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Chapter 6

Using environmental niche modeling to study the Late Devonian biodiversity crisis

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Abstract

Geographic ranges are estimated for brachiopod and bivalve species during the late Middle (mid-Givetian) to the middle Late (terminal Frasnian) Devonian to investigate range changes during the time leading up to and including the Late Devonian biodiversity crisis. Species ranges were predicted using GARP (Genetic Algorithm using Rule-set Prediction), a modeling program developed to predict fundamental niches of modern species. This method was applied to fossil species to examine changing ranges during a critical period of Earth's history. Comparisons of GARP species distribution predictions with historical understanding of species occurrences indicate that GARP models predict accurately the presence of common species in some depositional settings. In addition, comparison of GARP distribution predictions with species-range reconstructions from geographic information systems (GIS) analysis suggests that GARP modeling has the potential to predict species ranges more completely and tailor ranges more specifically to environmental parameters than GIS methods alone. Thus, GARP modeling is a potentially useful tool for predicting fossil species ranges and can be used to address a wide array of palaeontological problems.

The use of GARP models allows a statistical examination of the relationship of geographic range size with species survival during the Late Devonian. Large geographic range was statistically associated with species survivorship across the crisis interval for species examined in the *linguiformis* Zone but not for species modeled in the preceding Lower *varcus* or *punctata* zones. The enhanced survival benefit of having a large geographic range, therefore, appears to be restricted to the biodiversity crisis interval.

Keywords: prediction, invasion, extinction, survival, biogeography

1. Introduction

The geographic distribution of species is controlled by a variety of factors: biotic; environmental; and historical (Brown and Lomolino, 1998). The fundamental ecological niche of a species exerts a primary control on the geographic distribution of a species. Reconstructing species niches is an essential step in predicting the area a species could

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inhabit (Peterson, 2001). The fundamental niche is the set of environmental tolerances and limits in multidimensional space that define where a species is potentially able to maintain populations (Grinnell, 1917; Hutchinson, 1957). Species, however, rarely occupy their entire fundamental niche due to historical contingencies (e.g. their ancestors never inhabited the regions) or biological factors (e.g. competitive exclusion) (Brooks and McLennan, 1991, 2002; Brown and Lomolino, 1998). Modeling species ranges based on the fundamental niche is a major research area in modern biology and can be used to provide insight into geographic range changes, to predict new regions where species could occur, and to predict the effects of climate change on geographic distribution. Ranges of species in the fossil record are also controlled by the same types of ecological variables, so understanding the interplay between species fundamental niches and realized ranges is also important for palaeontologists. Numerous methods exist for reconstructing species ranges, including simplistic models designed around one variable and sophisticated computer learning-based systems (e.g. Stockwell and Peters, 1999; Haltuch et al., 2000). The GARP (Genetic Algorithm using Rule-set Prediction) modeling system, a computer learning-based system, predicts species ranges based on the fundamental ecological requirements modeled using the environmental characteristics of a set of known occurrence sites (Stockwell and Peters, 1999). This method has been successful at predicting species ranges and as a tool for investigating ecological and evolutionary questions in the modern biota (e.g. Peterson et al., 1999, 2001, 2002a–c; Anderson et al., 2002; Feria and Peterson, 2002). In this paper, we will explore the use of GARP for reconstructing ranges of shallow-marine brachiopod and bivalve species during the Givetian and Frasnian Ages (late Middle and early Late Devonian).

The Late Devonian is an excellent time to examine changing geographic ranges for several reasons. Firstly, the Middle to Late Devonian transition involved a dramatic change from a highly endemic Middle Devonian fauna to a cosmopolitan Late Devonian biota (Oliver, 1976, 1990; McGhee, 1989, 1996). In addition, the Late Devonian was a time of major biodiversity decline associated with the Frasnian–Famennian biodiversity crisis (McGhee, 1988, 1996). This crisis event was characterized by elevated extinction levels, reduced speciation rates, and ecological reorganization (McGhee, 1988, 1990, 1996; Oliver and Pedder, 1994; Droser et al., 2000; Rode and Lieberman, 2002). Finally, changing patterns of geographic range, particularly range expansions or species invasions during the Middle to Late Devonian transition, have been implicated in species survival during the biodiversity crisis interval (McGhee, 1996; Rode and Lieberman, 2004).

