah section (Nevada) [left], and upper Desmoinesian deposits in the Skunk Springs section (Utah) [right].

plant material, especially oxidized leaf remains, but no woody material. This plant material is abundant at the top of the cycles, and decreases in abundance down cycle indicating decreasing water depth from bottom to top within each cycle. Slabs were dissolved using acetic acid to remove carbonate and some residual mineral phases, leaving silicified fossil associations of brachiopods although carbonate brachiopod specimens were also found and removed using mechanical procedures.

3.2. Geochemistry

In both Utah and Nevada, samples for geochemical analysis were collected from different sedimentary facies (Fig. 3) within the depositional cycles representing different water depths. Samples without fossils were coarsely crushed and then sent to ALS Chemex of Vancouver, B.C. to be analyzed using ICP–MS. The results (see Supplemental Data-A) were examined using various measurements of nutrient levels (molar elemental ratios normalized to Al; Schmitz et al., 1997; Yudina et al., 2002) and terrestrial weathering including the molar ratio of total bases (Ca, Na, K, and Mg) to alumina. Total bases to alumina is used as a weathering ratio when describing terrestrial rocks because most weathering involves hydrolysis of base-bearing silicates, which leaves behind resistant cations such as Si and Al (e.g., Sheldon et al., 2002). Fe and P were selected as indications of nutrient levels because increasing abundances of either element stimulate primary productivity in modern shallow marine ecosystems (e.g., see references in Black and Shimmield, 2003), thereby increasing the available food supply.

3.3. Determining brachiopod associations

Six fossiliferous bulk samples were collected at each stratigraphic level for both localities. Brachiopods were collected in wackestone and packstone facies at six stratigraphic levels along three sedimentary cycles in the Illipah section, Nevada (Fig. 2). Eleven stratigraphic levels were surveyed in total, with six among the three sedimentary cycles in the Skunk Springs section, Utah (Fig. 2). Brachiopods were collected from intercalations of shales and wackestone limestones, wackestone, packstone, and grainstone facies. All brachiopods were identified at species level with eleven species (142 specimens)

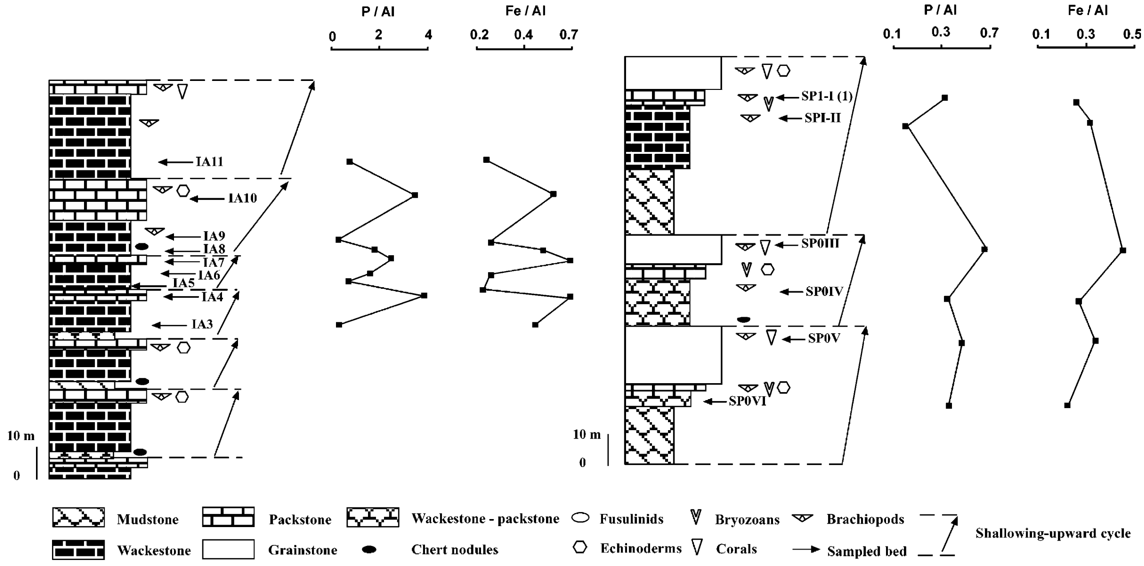

Fig. 3. Stratigraphic sections and geochemical results. Upper Atokan strata from the Illipah locality in Nevada (left column); Upper Desmoinesian strata from the section near Skunk Springs in the Conger Range in Utah (right column). [Note: differences in scale for P/Al and Fe/Al values for both localities are related to proximity to the continent as reflected in paleogeographic reconstructions; see Snyder et al., 1990].

recovered in Illipah (Table 1) and twenty species (607 specimens) in Skunk Springs (see Supplemental Data-B).

