Palaeoecological patterns within the dysaerobic biofacies: Examples from Devonian black shales of New York state

Diana L. Boyera,⁎, Mary L. Droserb

a Department of Earth Sciences, SUNY Oswego, 240 Pez Hall, Oswego, NY 13126, United States
b Department of Earth Sciences, University of California, Riverside, CA 92521, United States

1. Introduction

Nearly all of the preserved Palaeozoic marine record is interpreted to represent deposition in shallow epeiric seaways, which are susceptible to stratification and reduced bottom water oxygen conditions that can result in widespread black shale deposition (Klemme and Ulmishek, 1991; Tyson and Pearson, 1991; Arthur and Sageman, 1994; Schieber, 1998; Negri et al., 2006). Black shales are particularly abundant in Devonian aged strata (see Negri et al., 2006 and references within), supporting the idea that dysaerobic, or reduced but non-zero bottom water oxygen conditions were not only common and extensive during this time, but also exerted a major control over Devonian benthic community structure. Taxa interpreted to be adapted to reduced bottom water oxygen conditions occur throughout the Phanerozoic record, and the Devonian is noted for its dysaerobic assemblages (Kammer et al., 1986; Allison et al., 1995). Typically, assemblages of taxa associated with low oxygen conditions are grouped into the broadly defined dysaerobic biofacies (Rhoads and Morse, 1971; Byers 1977). Recurring taxonomic associations, known as biofacies, are associated with specific environmental conditions in oxic epeiric seas (e.g. Cisne and Rabe, 1978; Gray et al., 1981; Forney and Droser, 1996; Brett et al., 1991; Patzkowsky, 1995; Boucot and Lawson, 1999; Bonelli et al., 2006). However, the dysaerobic biofacies, customarily defined by low species richness and the presence of a few specific fossils, is characterized by numerous depositional environments. This paper tests the hypothesis that discrete patterns in taxonomic and ecological distribution of benthiic macrofauna can be recognized in association with what are interpreted as variable levels of bottom water oxygen and then further used to delineate environmental variation within these broad oxygen-deficient settings. The recognition of such patterns through the dysaerobic zone is important to understand the palaeoecological signal of much of our Palaeozoic stratigraphic record.

Studies of modern reduced oxygen settings reveal that patterns of diversity and life habits are associated with specific levels of bottom water oxygen as follows: 1) In general, polychaetes, echinoderms, and molluscs are the taxa most tolerant of oxygen stress (Levin and Gage, 1998; Wu, 2002; Levin, 2003), and soft bodied organisms, preserved as trace fossils in the rock record, are typically the last organisms to be excluded as oxygen levels decrease to zero (Savrda et al., 1984; Thompson et al., 1985; Savrda, 1992). 2) Reduced species richness is strongly correlated with reduced oxygen conditions from a range of modern settings (Diaz and Rosenberg, 1995; Levin and Gage, 1998; Wu, 2002; Levin, 2003); however, evenness, or the distribution of...
individuals among an assemblage, is less strongly tied to relative bottom water oxygen levels (Levin and Gage, 1998; Levin, 2003). Variability in dominant taxa is observed through the dysaerobic zone in association with changing levels of oxygen stress and one group is not typically dominant throughout the entire range of the dysaerobic zone (Allison et al., 1995; Levin, 2003). 3) In modern settings, as oxygen levels decrease, deposit feeding becomes the dominant life habit (Wu, 2002). 4) The size of metazoan organisms is correlated with physiological oxygen demands, and as a result, size of individuals is also observed to decrease under decreased relative oxygen levels (e.g. Rhoads and Morse, 1971; Pearson and Rosenberg, 1978; Thompson et al., 1985; Savrda, and Bottjer, 1986; Savrda, 1992). These established ecological patterns, either individually or in combination, are the basis for recognizing and interpreting reduced oxygen conditions from the rock record (e.g. Savrda and Bottjer, 1986; Wignall and Myers, 1988; Savrda, 1992; Allison et al., 1995; Sageman and Bina, 1997; Martin, 2004).

The dysaerobic zone is recognized in the rock record largely by decreased bioturbation and body fossil diversity (Rhoads and Morse, 1971; Byers, 1977; Wignall and Myers, 1988; Wignall and Hallam, 1991; Savrda, 1992), and the presence of specific taxa interpreted to be restricted to low oxygen conditions (Bromley and Ekdale, 1984; Savrda and Bottjer, 1986; Thompson and Newton, 1987; Gaines and Droser, 2003; Boyer and Droser, 2007). Dysaerobic conditions represent a wide range of relative oxygen levels and environmental settings (see Tyson and Pearson, 1991), however, variability within and between low diversity macrofaunal communities interpreted to be dysaerobic is rarely recognized. The Devonian has a particularly high number of taxonomically disparate groups that have been interpreted as dysaerobic and provides a unique opportunity to investigate the palaeoecology of a wide range of taxa inhabiting reduced oxygen settings (Allison et al., 1995).