Quantifying invertebrate fossil ranges is currently a promising area of palaeontological study. Recent geographic information systems (GIS) work with Palaeozoic invertebrates (e.g. Rode and Lieberman, 2003, 2004, 2005) has built on the earliest use of GIS methods in palaeontology (e.g. Juliusson and Graham, 1999; Graham, 2000; Ferguson et al., 2001). Computer learning-based genetic algorithms, however, have not been previously attempted in palaeontology, because most traditional range reconstruction methods are based on determining areas that surround known occurrence points, and do not allow simultaneous consideration of multiple variables under multiple rule sets. The use of the GARP algorithm to explore Palaeozoic species ranges, therefore, provides a potentially useful step quantifying species ranges and producing additional information for palaeoecological and macroevolutionary studies.

2. Methods

2.1. Geographic and stratigraphic intervals examined

2.1.1. Geographic extent

The focus of this analysis is to reconstruct species ranges of brachiopod and bivalve species for three time intervals during the Givetian and Frasnian Ages. The geographic area of this study is restricted to the northern Appalachian Basin of eastern North America including the Devonian outcrop belt in the states of New York, Maryland, Pennsylvania, West Virginia, and Virginia (Fig. 1). This region was chosen for study because the area represents one of the most complete Devonian sequences in the world with an extensively studied, well-preserved fauna. Within the region, the area of interest was divided by a grid system into smaller areas of 0.5° latitude by 0.5° longitude (Fig. 1), which is a standard

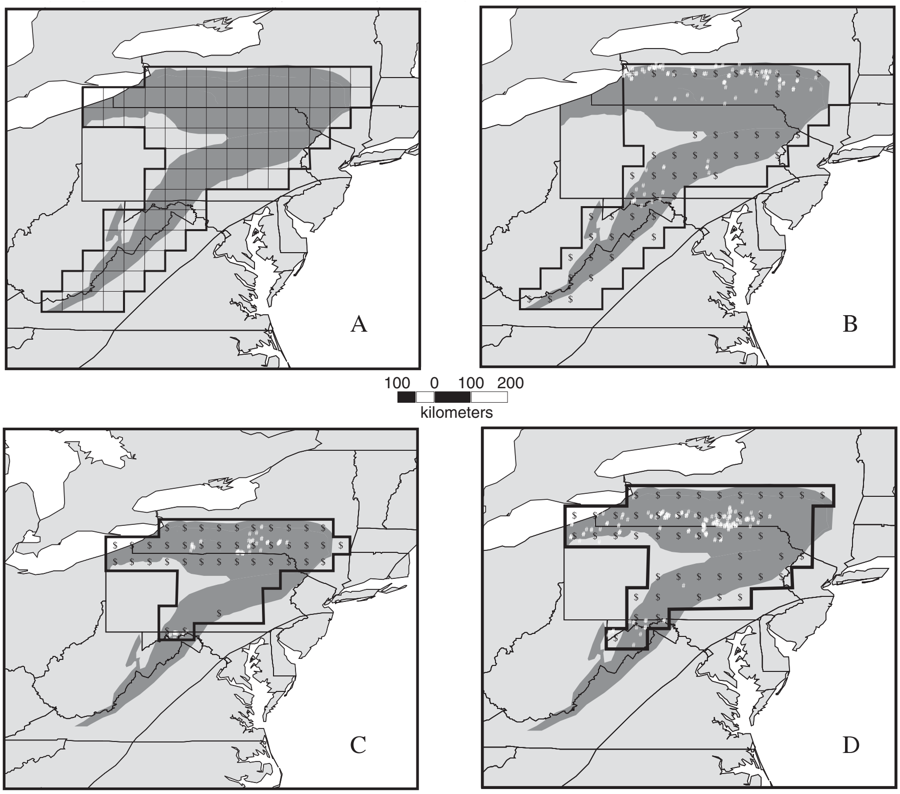

Figure 1. (A) Devonian outcrop belt of New York, Pennsylvania, West Virginia, Virginia, and Maryland with 0.5° × 0.5° grid overlain. Distribution of environmental data (black triangles), and species occurrence data (white circles), and geographic area considered within the modeling experiment (black outline) for the (B) Lower *varcus* Zone, (C) *punctata* Zone, and (D) *linguiformis* Zone.

procedure when using the GARP modeling system (R. Scachetti-Pereira pers. comm., 2002). Stratigraphic and environmental information (as discussed below) was obtained for each grid box individually.