Total specimen count displayed in abundance matrix was used to determine brachiopod associations. Two multivariate techniques were applied to resolve these associations and to relate them to environmental gradients. Detrended correspondence analysis (DCA) was the main technique because it is a method of ordination based on correspondence analyses but corrects the arch effect (Hill and Gauch, 1980; Etter, 1999). Also, this method has been reported successful in linking stratigraphic and paleoecological data (Scarponi and Kowalewski, 2004). For the present study, axis 1 (DCA 1) represents variation of facies along the cycle in which brachiopod species are recorded. It is possible to determine the relative water depth represented in this cycle through sedimentological analysis of these facies, and therefore axis 1 also represents variations in water depth. Sedimentological and paleontological data cannot resolve the meaning of axis 2 (DCA 2), but it is likely to reflect water energy by comparison with similar cycles described in the region (Heath et al., 1967). The DCA method of ordination clusters together those species that share the highest number of specimens present in the same facies and relative water depth. The use of DCA approach facilitates the determination of original associations based on recurrence of associated taxa present in the same ecosystem. This method, however, presents complications in establishing associations when species are recorded from more than three different stratigraphic levels (see Pérez-Huerta, 2004). Cluster analysis with Morisita's index (e.g., Etter, 1999) were used in combination with DCA to overcome these difficulties. This was necessary for the brachiopod associations determined from the Skunk Springs section, Utah (see Supplemental Data-C).

4. Results

Molecular weathering ratios Fe/Al and P/Al track changing water depth in both sections of Nevada and Utah (Fig. 3). In both cases, shallower water depths had a greater abundance of both Fe and P, and a higher total bases to alumina ratio (not shown). There is also a fairly strong relationship ($R^2=0.68$) between the Fe/Al and P/Al ratios and the ratio of total bases to alumina (Fig. 4). To ensure that the weathering ratios reflected depositional rather than diagenetic chemistry, we also examined the molar K/Al ratio of our samples. In cases of metasomatic alteration or of post-burial fluid migration, K is often redistributed, especially via depositional contacts between units (or bedding surfaces; e.g., Sheldon, 2003). There was no evidence of this, as K/Al ratios were relatively constant for both localities and K tracked the other labile cations with respect to sea level, i.e., there was no significant difference between say, K and Mg that would indicate preferential mobility of any of the individual chemical components.

Table 1
Late Atokan–Early Desmoinesian brachiopod data, number of specimens of each species at stratigraphic levels, from the Illipah section (Nevada)

Taxa	Stratigraphic levels					
	S51 (0)	S52 (0)	S51 (1)	S52 (1)	S51 (2)	S52 (2)
Kozlowskia splendens (1)	5	2	3	3	2	2
Eomarginifera cf. *E. haydensis* (2)	7	4	9	6	2	7
Linoproductus sp. (3)	0	4	0	3	0	3
Linoproductus ? *L. prattenianus* (4)	3	0	6	0	1	0
Crurithyris planoconvexa (5)	2	1	1	0	2	0
Composita subquadrata (6)	0	3	0	6	0	3
Composita aff. *C. subtilita* (7)	0	2	0	2	0	1
Cleiothyridina elegans (8)	2	2	4	3	3	5
Neospirifer cf. *N. cameratus* (9)	0	3	0	0	0	0
Anthracospirifer opimus (10)	0	1	0	0	0	1
Brasilioproductus cf. *B. welleri* (11)	7	0	8	0	2	0

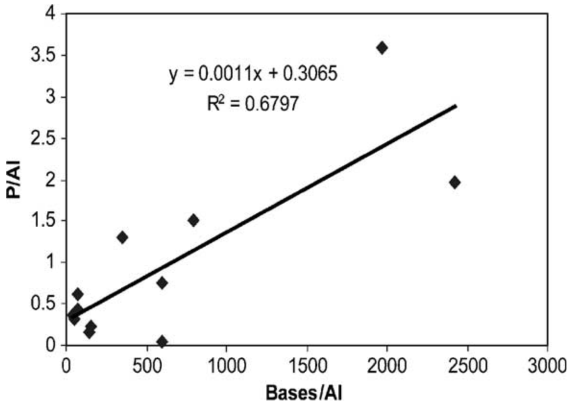

Fig. 4. P/Al versus total bases/Al.

Within a given species of brachiopod, the size of an individual specimen is strongly dependent on its depositional facies. Specimens of the athyridid *Cleiothyridina elegans* ($N=13$) and of the productid *Kozlowskia splendens* ($N=20$) were collected in wackestone and packstone facies along three consecutive sedimentary cycles (Fig. 5). Measurements of size, taking into account both length and width, were compared for both species found in different facies using a "box plot" diagram (Fig. 5). When values of mean size are compared, larger brachiopod specimens of *Cleiothrydina elegans* are associated with shallower depositional facies, while for specimens of *Kozlowskia splendens*, the opposite is true (Fig. 5). With a larger number of specimens recovered from facies reflecting greater differences in water depth, the results are more robust. Similar "box plot" diagrams were generated for two athyridid species, *Composita argentea* and *Composita trilobata*, recorded in wackestone and grainstone facies in the Skunk Spring section, Utah (Fig. 5). When the mean sizes of 30 specimens of each species are compared, larger brachiopod specimens of both species are associated with shallower depositional facies and smaller ones with deeper facies (Fig. 5). When separated temporally, between 20–50% of brachiopod species from a sequence of three consecutive cycles at each locality, Illipah (Nevada) and Skunk Springs (Utah), occurred in more than one facies and water depth, and 70–80% of the specimens of these taxa show different body size and biomass distribution when recorded from different facies and water depths. This tendency is not observed equally in dissimilar major groups of brachiopods. Some taxa belonging to the orders Productida and Athyridida show a size–water depth relationship but only within certain groups, whereas all recorded spiriferids show the trend. Among productid brachiopods, only the taxa within the tribe Kozlowskiini (Brunton et al., 1995) show a strong size–water depth relationship. In the order Athyridida, species of the genera *Composita* and *Cleiothyridina* show a size water–depth relationship, while species belonging to the order Terebratulida do not.