The Devonian of upstate New York provides an ideal succession to examine palaeocommunity scale patterns associated with variable bottom water oxygen levels through the dysaerobic zone on a microstratigraphic scale, as numerous, black shale intervals are well exposed, biostratigraphically well constrained (e.g. Thayer, 1974; Woodrow and Isley, 1983; Kirchgasser et al., 1988; Brett et al., 1991; Baird et al., 1999) and preserve abundant body fossils (Cleland, 1903; Cooper, 1930; Thompson and Newton, 1987; Baird and Brett, 1991; Brett et al., 1991). The “Leiorhynchids,” a clade of rhyynchonelliform brachiopods that are recognized globally in Devonian aged black shales, are particularly abundant within Middle Devonian aged mudstones of upstate New York, repeatedly dominating many bedding plane surfaces and are commonly used as a low oxygen indicator (Cleland, 1903; Cooper, 1930; Thompson and Newton, 1987; Baird and Brett, 1991; Brett et al., 1991). These occurrences are so conspicuous within several stratigraphic intervals that a Leiorhyncha biofacies was defined, named for this characteristic genus (Cleland, 1903). Curiously, unlike most taxa typical of the dysaerobic zone (Diaz and Rosenberg, 1995; Levin 2003), some of these rhyynchonellids are also present in assemblages of much higher diversities, within what are interpreted to be fully oxygenated depositional settings (Boyer and Droser, 2007; Brett et al., 2007).

In order to evaluate ecological change associated with bottom water oxygen levels, dysaerobic strata must be identified using distinct and independent methods. We utilize geochemical proxies, sedimentological and ichnological data, and reduce species richness. Once dysaerobic strata have been identified, the combination of various aspects of these palaeooxygenation proxies from continuously sampled stratigraphic intervals allows for the entire range of relative oxygen levels through the dysaerobic zone to be recognized, and provides a framework for detailed investigation of the palaeoecological variability within the dysaerobic zone. This study identifies predictable taxonomic and ecological distributions that vary with interpreted bottom water oxygen levels through the dysaerobic zone.

2. Geologic setting

Devonian mudstones of the Appalachian Basin record deposition in a fore-land basin and represent the combined influence of sediment influx from the Catskill delta to the east and tectonic activity associated with the Acadian Orogeny (Johnson et al., 1985; Kent, 1985; Ettensohn, 1985a,b; Woodrow and Sevon, 1985; Woodrow et al., 1989). The areas of central and western New York represent deposition within a broad epeiric sea and have been influenced by the Acadian Orogen to the east as a sediment source (Woodrow and Sevon, 1985; Ettensohn, 1985a,b). Variations in tectonic activity and eustatic fluctuations are expressed as alternating carbonate and siliciclastic deposition across the Appalachian Basin (Ettensohn, 1985a,b, 1987; Murphy et al., 2000a,b). The classic Hamilton Group (latest Eifelian–Givetian) represents the onset of about 5–7 million years of terrigenous sedimentation from the Acadian Orogen preserved in the Marcellus sub-group and overlying Skaneateles, Ludlowville, and Moscow Formations (Rickard, 1975; Ver Straeten et al., 1994) (Fig. 2). Stratigraphically above this group is the Genesee Formation, in which the Middle/Upper Devonian (Givetian–Frasnian) boundary is placed (Ver Straeten et al., 1994). The Genesee Formation is dominated by black shale deposition and comprised of several members including the Genesee and Penn Yan Shales (Thayer, 1974; Kirchgasser et al., 1988) (Fig. 2).

Black to grey shales are abundant through this interval and were sampled at several levels listed in ascending order, the Cardiff Shale of the Oatka Creek Formation, Marcellus sub-group (Ver Straeten et al., 1994), the Levanna member of the Skaneateles Formation, several intervals through the Ledyard Shale of the Ludlowville Formation, the Windom Shale of the Moscow Formation and the Genesee and Penn Yan members of the Genesee Formation (Figs. 1 and 2) (see Boyer, 2007).

3. Methods

Fossiliferous mudstone units from the Hamilton Group and overlying Genesee Formation were sampled continuously from 14 localities (Fig. 1). Sampled intervals include laminated to fully bioturbated shales.

Sedimentary features were recorded from both polished cross-sectional views in hand samples and thin sections. X-ray diffraction of whole rock samples representing less than 3 mm of total thickness.

Fig. 1. Locality map of Middle and Upper Devonian aged sites in western New York. Exposed formations or members are given in parenthesis. LA = Lake Ave. (Marcellus), BC = Browns Creek (Levanna), M = Manterh Creek (Penn Yan), K = Kashong Glen (Levanna), W = Wilson Creek (Ledyard), F = Fayette (Levanna), HQ = Hubbard Quarry (Genesee), PC = Faines Creek (Ledyard), MC = Mill Creek (Penn Yan), LH = Long Hill road cut (Windom), AR = Abbey Rd. (Marcellus), CF = Cheese Factory/Gulf Rd. (Marcellus), TF = Tinker Falls (Windom), HF = Highland Forest (Windom).
was used to most closely describe lithologic composition associated with individual bedding plane assemblages of fossils.

Framboid diameters from individuals on polished surfaces approximately 2 cm² were recorded from ten samples at five localities. Each sample was sub-sampled from hand samples with known cm scale paleontological and sedimentological information. Images were captured on a Philips XL30 instrument at the Analytical Electron Microscopy Facility at the University of California, Riverside. Individual framboids were then measured using the Image J 1.34n software from the National Institute of Health. Samples from intervals correlated with each bedding plane assemblage (Wignall and Myers, 1988; Savrda et al., 1984; Savrda, 1992), and the species richness associated with fundamental physiological oxygen demands of the trace-making organism (Rhoads, 1975; Pearson and Rosenberg, 1978; Savrda and Bottjer, 1986; Savrda, 1992), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Oschmann, 1991; Brett et al., 1991; Wignall, 1994; Allison et al., 1995). Species richness data, used to supplement the ichnological oxygen signal, is based simply on number of different taxa present, independent of the specific taxonomic or ecological associations investigated in this paper. In contrast to previous works, taxonomic and ichnological data in this study are collected at an extremely fine scale.