2.1.2. Temporal range

To examine changes in species ranges through time, three time intervals were investigated, each approximating a conodont zone. The intervals examined were the Lower *varcus* (middle Givetian), *punctata* (middle Frasnian), and *linguiformis* (terminal Frasnian) conodont zones, which are estimated at 1.5, 0.6, and 0.4 million years, respectively [zone durations approximated based on the relative durations of conodont zones in Sandberg and Ziegler (1996) calibrated against the Devonian time scale of Tucker et al. (1998)]. Both the Lower *varcus* and *punctata* zones precede the Late Devonian biodiversity crisis, providing necessary baseline information, whereas the *linguiformis* Zone is within crisis interval (McGhee, 1996). Species survivorship through the biodiversity crisis interval is further examined by comparing the temporal range of species into the Famennian in statistical analyses.

2.1.3. Stratigraphic framework

During the Middle to Late Devonian, the depositional setting of the northern Appalachian Basin was dominated by a shallow siliciclastic ramp system, the Catskill Delta (Woodrow, 1985). The Catskill Delta is a progradational system derived from the weathering of the Acadian highlands formed by several progressive tectophases of the Early to Late Devonian Acadian orogeny (Ettensohn, 1985). Progressive weathering and subsidence produced thick and laterally extensive deposits throughout the foreland basin beginning in the Middle Devonian. The depositional setting during this time was a gently sloping siliciclastic shelf with storm processes dominating in the platform setting and tidal influences dominating in the nearshore (Brett and Baird, 1994; Prave and Duke, 1991). The shoreline migrated progressively westward as the foreland basin filled from the Middle to Late Devonian (Rickard, 1975; de Witt et al., 1993). Consequently, the area of marine deposition in the study area becomes progressively smaller in younger stratigraphic intervals. Hence, the areal extent of marine rocks available for study in the *punctata* Zone is smaller than in the Lower *varcus* Zone and so on (Fig. 1). The westward progression of facies does not pose a problem in this analysis, because the full complement of environments examined in the oldest time intervals remains present in the basin during the youngest intervals. Cross-environmental analyses, therefore, remain possible and the reduction in depositional area is accounted for by examining relative areas in statistical analyses. Table 1 lists the stratigraphic references used in determining palaeoenvironmental conditions.

Stratigraphic data for depositional environments within each conodont zone were collected from stratigraphic units interpreted to approximately correlate to the zone of interest. While the boundaries of these units may not precisely coincide with the temporal boundaries of the conodont zone of interest, they do represent the best approximation and provide the most accurate data available to reconstruct sedimentary conditions during the temporal intervals under investigation.

The Lower *varcus* Zone of the middle Givetian includes the well-characterized stratigraphic units of the Hamilton Group of New York and the Mahantango Formation of

Table 1. Stratigraphic information references by conodont zone.