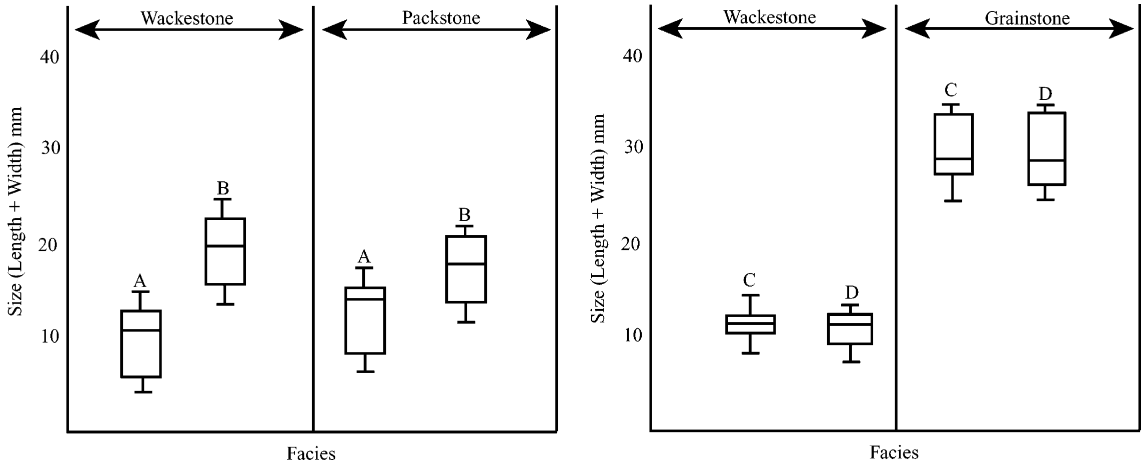

Fig. 5. Box plot diagrams of brachiopod size [mean size: cross bars inside box] for *Cleiothyridina elegans* (A) [$N=13$] and *Kozlowskia splendens* (B) [$N=20$] from the Illipah section [left] and for *Composita argentea* (C) [$N=30$] and *Composita trilobata* (D) [$N=30$] from the Skunk Springs section [right].

5. Discussion

5.1. Nutrient availability

The term food supply is used herein to include potential food resources for filter-feeders as well as those nutrients required for metabolic functions. The potential food resources for filter-feeders are: a) phytoplankton; b) organic detritus; c) dissolved or colloidal organic matter; d) heterotrophic microbial organisms (e.g., Fürsich and Hurst, 1974). Brachiopods can potentially feed from any of these groups (e.g., James et al., 1992), though early studies suggested that brachiopods feed mainly on diatoms and dinoflagellates (Rudwick, 1962) or dissolved organic matter (e.g., McCammon, 1969). However, more recent work indicates that brachiopods prefer phytoplankton whenever it is available, and that they rely on dissolved or colloidal organic matter only when phytoplankton are scarce (e.g., James et al., 1992). Less attention has been given to the study of the amount of nutrients used by brachiopods in their metabolic functions (James et al., 1992). Unless traces of phytoplankton or presence of diatoms and dinoflagellates are found, the use of paleoproductivity indices is the best estimate for availability of food supply, because the availability of nutrients as well as of food resources are linked in areas of present-day oceanic productivity (e.g., upwelling).

The relationship between Fe/Al and P/Al ratios and the weathering ratio of total bases to alumina (Fig. 4) indicate that Fe and P supply were in large part controlled by terrestrial inputs. This idea is also supported by the observation that terrestrial plant material is more abundant in the shallower facies than in the deeper ones. Within the shallower-water parts of the depositional cycles, terrestrial inputs were volumetrically more important than in the deeper parts. As a result, the shallower facies were richer in Ca, Na, Mg, K, Fe, and P, which represent a richer potential food supply for both primary producers and the brachiopods that fed on them.

Given the strong size-water depth relationships for many brachiopod species (Fig. 5) found in multiple sedimentary facies, it is suggested that the greater potential for primary productivity in the shallower facies directly controlled the distribution of the brachiopod fauna. Though the estimated difference in water depth between the top and bottom of the sedimentary cycles is at most 50 m based on carbonate sedimentation in modern carbonate ramps (e.g., Wilson and Jordan, 1983), there are significant differences in nutrient availability and primary productivity even within the photic zone in modern marine systems (see references in Black and Shimmield, 2003).

5.2. Brachiopod associations and species differences

The brachiopod associations based on DCA analyses (see Fig. 6 and Supplemental Data-C) show many species that cannot be ascribed to a certain facies. If any given species is present in more than one facies at different water depths, scores for these species will cluster together independently instead of overlapping. This will denote that the distribution of those species is not controlled by any of those two factors. An example of this is shown in the DCA analysis for taxa recorded in upper Atokan–lower Desmoinesian deposits from the stratigraphic section at the Illipah locality (Nevada) where three species demonstrate this behaviour: *Kozlowskia splendens* (1), *Eomarginifera* cf. *E. haydensis* (2), and *Cleiothyridina elegans* (8) (Fig. 6).