At every cm through sampled intervals, bedding plane exposures were exhumed to reveal maximum exposure, typically >2500 cm², in association with ichnological data. Diversity and abundance/m² data were recorded from each bedding plane. Specimens are identified using Linsley (1994) and the revised brachiopod treatise (Savage, 2002), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Martin, 2004). Specifically, variations in relative oxygen are identified first by the relative amount of bioturbation measured as ichnofabric index (ii) (Droser and Bottjer, 1986), and further resolution is then interpreted using maximum burrow width, which has been found to be associated with fundamental physiological oxygen demands of the trace-making organism (Rhoads, 1975; Pearson and Rosenberg, 1978; Savrda et al., 1984; Savrda, 1992), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Oschmann, 1991; Brett et al., 1991; Wignall, 1994; Allison et al., 1995). Species richness data, used to supplement the ichnological oxygen signal, is based simply on number of different taxa present, independent of the specific taxonomic or ecological associations investigated in this paper. In contrast to previous works, taxonomic and ichnological data in this study are collected at an extremely fine scale.

At every cm through sampled intervals, bedding plane exposures were exhumed to reveal maximum exposure, typically >2500 cm², in association with ichnological data. Diversity and abundance/m² data were recorded from each bedding plane. Specimens are identified using Linsley (1994) and the revised brachiopod treatise (Savage, 2002), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Martin, 2004). Specifically, variations in relative oxygen are identified first by the relative amount of bioturbation measured as ichnofabric index (ii) (Droser and Bottjer, 1986), and further resolution is then interpreted using maximum burrow width, which has been found to be associated with fundamental physiological oxygen demands of the trace-making organism (Rhoads, 1975; Pearson and Rosenberg, 1978; Savrda et al., 1984; Savrda, 1992), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Oschmann, 1991; Brett et al., 1991; Wignall, 1994; Allison et al., 1995). Species richness data, used to supplement the ichnological oxygen signal, is based simply on number of different taxa present, independent of the specific taxonomic or ecological associations investigated in this paper. In contrast to previous works, taxonomic and ichnological data in this study are collected at an extremely fine scale.

At every cm through sampled intervals, bedding plane exposures were exhumed to reveal maximum exposure, typically >2500 cm², in association with ichnological data. Diversity and abundance/m² data were recorded from each bedding plane. Specimens are identified using Linsley (1994) and the revised brachiopod treatise (Savage, 2002), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Martin, 2004). Specifically, variations in relative oxygen are identified first by the relative amount of bioturbation measured as ichnofabric index (ii) (Droser and Bottjer, 1986), and further resolution is then interpreted using maximum burrow width, which has been found to be associated with fundamental physiological oxygen demands of the trace-making organism (Rhoads, 1975; Pearson and Rosenberg, 1978; Savrda et al., 1984; Savrda, 1992), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Oschmann, 1991; Brett et al., 1991; Wignall, 1994; Allison et al., 1995). Species richness data, used to supplement the ichnological oxygen signal, is based simply on number of different taxa present, independent of the specific taxonomic or ecological associations investigated in this paper. In contrast to previous works, taxonomic and ichnological data in this study are collected at an extremely fine scale.

At every cm through sampled intervals, bedding plane exposures were exhumed to reveal maximum exposure, typically >2500 cm², in association with ichnological data. Diversity and abundance/m² data were recorded from each bedding plane. Specimens are identified using Linsley (1994) and the revised brachiopod treatise (Savage, 2002), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Martin, 2004). Specifically, variations in relative oxygen are identified first by the relative amount of bioturbation measured as ichnofabric index (ii) (Droser and Bottjer, 1986), and further resolution is then interpreted using maximum burrow width, which has been found to be associated with fundamental physiological oxygen demands of the trace-making organism (Rhoads, 1975; Pearson and Rosenberg, 1978; Savrda et al., 1984; Savrda, 1992), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Oschmann, 1991; Brett et al., 1991; Wignall, 1994; Allison et al., 1995). Species richness data, used to supplement the ichnological oxygen signal, is based simply on number of different taxa present, independent of the specific taxonomic or ecological associations investigated in this paper. In contrast to previous works, taxonomic and ichnological data in this study are collected at an extremely fine scale.

At every cm through sampled intervals, bedding plane exposures were exhumed to reveal maximum exposure, typically >2500 cm², in association with ichnological data. Diversity and abundance/m² data were recorded from each bedding plane. Specimens are identified using Linsley (1994) and the revised brachiopod treatise (Savage, 2002), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Martin, 2004). Specifically, variations in relative oxygen are identified first by the relative amount of bioturbation measured as ichnofabric index (ii) (Droser and Bottjer, 1986), and further resolution is then interpreted using maximum burrow width, which has been found to be associated with fundamental physiological oxygen demands of the trace-making organism (Rhoads, 1975; Pearson and Rosenberg, 1978; Savrda et al., 1984; Savrda, 1992), and the species richness associated with each bedding plane assemblage (Wignall and Myers, 1988; Oschmann, 1991; Brett et al., 1991; Wignall, 1994; Allison et al., 1995). Species richness data, used to supplement the ichnological oxygen signal, is based simply on number of different taxa present, independent of the specific taxonomic or ecological associations investigated in this paper. In contrast to previous works, taxonomic and ichnological data in this study are collected at an extremely fine scale.