Lower *varcus* Zone	*punctata* Zone	*linguiformis* Zone
Batt, 1996	*Adams et al., 1956	Babcock and Wegweiser, 1998
*Batt, 1999	Applebaum, 1993	*Dennison, 1985
*Brett and Baird, 1994	*Bishuk et al., 1991	*Dennison et al., 1979
*Brett et al., 1986	*Bridge and Dingman, 1981	*de Witt, 1960
Dennison, 1985	*Bowen et al., 1970	*de Witt et al., 1993
*Dennison and Hasson, 1976	*Bowen et al., 1974	Ehrets, 1981
*Dennison et al., 1979	*Colton and de Witt, 1958	Frakes, 1963
Ellison, 1963	*Dennison, 1985	*Frakes, 1964
Ellison, 1965	*Dennison et al., 1979	*Jacobi and Smith, 1999
Epstein, 1986	*de Witt et al., 1993	Karman, 1968
*Faill et al., 1973	*Fletcher, 1962	*Kirchgasser et al., 1994
*Hasson and Dennison, 1979	Jacobi and Smith, 1999	*Krajewski and Williams, 1971
Lafferty et al., 1994	Kirchgasser, 1965	*Leighton, 2000
Linsley, 1994	*Kirchgasser, 1983	*McGhee, 1976
*Mayer, 1994	*Kirchgasser et al., 1994	*McGhee and Sutton, 1981
*Mayer et al., 1994	*Krajewski and Williams, 1971	*McGhee and Sutton, 1983
*Miller, 1986	*Lundegard et al., 1985	*McGhee and Sutton, 1985
*Oliver and Klapper, 1981	*McGhee and Sutton, 1985	*Metzger et al., 1974
*Prave and Duke, 1991	*Oliver and Klapper, 1981	*Oliver and Klapper, 1981
*Prave et al., 1996	*Over et al., 1999	*Over, 1997
*Rickard, 1975	Patchen and Dugolinsky, 1979	*Over et al., 1999
Rodeheaver, 1992	*Rickard, 1975	Patchen and Dugolinsky, 1979
*Savarese et al., 1986	Sutton, 1963	*Pepper and de Witt, 1950
Sevon, 1985	*Sutton and McGhee, 1985	*Rahmanian, 1979
*Ver Straeten and Brett, 1999	*Sutton et al., 1970	*Rickard, 1975
Willard, 1935a	*Tesmer, 1966	*Roe, 1976
Willard, 1935c	Willard, 1934	*Schultz, 1974
Woodrow, 1985	Willard, 1935b	*Smith and Jacobi, 2000
*Wygart, 1986	Woodrow, 1985	Sutton, 1963
		*Sutton and McGhee, 1985
		*Tesmer, 1966
		*Tesmer, 1974
		Walker and Sutton, 1967
		Willard, 1934
		Willard, 1935b
		*Williams and Slingerland, 1985
		Woodrow, 1985

*key citation.

Pennsylvania, Maryland, and West Virginia. The stratigraphic units used to estimate environmental parameters within the interval are the Ludlowville Formation of the Hamilton Group, the Panther Sandstone, the Plattekill Formation, the Millboro Shale Member of the Mahantango Formation, and the Mahantango Formation undivided (Appendix 1.1).

Environmental parameters during the *punctata* Zone of the middle Frasnian were estimated by using the characteristics of the Sonyea Group of New York, specifically the correlative Cashaqua, Rock Stream, Glen Aubrey, and lower Walton formations. Correlative portions of the Trimmers Rock Formation and Bralier Formation as well as the correlative strata of the Chemung, Portage, and Catskill magnafacies of Pennsylvania, Maryland, and West Virginia were also considered (Appendix 1.2).

The *linguiformis* Zone environment was estimated using the characteristics of the upper Java Formation (upper portion of the Hanover and Wiscoy members), Mansfield Shale, and Slide Mountain Formation of New York. Parts of the Trimmers Rock Formation, Foreknobs Formation, and other correlative strata of the Chemung, Portage, and Catskill magnafacies of Pennsylvania, Maryland, and West Virginia were also examined (Appendix 1.3).

2.2. Species occurrence information

Species geographic distribution data included in this analysis were assembled from examination of museum collections. Museums with extensive taxonomic and stratigraphic material from the northern Appalachian Basin of North America were visited and occurrence data collected for brachiopod and bivalve species. These occurrence data include species identifications (verified by A.L.S.), geographic location from which the fossil was collected, keyed to latitude and longitude values with maps, and the stratigraphic position of each specimen. Stratigraphic information was then converted to the approximate correlative conodont zone based on current literature (Rode and Lieberman, 2004). Only material with sufficient stratigraphic and locality information to identify a specimen's presence within a narrow geographic region and particular conodont zone were included within the database. Taxonomic identifications were based on comparison of specimens with the most up-to-date references available. Collection from the following museums were used: American Museum of Natural History; the Carnegie Museum of Natural History; the Museum of Comparative Zoology (Harvard University); the Peabody Museum of Natural History (Yale University); the University of Iowa Museum of Paleontology; the University of Michigan Museum of Paleontology; and the United States National Museum of Natural History. The entire database created from the museum data and further details on its assembly is published in Rode and Lieberman (2004).