These species are recorded in both wackestone and packstone facies and are associated with different water depths. Specimens of these taxa, however, do not have the same body size and biomass in both sedimentary contexts. Specimens of *Cleiothyridina elegans* have larger body sizes (up to 14 mm in length and 18 mm in width) in packstone facies at the top of the cycles (Fig. 7). Specimens of the same species do not reach more than 10 mm in width and 8 mm in length when in wackestone facies (Fig. 7). A similar trend is observed for specimens of *Kozlowskia splendens* in the same stratigraphic sequence. Specimens of about 20 mm in length and 25 mm in width are recorded in wackestone facies, while specimens do not usually reach more than 20 mm in width when present in packstone facies (Fig. 7). This trend in brachiopod size and biomass distribution suggests a correlation with changes in food supply when compared with the paleoproductivity indices (see Figs. 3 and 7). Specimens of *Cleiothyridina elegans* attain larger size and volume in correlation with high levels of food supply. Specimens of *Kozlowskia splendens* as well as of *Eomarginifera* cf. *E. haydensis* show an opposite tendency with larger size associated to

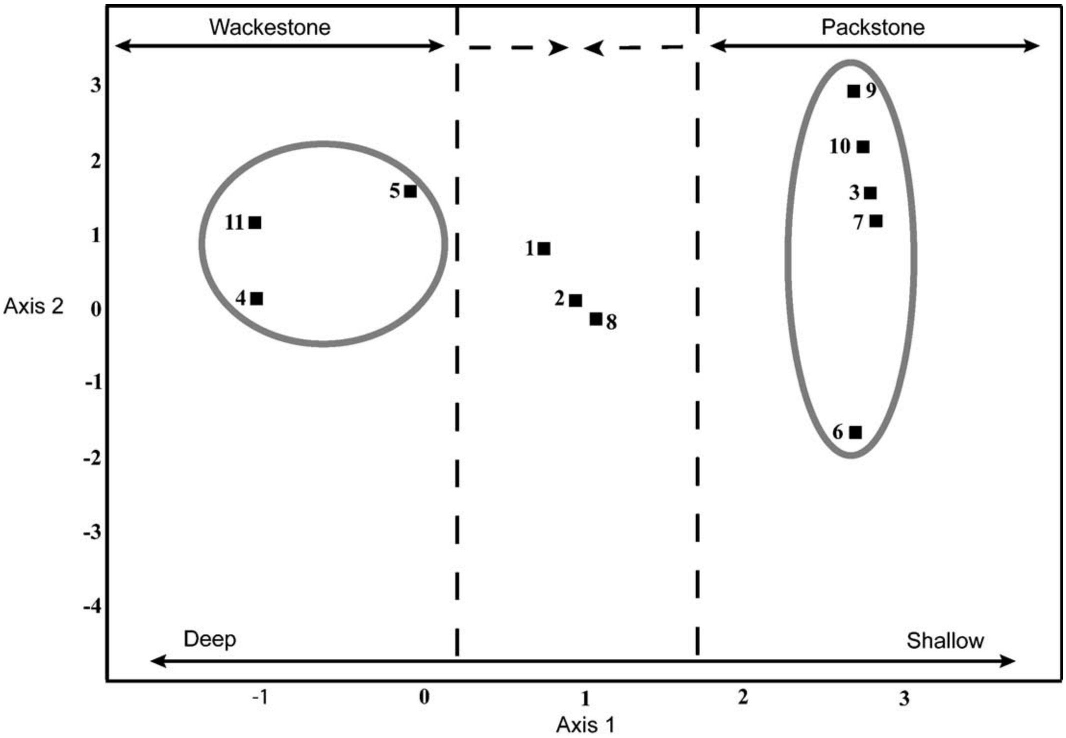

Fig. 6. DCA scores for brachiopod data (Table 1) from the upper Atokan strata at the Illipah locality in Nevada. Detrended correspondence analysis (DCA) relates the distribution of brachiopod species to water depth and sedimentary facies. 1. *Kozlowskia splendens*; 2. *Eomarginifera* cf. *E. haydensis*; 3. *Linoproductus* sp.; 4. *Linoproductus* ? *L. prattenianus*; 5. *Crurithyris planoconvexa*; 6. *Composita subquadrata*; 7. *Composita* aff. *C. subtilita*; 8. *Cleiothyridina elegans*; 9. *Neospirifer* cf. *N. cameratus*; 10. *Anthracospirifer opimus*; 11. *Brasilioproductus* cf. *B. welleri*. Circles represent brachiopod associations based on stratigraphic occurrence in consecutive depositional cycles (details in Pérez-Huerta, 2004).

depletion in food supply. Similar results are obtained from brachiopod species in upper Desmoinesian deposits from Skunk Springs (Utah), as previously shown for the brachiopod species *Composita argentea* and *Composita trilobata*. These results suggest a correlation between changes in body size and availability of food supply at the species level. If analyses are extended to generic levels, results are more conclusive and robust. This result supports the hypothesis proposed by Fürsich and Hurst (1974) that environmental factors play a crucial role in dictating the structure of brachiopod associations.

5.3. The role of lophophore filtering efficiency in food supply processing

The established brachiopod associations demonstrate that spire-bearing brachiopods (athyridids and spiriferids) are dominant at the top of shallowing-upward cycles within packstone and grainstone facies. Specimens of taxa included in this group are also larger and constitute a higher fraction of biomass at these levels in correlation with high primary paleoproductivity. In contrast, productid brachiopods are dominant and larger in deeper waters (predominantly wackestone facies) within the cycles. The dominance of productid brachiopods at these levels correlates with depletion in nutrients and food resources. One possible explanation for these differences in structure and composition of these brachiopod communities is that different groups of brachiopods had different types of lophophore, better adapted to either high or low nutrient conditions, because lophophores control the efficiency of filtering systems in both groups (e.g., Fürsich and Hurst, 1974; Vogel, 1975; Williams et al., 1997).