4. Establishment of dysaerobic framework

4.1. Sedimentology, ichnology, and species richness results

Sampled units are grey to black mudstones with variable silt and carbonate composition. Significant but variable silt compositions (20–

---

Table 1

<table>
<thead>
<tr>
<th>Terminology used in this paper</th>
<th>Equivalent ranges through the dysaerobic zone</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extremely reduced</td>
<td>Lower</td>
<td>ii values 1–2, ranging from laminated with body fossils, typically monospecific, to rare isolated burrows</td>
</tr>
<tr>
<td>Moderately reduced</td>
<td>Middle</td>
<td>ii 2–3 slight to moderate bioturbation with low to moderate (3–8) species richness</td>
</tr>
<tr>
<td>Slightly reduced</td>
<td>Upper</td>
<td>ii 4–5 abundant burrows, commonly large with moderate to high (5–20) species richness</td>
</tr>
</tbody>
</table>
50% quartz silt) allow for recognition of individual laminations and burrows through these units. Carbonate composition is consistently low, contributing typically less than 10% to the total composition of the mudstones. The clay composition is dominated by illite with a lesser component of chlorite based on X-ray diffraction (Boyer, 2007). Rare sedimentary features indicative of energy include grading, ripple and scour marks. Laminations are the most common sedimentary structure.

Ichnofabric ranges from laminated to fully bioturbated. Relative amount of bioturbation quantified using ichnofabric index ranges from 1–5 and laminated intervals (ii 1) are common. Most traces are horizontal to sub-horizontal in orientation and without internal structure. A total of 5 ichnogenera were identified including Planolites, Chondrites, Teichichnus, Zoophycos and Thalassinoides from nearly 650 individual identified burrows. A majority of the traces were assigned to the ichnogenus Planolites, however ichnogeneric diversity of trace fossil assemblages increases with higher ichnofabric indices.

Burrow width and depth ranged from 0.02 to 1.45 cm and 0.02 to 1.82 cm respectively. In general, burrow diameters and depth of penetration are consistently small. Over 97% of the burrows penetrate the substrate less than 1 cm and approximately 90% are less than 0.5 cm in burrow depth. Nearly all burrows are less than 1 cm in width and over 94% of burrows are less than 0.5 cm in width. However, it is likely that larger burrows are obscured within more bioturbated intervals (ii 4–5) resulting in less data on individual burrow morphology from these intervals.

Species richness is well documented to decrease with decreasing oxygen in modern marine environments (e.g. Rhoads and Morse, 1971; Teichichnus, Chondrites, and Zoophycos; see Fig. 1 for locality abbreviations.) Pyrite varies in morphology and density of packing along polished surfaces; however frambooids are common in all selected samples. Seven assemblages were measured from four localities (Table 3). All samples had a narrow size range and mean frambooid diameter of less than 6 μm.

The trace metals of Mo and V are recognized to reflect redox conditions (Tribovillard et al., 2006). These values are given for several samples throughout the study area on Table 3. Upper crustal values of Mo and V are 1.5 and 60 ppm respectively (Tayor and McLennan, 1985), with enriched values associated with reducing conditions that are commonly associated with reduced oxygen conditions. Mo shows crustal values to more than 10 times enrichments and V shows 2 to nearly 3 times enrichment. All V/V+ Ni values are greater than 0.6. Sedimentological, ichnological, geochemical and species richness data all support that these units were deposited under reduced oxygen conditions. Importantly these proxies vary in concert. However, an increase in species richness is not always correlated with inferred increased oxygen levels interpreted from other proxies. Although some of these proxies are more sensitive to small scale fluctuations, the combined data set supports the dysaerobic nature of these units and allows for fine scale variation in relative oxygen to be constrained.

## 5. Palaeoecology through the dysaerobic zone

### 5.1. Taphonomy

In this study, 8643 individual body fossil specimens and associated ichnological data were collected from nearly 9 m of section that were