This database was further culled, with only species represented by five or more occurrences during a conodont zone of interest retained for the present analysis. The GARP modeling algorithm (see discussion below), has been shown to be effective with sample sizes as small as five species occurrences (Peterson and Cohoon, 2002; Stockwell and Peterson, 2002), so five spatially distinct occurrence points within a conodont zone was used as the lower cutoff for species inclusion in this analysis. Included species are listed in Table 2, and species occurrence data used in this analysis are presented in Appendix 2.

2.3. Acquisition of environmental data and creation of base layers

The niche of shallow-marine species is controlled by a variety of environmental factors, such as water depth, wave energy, substrate type, oxygenation levels, and biotic interactions. The factors included in this study are primarily abiotic in nature and include the variables

Table 2. List of species and the conodont zones in which they were modeled using GARP.

Species	Conodont Zone
Ambocoelia gregaria (Hall)	*linguiformis*
Ambocoelia umbonata (Conrad)	*linguiformis*
Athyris angelica (Hall)	*linguiformis*
Athyris cora (Hall)	*varcus*
Athyris spiriferoides (Eaton)	*varcus*
Cariniferella carinata (Hall)	*varcus, linguiformis*
Cariniferella tioga (Hall)	*linguiformis*
Cupularostrum contracta (Hall)	*linguiformis*
Cupularostrum exima (Hall)	*punctata, linguiformis*
Cypricardella bellistriata (Conrad)	*varcus*
Cyrtospirifer chemungensis (Hall)	*linguiformis*
Douvillina cayuta (Hall)	*linguiformis*
Eoschizodus chemungensis (Conrad)	*punctata*
Floweria chemungensis (Conrad)	*linguiformis*
Floweria prava (Hall)	*linguiformis*
Goniophora chemungensis (Vanuxem)	*punctata*
Grammysia elliptica Hall and Whitfield	*punctata*
Leptodesma nitida (Hall)	*punctata*
Leptodesma spinerigum (Conrad)	*varcus, linguiformis*
Mucrospirifer mucronatus (Conrad)	*varcus*
Nervostrophia nervosa (Hall)	*linguiformis*
Palaeoneilo constricta (Conrad)	*varcus, punctata*
Paracyclas lirata Conrad	*varcus*
Praewaagenoconcha speciosa (Hall)	*punctata, linguiformis*
Productella rectispina (Hall)	*linguiformis*
Pseudatrypa devoniana (Webster)	*linguiformis*
Ptychopteria chemungensis Conrad	*punctata*
Schizophoria impressa (Hall)	*linguiformis*
Spinatrypa spinosa (Hall)	*varcus, linguiformis*
Spinocyrtia granulosa (Conrad)	*varcus*
Strophonella hybrida Hall and Whitfield	*linguiformis*
Tylothyris mesacostalis (Hall)	*punctata, linguiformis*

considered to be most important for determining habitable areas for benthic marine organisms (Brenchley and Harper, 1998) as well as the types of data typically compiled by sedimentary geologists interested in reconstructing depositional environments.

Eleven environmental factors were used to predict species ranges in this analysis (Table 3). Successful GARP analyses have been produced with as few as four and as many as 19 environmental variables (e.g. Feria and Peterson, 2002; Anderson et al., 2002; Peterson et al., 2002). Statistical analyses by Peterson and Cohoon (1999) have shown that although as few as five environmental variables can achieve nearly maximum accuracy in results, the inclusion of additional variables enhances detail and does not reduce accuracy. In addition, although some covariation is present within the environmental variables (e.g. water

Table 3. Explanation of coding strategy for variables used in construction of environmental base maps.

Percent mud, silt, or sand:

- Approximate fraction of each grain size within the sedimentary package

Percent limestone:

- Approximate percentage of limestone beds within the sedimentary package

Bedding style:

- Approximate thickness of sedimentary beds. Decimals indicate the relative abundance of each bedding type.