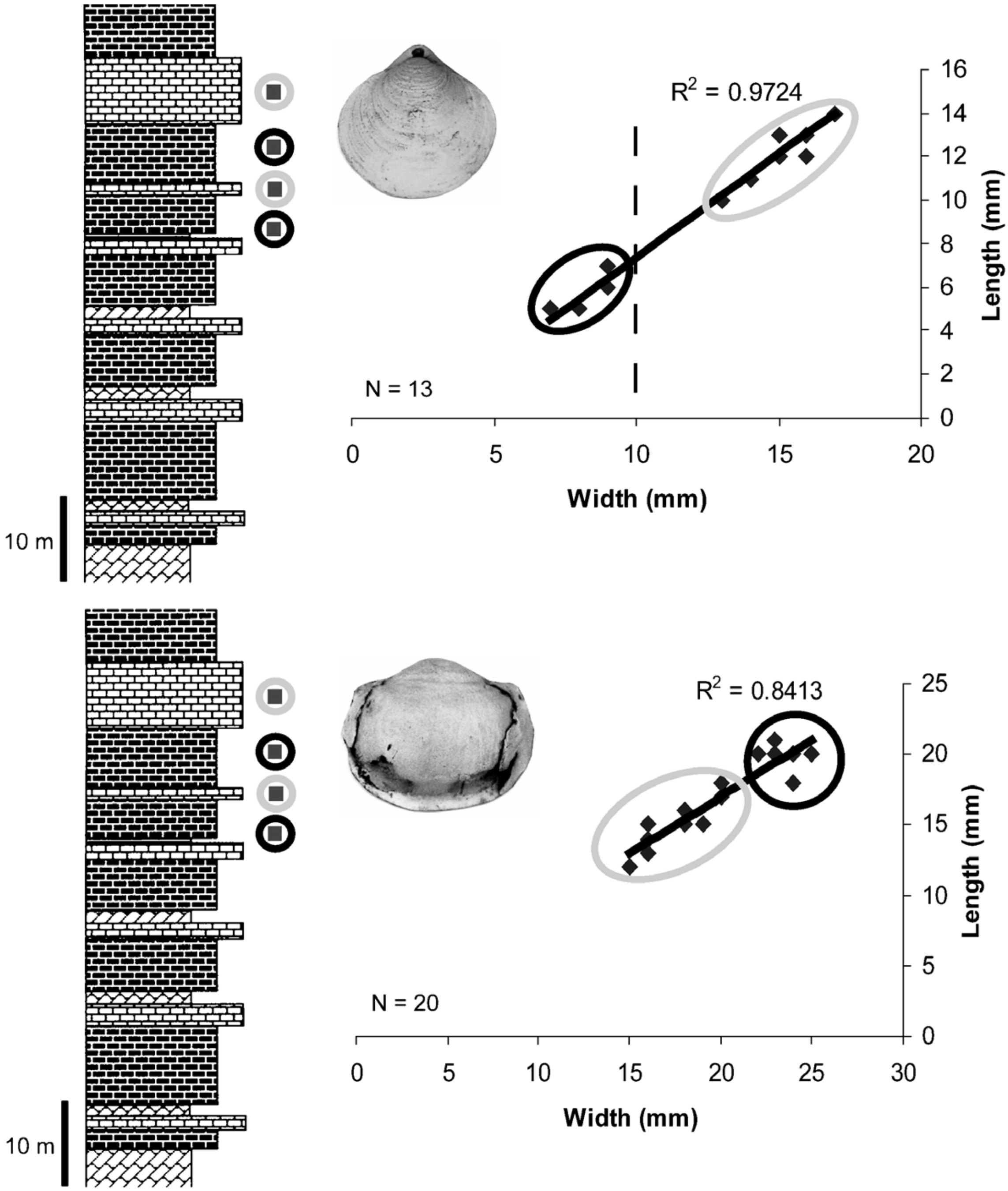

Fig. 7. Length–width distribution for specimens [dark squares] of *Cleiothyridina elegans* [upper diagram] and *Kozlowskia spendens* [lower diagram]. The length–width distribution for specimens of *Cleiothyridina elegans* shows two distinct populations, with larger specimens occurring exclusively in shallower water and the opposite trend shown for specimens of *Kozlowskia splendens* [Black and grey circles for specimens collected at wackestone and packstone facies, respectively].

The evaluation of lophophore efficiency in food supply processing is speculative because taxa within the groups of spire-bearing and productid brachiopods do not have extant representatives, which complicates the reconstruction of inhalant and exhalant currents. The absence of these data does not allow a quantitative determination of the efficiency of filtering systems in both groups. Some studies of modern brachiopods, however, can provide guidance about lophophore filtering efficiency. Brachiopods are "facultative active suspension feeders" (LaBarbera, 1977) that maximize efficiency of water transport (LaBarbera, 1981). The implication is that the filtering capacity mostly depends on their own ability to generate efficient inhalant and exhalant currents. Those studies were conducted primarily in extant brachiopod species of the order Terebratulida (e.g., LaBarbera, 1981). However, these brachiopods have a plectolophous type of lophophore that cannot be compared directly to the lophophore that was present in spire-bearing and productid brachiopods. This situation limits the applicability of analyses on living brachiopods in understanding lophophore filtering efficiency in fossil faunas of the present work.