#### Table 2
An overview of large-scale diversity and life habit patterns across the palaeobasin.

<table>
<thead>
<tr>
<th>Locality</th>
<th>M</th>
<th>MC</th>
<th>HQ</th>
<th>F</th>
<th>AR</th>
<th>K</th>
<th>CF</th>
<th>LA</th>
<th>W</th>
<th>PC</th>
<th>BC</th>
<th>HF</th>
<th>TF</th>
<th>LH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diversity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sampled interval (cm)</td>
<td>33</td>
<td>36</td>
<td>106</td>
<td>195</td>
<td>18</td>
<td>26</td>
<td>113</td>
<td>38</td>
<td>56</td>
<td>77</td>
<td>34</td>
<td>32</td>
<td>26</td>
<td>89</td>
</tr>
<tr>
<td>Total species richness</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>10</td>
<td>15</td>
<td>31</td>
<td>28</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>Rarefied diversity</td>
<td>1.74</td>
<td>2.99</td>
<td>2.97</td>
<td>3.87</td>
<td>2.04</td>
<td>3.78</td>
<td>6.5</td>
<td>2.3</td>
<td>5.23</td>
<td>4.15</td>
<td>4.6</td>
<td>7.83</td>
<td>7.73</td>
<td>7.08</td>
</tr>
<tr>
<td>Number of individuals</td>
<td>238</td>
<td>65</td>
<td>299</td>
<td>105</td>
<td>501</td>
<td>103</td>
<td>51</td>
<td>605</td>
<td>89</td>
<td>166</td>
<td>521</td>
<td>1004</td>
<td>1852</td>
<td>824</td>
</tr>
<tr>
<td>Maximum abundance/m</td>
<td>700</td>
<td>53</td>
<td>457</td>
<td>670</td>
<td>5700</td>
<td>190</td>
<td>83</td>
<td>579</td>
<td>86</td>
<td>98</td>
<td>670</td>
<td>3090</td>
<td>4041</td>
<td>822</td>
</tr>
<tr>
<td>Range of ii values</td>
<td>1–3</td>
<td>1–3</td>
<td>1–1</td>
<td>1–4</td>
<td>1–4</td>
<td>1–3</td>
<td>2–4</td>
<td>2–5</td>
<td>1–3</td>
<td>1–4</td>
<td>3–5</td>
<td>3–5</td>
<td>2–5</td>
<td></td>
</tr>
<tr>
<td>Life habit (% total)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epifaunal Filter feeder attached</td>
<td>100</td>
<td>100</td>
<td>70.8</td>
<td>84.8</td>
<td>98.8</td>
<td>93.2</td>
<td>58</td>
<td>40.5</td>
<td>27</td>
<td>89.8</td>
<td>810</td>
<td>56.9</td>
<td>55.2</td>
<td>779</td>
</tr>
<tr>
<td>Epifaunal filter feeder reclining</td>
<td>6.0</td>
<td>1.0</td>
<td>3.8</td>
<td>2</td>
<td>1.3</td>
<td>3.8</td>
<td>2</td>
<td>183</td>
<td>5.8</td>
<td>15.9</td>
<td>36.8</td>
<td>40.4</td>
<td>8.9</td>
<td></td>
</tr>
<tr>
<td>Shallow embedded endobysate</td>
<td>14.3</td>
<td>0.4</td>
<td>1.9</td>
<td>32</td>
<td>40.7</td>
<td>64</td>
<td>5.1</td>
<td>16.0</td>
<td>1.1</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deep embedded endobysate</td>
<td>2.2</td>
<td>0.6</td>
<td>0.1</td>
<td>1.4</td>
<td>1.7</td>
<td>2.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epifaunal deposit feeder/herbivore</td>
<td>1.0</td>
<td>0.6</td>
<td>0.1</td>
<td>1.4</td>
<td>1.7</td>
<td>2.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Infaunal filter feeder</td>
<td>23.2</td>
<td>0.8</td>
<td>10.0</td>
<td>8</td>
<td>1.8</td>
<td>3.4</td>
<td>3.1</td>
<td>0.8</td>
<td>2.3</td>
<td>2.1</td>
<td>7.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Infaunal deposit feeder</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total # of life habits</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>5</td>
<td>7</td>
<td>7</td>
</tr>
</tbody>
</table>

Sample Pyrite framboid data

<table>
<thead>
<tr>
<th>Sample</th>
<th>Pyrite framboid data</th>
<th>Mo</th>
<th>V</th>
<th>V/V+ Ni</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>Std.</td>
<td>MFD</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>μm</td>
<td>dev.</td>
<td>(μm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC 45</td>
<td>4.746</td>
<td>2.750</td>
<td>22.319</td>
<td>121</td>
</tr>
<tr>
<td>PC 37</td>
<td>3.991</td>
<td>1.859</td>
<td>12.829</td>
<td>146</td>
</tr>
<tr>
<td>PC 28</td>
<td>5.334</td>
<td>3.097</td>
<td>21.177</td>
<td>233</td>
</tr>
<tr>
<td>M 27</td>
<td>4.495</td>
<td>2.506</td>
<td>16.570</td>
<td>111</td>
</tr>
<tr>
<td>M 6</td>
<td>4.544</td>
<td>2.249</td>
<td>14.644</td>
<td>119</td>
</tr>
<tr>
<td>PC 8</td>
<td>4.851</td>
<td>2.506</td>
<td>17.283</td>
<td>120</td>
</tr>
<tr>
<td>HQ 66</td>
<td>4.675</td>
<td>2.798</td>
<td>26.439</td>
<td>165</td>
</tr>
<tr>
<td>F 28</td>
<td>13</td>
<td>160</td>
<td>0.7017</td>
<td></td>
</tr>
<tr>
<td>K 17</td>
<td>4</td>
<td>144</td>
<td>0.6890</td>
<td></td>
</tr>
</tbody>
</table>

See Fig. 1 for locality abbreviations.
5.2. Taxonomic overview

A total of 56 species occur throughout these intervals, most occurring rarely (Table 4). Rhynchonelliform brachiopods consistently dominate assemblages (Fig. 4), and the camarotoechioidean and chonetidean brachiopods comprise more than 85% of the total population as 5298 and 2149 individuals respectively.

Members of the superfamily Camarotoechioidea are overwhelmingly the most abundant rhynchonelliform brachiopods including species of Eumetabolotoechia, Cherryvalleyrostrum, Camarotoechia, and Leiorhynchus. The six chonetidean species are associated to the genera “Chonetes”, Longispina, Sinochonetes, Eodevonaria, Arcuami- netes and Devonchonetes. Other rhynchonelliform brachiopods occurring in these units include spiriferid groups and less commonly atyrids. Pterochaenia is the numerically dominant bivalve, with Nuculoidea, Nuculites, Polunello, Glossities, and Modiomorpha species also common in some assemblages.