  1. Thin: centimeter scale bedding
  2. Moderate: decimeter scale bedding
  3. Thick: meter scale bedding

Substrate type:

- Character of the substrate on which benthic organisms reside. Decimals indicate the relative abundance of each substrate type.

  1. Muddy: fine grained, soupy sediment with abundant water in pore spaces for nutrients and deposit feeders
  2. Silty: intermediate substrate type
  3. Sandy: well sorted, coarser grained sediment

Inferred water depth/energy zone:

- Relative water depth with respect to storm and fair weather wave bases. Offshore settings within the Appalachian basin may have had water depths of 50 to 150 m (Prave et al., 1996). Decimals indicate the relative placement within the energy zone.

  0. Offshore: below storm wave base
  1. Subtidal: at storm wave base
  2. Lower intertidal: at the lower boundary of the fair weather wave base (low tide waves)
  3. Upper intertidal: at the lower boundary of high tide waves
  4. Subaerial: above the high tide interval

Depositional environment:

- Inferred sedimentary environment of deposition. Decimals indicate the relative placement within depositional environments.

  0. Basin
  1. Outer shelf
  2. Middle shelf
  3. Inner shelf
  4. Deltaic-estuarine
  5. Coastal plain/alluvial setting

Ichnofacies:

- Representative icnofauna found within the stratigraphic unit. Decimals indicate the relative placement within ichnofacies.

  0. Anoxic, traces absent
  1. *Zoophycus* ichnofacies
  2. *Cruziana* ichnofacies
  3. *Skolithos* ichnofacies

Table 3. (*Continued*)

4. *Tubiphytes* ichnofacies
5. *Scoyenia* ichnofacies

Oxygenation:

- Inferred oxygen content of the water column at the water–substrate interface. Decimals indicate the relative placement within oxygenation zones.

1. Anaerobic
2. Dysaerobic
3. Normal marine
4. Subaerial

Biofacies

- Community of species present. Community names and associations follow Bowen et al. (1974), McGhee (1976), McGhee and Sutton (1981, 1983, 1985), and Sutton et al. (1970).

Lower *varcus* Zone:
1. Anoxic, fossils rare
2. Dysaerobic, *Ambocoelia*, *Palaeoneilo*, chonetids
3. Open marine, *Cypricaridella*, *Tropidoleptus*, *Athyris*, and *Ambocoelia*
4. Continental, root traces

punctata Zone:
1. Ammonites, conodonts
2. *Rhipidomella* fauna
3. *Cypricardella* fauna
4. Continental, root traces, plant material

linguiformis Zone:
1. Ammonites, cephalopods
2. *Ambocoelia-Cariniferella* fauna
3. *Tylothyris-Schizophoria* fauna
4. *Cyrtospirifer-Douvillina* fauna
5. Continental

depth and depositional environment), the GARP algorithm (discussed below) is designed to analyze poorly structured domains and is not sensitive to environmental covariation (Stockwell and Peters, 1999).

Environmental variables were coded for each grid box (Fig. 1) from published stratigraphic columns and descriptions. The raw data are presented in Appendices 1.1-1.3 and include all environmental data as well as the key references from which the data were derived. The raw data were converted to numerical values appropriate for use in the modeling program using the coding scheme presented in Table 3. The coded data are presented in Tables 4–6. Because each grid box encompasses an area of roughly 43 × 56 km, variability in environmental conditions occurs commonly within regions. Environmental variability also occurs temporally through the stratigraphic interval considered. This variability in environmental parameters within a single grid box was incorporated by coding the variable with a value intermediate between the end member states present within the region.

Table 4. Data used in reconstructing environmental base maps for the Lower *varcus* Zone.