Although some studies (e.g., Ager and Wallace, 1966) have tried to address the filtering efficiency in fossil faunas, there is still not sufficient and accurate information for such interpretations. Analyses of internal morphology of fossil faunas, however, allow us to reconstruct lophophore morphology and to determine a hypothetical reconstruction of inhalant and exhalant currents. The problem is that a proper analysis should take in consideration water currents around the organism (LaBarbera, 1981), 3D distribution of the incoming and outgoing flow patterns, and the possible orientation of brachiopods to water movement (LaBarbera, 1977). However, this is not possible in many cases when dealing with fossil faunas. For example, no evidence of water current directions or of preferred orientation of brachiopod faunas were found during our field work. For most of these reconstructions, we have to assume a scenario with faunas living in "still water" conditions. LaBarbera (1981) demonstrated that flow patterns (inhalant–exhalant currents) generated by brachiopods are similar under "still and current water" conditions, since their high efficiency in transporting water in and out of the shell independently of the surrounding conditions.

"Spire-bearing brachiopods", including taxa within the orders Athyridida and Spiriferida, developed a skeletal support for their lophophores in the form of a laterally extended pair of spiral lamellae (spiralium) (Williams et al., 1997). This skeletal structure is thought to mainly support a spirolophe type of lophophore as in extant rhynchonellids (Williams et al., 1997) or alternatively a deuterolophe type (Williams and Wright, 1961). This type of lophophore of spire-bearing brachiopods is thought to represent an efficient filtering system (e.g., Fürsich and Hurst, 1974; Vogel, 1975), since it is one of the most complex and largest types of lophophore. There is a general agreement about the reconstruction of inhalant and exhalant currents in spiriferid (e.g., Williams and Wright, 1961; Ager and Wallace, 1966; Vogel, 1975) and athyridid brachiopods (see work and references in Alvarez and Rong, 2002). According to the reconstructions by Vogel (1975), spire-bearing brachiopods could generate strong unidirectional inhalant currents through the antero-lateral margins of the shell (Fig. 8). The presence of the spiralium, however, would limit the extension of the lophophore, reducing the area to filter food supply. The inhalant currents would be confined to the anterior margin of the shell filtering resources from an area of less than 180° laterally respect to the plane of bilateral symmetry (Fig. 8). This filtering system represents a significant advantage for brachiopods living in areas of elevated concentrations of food supply, although it would be less efficient where the food supply is less abundant. Low concentrations result in dispersion of nourishment, which does not favor systems based on unidirectional currents in limited areas around the shell. The dominance and larger size attained by spire-bearing brachiopods in shallow waters with high levels of paleoproductivity at the top of the cycles correlates with these factors. This may also explain why spire-bearing brachiopods are recorded with smaller body sizes and in less abundance in deeper waters. These results are in contrast to those of Silurian–Devonian brachiopod associations as described by Fürsich and Hurst (1974). For example, these authors showed that Silurian spiriferids do not decrease in size, along with pentamerids, toward deeper waters, because of their highly efficient lophophore.

Our observations on spiriferid brachiopods may represent a difference with respect to living rhyncho-

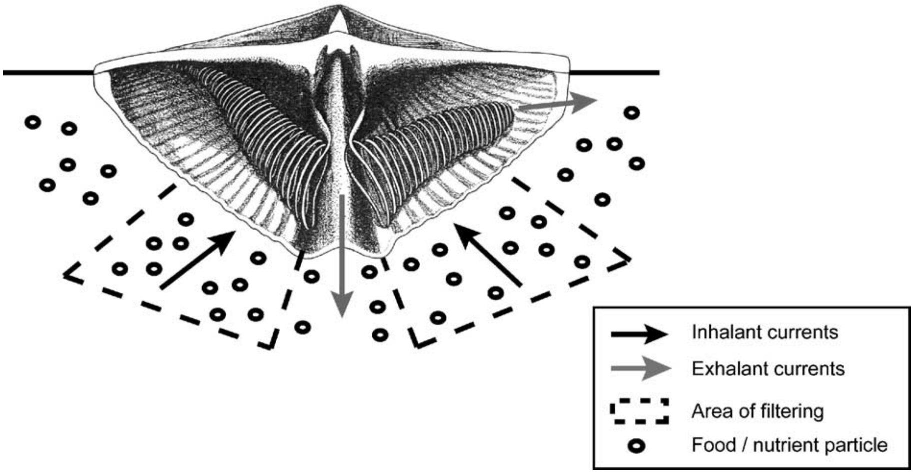

Fig. 8. Hypothetical representation of efficiency of the filtering system of some extinct spire-bearing brachiopods showing flow patterns and extension of area for trapping food resources. Inhalant and exhalant currents according to Vogel (1975) and diagram modified from Ager and Riggs (1964).

nellid brachiopods because they can uncoil and extend the lophophore beyond their shells. It is well known since the end of the 19th century (e.g., in *Hemithyris psittacea* described by Morse, 1869) and it has been also shown in the rhynchonellid brachiopod *Notosaria nigricans* (Hoverd, 1985). Such a capability is an advantage for suspension-feeders because greatly extends the area for trapping food particles (Ager, 1987). However, Fürsich and Hurst (1974) also showed that species of Silurian rhynchonellids decrease in size toward deeper water even having such potential capability.