The five most abundant groups within these units, species of Camarotoechioidea and Chonetidea, Pterochaenia, Lingula, and Orbi- culoids, are typically interpreted as “dysaerobic taxa” (e.g. Thompson and Newton, 1987; Brett et al., 1991; Brower and Nye, 1991; Allison et al., 1995) and are present in monospecific assemblages within laminated sediments (Boyer and Droser, 2007). However, these same taxa also occur in higher diversity assemblages associated with high levels of bioturbation (ii 4–5) (Table 4).

5.2.1. The Camarotoechioidea

Four common species, Cherryvalleyrostrum limitare, Leiorhynchus quadracostata, L. simae, and Eumetabolotoechia multicostata, were identified from over 5000 individual camarotoechioidea brachiopods, and over 400 individuals were measured in detail (Appendix A). Several specimens of Camarotoechia pauciplicata occur uncommonly at the Browns Creek locality, but are stratigraphically and geographically restricted. Camarotoechioidea brachiopods are typically preserved as external moulds with only rare preservation of internal features. Those specimens that were crushed or distorted obliquely were not measured. Other features such as the orientation of the fold and sulcus, as well as characteristics of costae including relative size and shape, number in fold and sulcus, and distribution (i.e. present on flanks, restricted to fold and sulcus) were also noted. Details of species are described below in order of stratigraphic appearance.

Within the Family Camarotoechidae (Schuchert, 1929) the monospecific genus Cherryvalleyrostrum (Fig. 5A), as described by...
Sartenaer (2004), is present within the Marcellus sub-group, in the first of the originally defined Leiorhynchus zones. Cherryvalleyrostrum limitare is small to moderate in size ranging from 0.5 to nearly 2 cm in length (Appendix A). Individuals have well pronounced folds and sulci that do not start at the beak. Costae in general are wide, low, and rounded. Within the fold and sulcus, costae are wider and more pronounced than on the flanks of the valves. The number of costae in the fold region is commonly 4 or 5, but rarely 6. This species is preserved moderately inflated to flattened.

Cherryvalleyrostrum limitare occurs most commonly in moderately to densely packed, low diversity assemblages with a range of species richness of 1–5. This species is associated with ii 2–5 and commonly occurs in homogenized mudstones (Fig. 6). Rare individuals are preserved as articulated specimens, while nearly all are complete valves without significant fragmentation or abrasion.

Within the family Leiorhynchidae, the genus Eumetabolotoechia, in the sense of Sartenaer, 1975 (Fig. 5B), is present in assemblages within these units. E. multicoastata is the only member of this genus within these units and occurs in the upper three Leiorhynchus zones. It is moderately inflated to flattened with many costae on the flanks, as well as the fold and sulcus. Individual costae in the fold/sulcus range from 6–8 and costae are thin and rounded. This taxon commonly is more transversely ovate that other Camarotoechioidea and has more abundant costae than the other rhynchonellids in these units. This species shows a range in size of individual valves discussed in detail below.

Eumetabolotoechia multicoastata is the most common rhynchonellid brachiopod occurring in assemblages ranging from monospecific to a diversity of 18 and in mudstones ranging from laminated to fully bioturbated (ii 1–5) within the Skaneatles, Ludlowville, and Moscow Formations of the Hamilton group (Fig. 6). E. multicoastata typically dominates assemblages regardless of species richness. Individuals are uncommonly preserved articulated.

The genus Leiorhynchus, family Leiorhynchidae, originally described by Hall, 1860 from these units, and revised by Sartenaer (1961), is present as two species in sampled intervals; L. quadracostata and L. sinuata. L. quadracostata (Fig. 5C) occurs only in the Genesee Shale Member of the Genesee Formation in close geographic proximity to the type locality. Specimens are inflated to compressed, with original shell material rarely preserved. L. sinuata (Fig. 5D) is reported from several localities within the Penn Yan Shale Member of the Genesee Formation (Fig. 1) and is exclusively preserved as flattened molds. In both species, costae are most pronounced in the fold and sulcus region, but still visible on flanks. L. quadracostata has a pronounced trapezoidal tongue and typically four costae in the fold/sulcus. L. sinuata is typically smaller and more rounded in outline with more variability in number of costae in the fold, ranging from 3–6. L. sinuata is relatively small, with the largest specimen collected measured at 1.7 cm in length. L. quadracostata is comparatively large, ranging to over 3 cm in length (Appendix A).

Leiorhynchus quadracostata and L. sinuata are both associated with ii 1–3 (Fig. 6) and occur in dispersed to densely packed monospecific assemblages and in association with no more than one other species on bedding plane surfaces. Articulated L. quadracostata are rare but nearly all Leiorhynchus specimens are preserved as complete valves.

**Fig. 5.** A. Cherryvalleyrostrum limitare from Abbey Rd., B. Eumetabolotoechia multicoastata from Highland Forest, C. Leiorhynchus quadracostata from Hubbard Quarry, D. Leiorhynchus sinuata from Manteth Creek. Scale bars are 1 cm.

**Fig. 6.** Distribution of three dominant Camarotoechioidea genera in association with a range of ii values.
5.2.2. Descriptions of other taxa

In addition to the Camerotoechoidea, 47 other taxa occur in these units. There are 22 additional species of rhyynchonelliform brachiopods that range in distribution from within shales interpreted to represent extremely reduced oxygen conditions to only occurring in fully bioturbated units (ii 5), and some groups are common in all interpreted oxygen levels (ii 1–5) (Table 4). These rhyynchonelliform taxa are all either attached or reclining epifaunal filter feeding groups (Brett et al., 1991; Brower and Nye, 1991; Newman et al., 1992).

Several groups of linguliform brachiopods occur in these units including species of Lingula and Orbiculoidea. They are all relatively small, flat taxa, with the largest species, Lingula punctata, reaching over 1 cm in length. With the exception of L. punctata exclusively associated with ii 4, the other groups are broadly associated with a range of bioturbation (ii 1–5). These Lingula species are interpreted to be shallow to deep infaunal filter feeders and Orbiculoidea groups are interpreted as epifaunal filter feeders (Brower and Nye, 1991).

Twelve bivalve taxa are widely distributed occurring either only in shales interpreted as slightly reduced oxygen levels (ii 4–5) or occurring throughout the entire range of dysaerobic conditions (ii 1–5). Individuals of the genus Paneka reach over 6 cm in valve length, while other taxa are consistently much smaller. Pterochaenia fragilis are the smallest group at less than 0.80 cm in valve length. P. fragilis is most common under what are interpreted as extremely reduced oxygen levels (ii 1–2), although not restricted to these settings (Table 4). P. fragilis is interpreted to be a shallow infaunal to epifaunal (shallow embedded endobysate) filter feeder, while other bivalve groups are interpreted to have had shallow to deep embedded endobysate filter feeding or infaunal deposit feeding life habits (Brower and Nye, 1991; Newman et al., 1992).

Four species of trilobites occur repeatedly through these units and include Viaphacops cristatus, Eldregeops rana, Hallandclarkeia jennyae, and Greenops boothi. Most specimens are preserved as individual pygidia and less commonly as crania. V. cristatus occurs in fully bioturbated (ii 5) intervals, H. jennyae and Greenops boothi occur through a wide range of ichnofabrics (ii 2–4) and E. rana occurs in moderately bioturbated intervals (ii 3–5). These groups are interpreted to have been epifaunal deposit feeders (Brett et al., 1991). Palaeozygopluera sp. is the only gastropod species occurring rarely in moderately to heavily bioturbated intervals (ii 3–5). These taxa are interpreted to have been epifaunal herbivores or scavengers (Brett et al., 1991; Newman et al., 1992).

5.3. Distribution of taxa

There are two distinct patterns in the distribution of taxa through the dysaerobic biofacies (Table 4, Fig. 7). 1) Cupularostrum orbicularis, Chonetes sp., Leiorhynchus quadracostata, and L. sinuata, Orbiculoidea lodensis are limited to laminated to minimally bioturbated intervals (Table 2) and are common in low diversity and high dominance, often monospecific assemblages restricted to the lowest dysaerobic zone (ii 1–2). These are represented by taxa A and B in Fig. 7. 2) Most of the taxa actually occur within fully oxygenated strata, however, under decreasing oxygen levels, taxa with what are interpreted as successively higher oxygen thresholds are excluded in a predictable order consistent across the paleo-basin. This results in a nested distribution pattern through much of the dysaerobic zone. Thus, taxa associated with ii 4, interpreted as slightly reduced oxygen conditions, are a subgroup of the taxa associated with ii 5 interpreted to represent fully oxygenated conditions. Within these units, predictable associations of
taxa are recognized as characteristic of specific relative oxygen levels. Although specialists adapted to reduced oxygen conditions are recognized in both modern and ancient reduced oxygen settings, a nested pattern of taxonomic distribution through a range of oxygen conditions is an unexpected result.

Relative abundance can also vary in association with inferred relative oxygen levels. Orbiculoides newberryi, Lingula spatulata, and Pterochaenia fragilis dominate bedding planes associated with lower oxygen levels and are rare or absent associated with higher inferred oxygen levels (Table 4). Conversely, Arcuaminetes scitulus is only abundant associated with higher oxygen levels. This distribution of relative abundance patterns supports the model that while many taxa may be distributed across a range of oxygen conditions, they are likely to be more dominant under particular conditions. Eumetabolotoechia

![Fig. 10. Interval through the Ledyard Shale at Paines Creek. Columns from left to right include a schematic representation of ichnofabric seen in cross-section, ichnofabric index as a measure of relative amount of bioturbation, relative oxygen curve based on combined ichnological and macrofaunal species richness data, and occurrences and life habits of individual taxa through the succession. FF = filter feeder; Shlw E = Shallow endobyssate filter feeder; IF = infaunal; EF D/H = epifaunal deposit and/or herbivore.](image-url)
multicostata is an exception. It is the only species that is numerically abundant within assemblages through the entire dysaerobic zone (Table 2). E. multicostata is highly unusual as it is dominant within assemblages associated with a broad range of oxygen levels and demonstrates a truly unique ecology.

5.4. Variation in valve size

Measured specimens of Eumetabolothetaea multicostata from five localities at several stratigraphic intervals through the Ludlowville and Moscow Formations are systematically smaller as amount of bioturbation, indicative of relative oxygen levels, decreases (Appendix A). A “box-and-whisker” plot is used to describe the size distribution of estimated valve areas of E. multicostata in association with ii values with the boxes ranging from quartile Q = 0.25 to quartile Q = 0.75 and divided by the mean value (Fig. 8). These data demonstrate that although there are overlapping ranges of sizes associated with each ii value, significant differences in the mean estimated areas can be recognized and generally increase with increasing ii values. Comparison of mean area values associated with different ii values using the Mann–Whitney significance test reveal that E. multicostata valves preserved in laminated strata (ii 1) are significantly (p<0.05) smaller than those associated with more bioturbated intervals (ii 4–5), but not statistically different than those associated with ii 2–3. Valves preserved in fully bioturbated sediments are statistically larger than those associated with valves interpreted to be associated with lower oxygen levels (ii 1–3).