There is less agreement about the reconstruction of inhalant and exhalant currents in productid brachiopods because there is a higher diversity of internal morphology within the order Productida. Also, less work has been done in terms of filtering efficiency and there are no analogous models for lophophore geometry in living brachiopods. However, we can discuss filtering efficiency in productid brachiopods based on internal morphological features. In contrast to spire-bearing brachiopod, productids have a lophophore with more coverage around the surface of the dorsal valve (see Brunton et al., 2000). The lophophore is thought to have been present in the mantle cavity attached to the brachial ridges and around the subperipherial and lateral ridges (Brunton et al., 2000). The absence of a skeletal support as in spire-bearing brachiopods suggests not only more coverage internally, but also that the lophophore could be extended freely beyond the shell as in living rhynchonellids. This would allow them hypothetically to get food resources from at least 270° around their shells (Fig. 9). Also, it might permit the possibility of creating multidirectional inhalant currents. Although multidirectional inhalant currents have not yet been observed in modern brachiopods, the reconstruction of lophophore geometry of these extinct forms does not preclude such a possibility. In fact, this has been proposed for taxa within the order Productida, such as the genus *Falafer* (Grant, 1972) and could even be applied to the new taxon *Muhuarina* (Baliński and Sun, 2005). Many of the taxa recorded in the study area, such as those belonging to the tribe Kozlowskiini (Brunton et al., 1995) (see Table 1), presumably had a less complex lophophore morphology than in *Falafer* and *Muhuarina*. Although this implies a more simple reconstruction of inhalant and exhalant currents (see Brunton et al., 2000), we think that they might facilitate the generation of multidirectional currents. The resultant filtering system, based on reconstructions of lophophore geometry, would permit them to obtain their food supply from a more extended area around the shell than in spire-bearing brachiopods (Fig. 9). This would benefit productid brachiopods under conditions of low productivity when nourishment is more dispersed. As a result, productid brachiopods

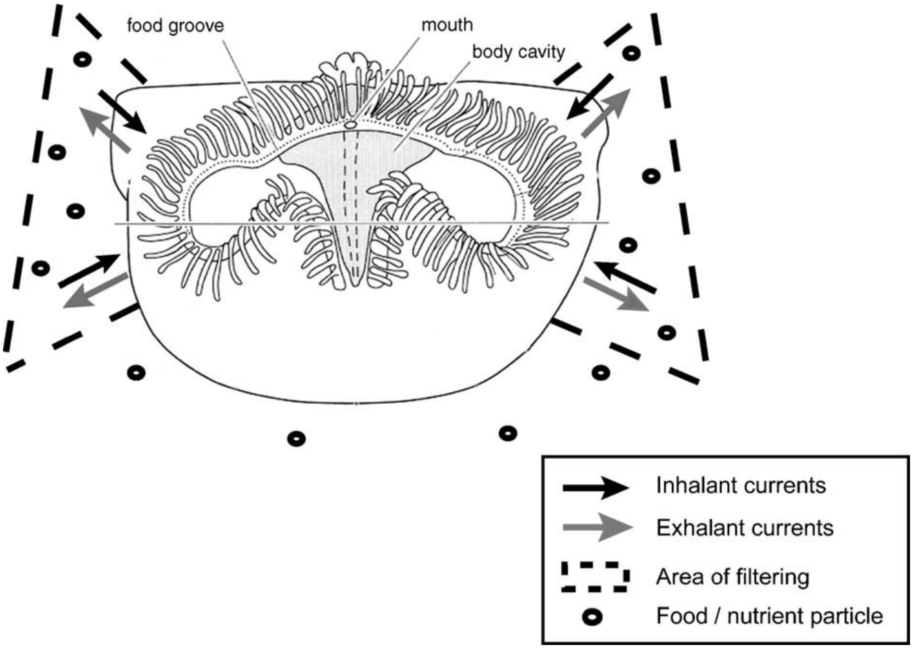

Fig. 9. Hypothetical representation of efficiency of the filtering system present in extinct productid brachiopods showing flow patterns and extension of area for trapping food resources. Inhalant and exhalant currents as in a similar model proposed for Falafer Grant (1972) and diagram modified from Brunton et al. (2000) without including his interpretations.

would dominate and be of larger size in deeper water with less food supply.

The reconstruction of lophophore filtering efficiency in spire-bearing and productid brachiopods explains the recorded spatial distribution and morphological changes in these faunas. Based on our other data it may be argued that the type of lophophore and the availability of nourishment in the water column determine the dominance and body size distribution of brachiopod faunas within the associations.

5.4. The role of physico-chemical parameters versus food supply as major paleoecological controls

Physico-chemical parameters such as oxygen availability, temperature, salinity, water depth, and substrate traditionally have been proposed as major paleoecological factors controlling the distribution of filter-feeders in benthic communities. For brachiopod faunas, these factors are thought as well to determine morphological variability and abundance. The fact that these physical and chemical parameters often can be inferred from stratigraphical and sedimentological evidence is the main reason to give them special consideration in paleoecological studies (e.g., Boucot, 1981), but they should be considered individually for a given study rather than simply assumed to be the primary controls.