5.5. Life habits

Seven life habits were interpreted from these taxa and are variable with interpreted relative oxygen levels (Table 2). The attached epifaunal filter feeding life habit is dominant in all but one locality (Wilson Creek) and two localities are comprised of exclusively epifaunal attached filter feeders (Manteth Creek and Mill Creek). The reclining epifaunal filter feeding life habit is the second most common, with shallow embedded endobyssate groups also common at some localities and dominant at the Wilson Creek locality. Other life habits are either absent or uncommon at all localities.

Epifaunal suspension feeders are the dominant ecological group largely because of the dominance of rhynchonelliform brachiopods at most localities and within most bedding plane assemblages. Several groups of Orbiculoidei, epifaunal suspension feeders, are most commonly associated with reduced oxygen levels (ii 2–3) (Fig. 9). The shallow embedded endobyssate life habit, of which Pterocharaenia accounts for most of the individuals, and the infaunal filter feeding habit, are most commonly associated with reduced amounts of bioturbation, but rarely with higher ii values. Taxa from all filter feeding groups, excluding the deep embedded endobyssate, are preserved within laminated sediments. Taxa interpreted to be infaunal or shallow embedded were typically small in size and clearly extremely shallow within the sediment to allow laminations to be preserved undisrupted. Individuals of Lingula, the only infaunal filter feeder, are very small, typically less than 0.5 cm in length, when preserved in association with laminated sediments. Epifaunal deposit feeders including trilobite and gastropod groups are rarely associated with ii 2–3, and become more common under increased interpreted oxygen levels, but are never numerically dominant in these units. Infaunal deposit feeders, including most abundantly Nuculoidae, Nuculitidae, and Paleonellidae, are associated with sub-laminated facies (Brett et al., 1991), and in these units gradually increase in abundance within assemblages correlated with increasing ii values. Deep embedded endobyssate groups, including Modiomorphia, Glossitidae, and Grammysioidea, among others, become common as a life habit only associated with ii 4–5, and are uncommon in association with ii 3 (Fig. 9).

Life habit distribution is variable on a cm scale in association with fluctuating oxygen conditions as illustrated through a 75 cm interval of the Ledyard Formation at the Paines Creek locality (Fig. 10). Taxa through this interval are representative of six life habits, however, the appearance of deposit feeders and/or herbivorous taxa consistently correlates with interpreted increased oxygen levels in these units.

6. Discussion

The sedimentological, ichnological and geochemical proxies utilized in this study support the interpretation that these units were dysaerobic and deposited under a range of relative oxygen levels. However, species richness, while generally correlated with patterns interpreted from other proxies is not always correlated with increased oxygen levels as inferred from other proxies. Rather, specific taxonomic occurrences associated with interpreted oxygen thresholds are more appropriate to recognize variation in bottom water oxygen conditions through the dysaerobic zone. Relative oxygen levels in these units, although commonly reduced, are recognized to fluctuate. This is consistent with previous investigations of fluctuating rather than stable oxygen conditions in the Hamilton group (Brett et al., 1991).

Several significant paleoecological patterns emerge from these data. The three identified camarotoechioidean genera are associated with different relative bottom water oxygen levels (Fig. 6). The distributions of Leiohynchus and Cherryvalleyrostrum are generally associated with extremely reduced and moderately reduced bottom water oxygen conditions respectively, but their distributions do overlap. Eumetabolothetaea multicostata is abundant throughout the full range of the dysaerobic zone (ii 1–5) and is, therefore, not diagnostic of specific bottom water oxygen conditions; however, the relative size of E. multicostata valves is interpreted to reflect variability in relative bottom water oxygen conditions.

Life habits also display correlation with interpreted relative oxygen levels. Under extremely reduced oxygen conditions within these units, all shelly benthic macrofauna are interpreted as filter feeders with the epifaunal attached life habit as most common. This is in contrast to observations in modern extremely reduced oxygen settings in which infaunal deposit feeders are common (Wu, 2002; Levin, 2003). Brachiopod groups, all functionally restricted to a filter feeding habit, dominated most environments during the Devonian and these data support that they also dominate nearly all reduced oxygen depositional settings. These brachiopod groups are epifaunal, with the exception of the genus Lingula. Further, the bivalve that is common within the lowest dysaerobic settings, Pterochaenia fragilis, is also interpreted as a shallow embedded filter feeder. The occurrence of 4 different life habits within laminated sediments (ii 1) indicates that a wide range of ecologically and taxonomically disparate groups were equally well adapted to extremely reduced oxygen condition.

The broadly defined “dysaerobic biofacies” can be subdivided based on predictable taxonomic distributions that vary in concert with bottom water oxygen levels as a single controlling factor. The Leiohynchus biofacies, as originally defined, is representative of a range of bottom water oxygen conditions and includes two distinct patterns in the distribution of body fossils. However, nested distributions of taxa through the dysaerobic zone are inconsistent with patterns observed in younger strata. These results support that bottom water oxygen levels were likely a major factor controlling shallow marine ecosystems due largely to the widespread distribution of epeiric seaways in the Devonian.

Acknowledgements

This study was funded in part by NSF grant EAR-0719841. This manuscript was greatly improved by reviews by Carl Brett and an anonymous reviewer. Thanks to Jeremy Owens for tremendous help.