5.4.1. Water depth

There is no direct evidence of changing brachiopod dominance and morphology with changes in water depth. More important herein are modifications of physico-chemical parameters associated with these changes, because water depth alone cannot explain the inter-group (e.g., productids versus spiriferids) variations (see Section 5.1 and 5.2). Fluctuations in temperature, oxygen availability, salinity, and water turbulence are directly related to water depth changes. Thus, some brachiopods present morphological adaptations, such as thick shells, large pedicle openings or wings, which are thought to be related to living conditions in turbulent or quiet waters (e.g., Alexander, 2001). Therefore, concluding that water depth is the sole control is at best an oversimplification because it plays a role in at least four other factors (temperature, oxygen availability, salinity, and turbulence) that may work either in concert or in competition with one to another.

5.4.2. Substrate type

Substrate type has traditionally been considered as one of the primary paleoecological controls on the distribution of brachiopods. Brachiopods are benthic organisms that spend the majority of their life "attached" to a surface and, therefore, type of substrate is likely to influence the occurrence of species within different paleoenvironments. We can assume that spire-bearing and productid brachiopods had lecithotrophic larvae as in other "articulated brachiopods". It has been long known that brachiopod with lecithotrophic larvae "are capable of making choices about the type of substratum they settle on, and they show behaviors interpreted as exploratory and directed toward identifying a suitable substratum prior to final attachment" (Peck, 2001b; p. 175; see also references in this paper). Several morphological adaptations have been linked to living in a certain type of substrates. For example, the presence of hollow halteroid and umbonal spines in productids are thought to prevent sinking (Brunton, 1982) or large flat ventral interareas to help stabilize some spiriferids on soft substrates (Alexander, 1984, 2001). However, it is not certain that substrate type controls the presence or absence of different species, but it might determine which species dominate a given population. Many brachiopod species recorded in a certain substrate type do not have specific morphological adaptations for stabilization or attachment but for filtering purposes. For example, some rhynchonellids developed a high linguiform extension (tongue) and strong angular costae to prevent coarse sediment entering the mantle cavity (e.g., Rudwick, 1964). A similar adaptation is found in the brachiopod species *Kochiproductus coronus* in which the trail is modified to trap sedimentary particles (Shiells, 1968). This also applies to most of the species of *Cleiothyridina* in the Pennsylvanian deposits of the Great Basin (Pérez-Huerta, 2004). These species are recorded in all facies, but are larger in size when recorded in wackestone facies or limestones associated with shales. Taxa within this genus are usually characterized by displaying flat spines at the anterolateral margins of the shell (Alvarez and Rong, 2002), which may prevent coarse inorganic particles from entering the mantle cavity.

5.4.3. Food supply

The influence of substrate type and water depth on brachiopods explains some morphological adaptations in specific taxa, and the structure and dominance in some associations. Neither changes in water depth and type of substrate can explain most of the observed paleoecological trends described in this study. The presence of brachiopod species in more than one facies and relative water depth but of different size requires additional explanations. Also, the dominance of spire-bearing brachiopods in shallow water and productid brachiopods in deeper water cannot be explained by changes in water depth and type of substrate. Because of these observations, it is thought that availability of nourishment plays a significant role in the paleoecology of brachiopods as well. Thus, body size distribution of brachiopods is unlikely to be dependent primarily on the amount of oxygen or temperature but rather by the availability of food. In general, it is difficult to determine which environmental factor, temperature, oxygen, and food availability, is the key driver influencing the metabolism of living brachiopods. However, a positive correlation between metabolic rate (oxygen consumption) and temperature has been shown previously. Experiments with modern brachiopods from high latitudes show that with increasing temperature brachiopods have to consume more oxygen (James et al., 1992; Peck, 2001a). However, it is clear that the bulk change of metabolism of brachiopods, and therefore growth, is mostly influenced by nourishment availability (James et al., 1992; Peck, 2001a). Temperature has a minor influence and oxygen availability only controls growth rates depending on seasonal cycles. This has been also shown for other marine invertebrates, such as sea urchins (Brockington and Clarke, 2001).

6. Conclusions

The availability of nutrients is enhanced by shallower seas in the Pennsylvanian of Utah and Nevada. Among brachiopod species preserved in these cyclical deposits, most spiriferids, some athyridids, and few productid brachiopods show a strong relationship between body size/biomass and nutrient variability as shown by paleoproductivity indices. Given these relationships for many brachiopod species found in multiple sedimentary facies and different water depths, it is suggested that the greater potential for primary productivity, and consequently, total food supply, in shallow water is an important paleoecological control. This factor influences the body size, abundance, and population variability of studied fossil brachiopod faunas. This conclusion is also supported by studies of extant brachiopods (Kowalewski et al., 2002) and other fossil faunas, such as microfossil taxa (e.g., Brasier, 1995). Because physicochemical factors influence the nourishment availability, we suggest that both components played an important role in controlling the distribution of brachiopod faunas. Consistent with the findings of Fürsich and Hurst (1974), the spatial distribution and structure of Pennsylvanian Great Basin brachiopod associations is also highly governed by filter-feeding efficiency of brachiopods besides the food supply. Thus, spire-bearing brachiopods dominate and attain larger size in shallow water with a large food supply because of their capacity to generate strong inhalant currents. Productid brachiopods in contrast, dominate and are of larger size in deeper water with less food supply because of their lophophore geometry and the possibility of creating multi-directional inhalant currents (see Section 5.3). Food supply also explains greatly the size distribution of fossil brachiopod faunas. Given the relationship between variations in oxygenation, temperature and nourishment availability and their influence on the metabolic functions, which determine growth rates, physiology may play a more important role in the paleoecology of brachiopods and other benthos than previously recognized.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2005.07.020.

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