Longitude	Latitude	% Mud	% Silt	% Sand	% ls	Bedding	Substrate	Water depth	Environ	Oxygen	Biofacies
−78.75	42.75	55	20	0	25	1	1	1	1.5	1.5	3
−78.25	42.75	50	30	0	20	1	1	1.5	1.5	1.5	3
−77.75	42.75	70	0	0	30	1	1	1.5	0.5	1	3
−77.25	42.75	70	15	0	15	1	1	0	0	1.5	2
−76.75	42.75	80	10	0	10	1	1	0	0	1	2
−76.25	42.75	60	20	0	20	1.5	2	1.5	2	1	3
−75.75	42.75	30	60	0	10	1.5	2	1	2	2	3
−75.25	42.75	15	10	75	0						
−74.75	42.75	20	0	80	0	3	3	3.5	4	4	4
−74.25	42.75	20	10	70	0	3	3	4	5	5	4
−75.25	42.25	20	10	70	0	3	3	4	5	5	4
−77.25	41.25	90	10	0	0	1.5	1.5	1	0.5	2	2
−76.75	41.25	80	20	0	0	1.5	1.5	1	0.5	2	2
−76.25	41.25	63	35	2	0	1.5	1.5	1	1.5	2	3
−75.75	41.25	43	47	10	0	1.25	1.5	1	1.5	2	3
−75.25	41.25	52	44	4	0	1.25	2	1.5	2	2.5	3
−74.75	41.25	20	28	52	0	2.5	2.5	2	2.5	2.5	3
−78.25	40.75	80	20	0	0	1.5	1.5	1	0.5	2	2
−77.75	40.75	57	40	3	0	1.5	1.5	1	1.5	2	3
−77.25	40.75	62	25	13	0	1.25	1.5	1	1.5	2	3
−76.75	40.75	27	40	33	0	1.25	2	1.5	2	2.5	3
−76.25	40.75	21	47	32	0	1.25	2	1.5	2	2.5	3
−75.75	40.75	14	46	40	0	1.25	2	1.5	2	2.5	3
−75.25	40.75	10	53	37	0	1.25	2	1.5	2	2.5	3

−78.75	40.25	48	52	0	0	1.25	1.5	1	0.5	2	2
−78.25	40.25	36	50	14	0	1.25	1.5	1	1.5	2	3
−77.75	40.25	28	50	22	0	1.25	2	1.5	2	2	3
−77.25	40.25	15	41	44	0	2.5	3	3	3	3	3
−76.75	40.25	0	6	94	0	2.5	3	2	3.5	3	3
−76.25	40.25							4	5	5	4
−75.75	40.25							4	5	5	4
−78.75	39.75	33	50	17	0	1.25	1.5	1.5	1.5	2	3
−78.25	39.75	25	50	25	0	1.25	2	1.5	2	2	3
−77.75	39.75	15	43	42	0	2.5	2.5	2	3	2.5	3
−79.75	39.25	100	0	0	0	1	1	0	0	0	1
−79.25	39.25	75	25	0	0	1.5	1.5	1	0.5	2	2
−78.75	39.25	31	50	19	0	1.25	1.5	1	1.5	2	3
−78.25	39.25	25	50	25	0	1.25	2	1	1.5	2	3
−79.75	38.75	100	0	0	0	1	1	0	0	0	1
−79.25	38.75	77	23	0	0	1.5	1.5	1	0.5	2	2
−78.75	38.75	35	50	15	0	1.25	1.5	1	2	2	3
−78.25	38.75	21	50	29	0	1.25	2	1	1.5	2	3
−80.25	38.25	100	0	0	0	1	1	0	0	0	1
−79.75	38.25	87	13	0	0	1.5	1.5	1	0.5	2	2
−79.25	38.25	46	40	14	0	1.5	2	1	2	2.5	3
−80.25	37.75	66	32	2	0	1.5	1.5	1	0.5	2	2
−79.75	37.75	34	50	16	0	1.25	2	1.5	2	2.5	3
−81.25	37.25	75	25	0	0	1.5	1.5	1	0.5	2	2
−80.75	37.25	38	62	0	0	1	1	0	1	2	3
−80.25	37.25	39	50	11	0	1.25	1.5	1	1.5	2	3

Table 5. Data used in reconstructing environmental base maps for the *punctata* Zone.

Longitude	Latitude	% Mud	% Silt	% Sand	% ls	Bedding	Substrate	Water depth	Environ	Oxygen	Biofacies
−78.75	42.75	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−78.25	42.75	80	0	0	20	1.00	1.00	0.00	1.00	2.00	2
−77.75	42.75	70	5	5	20	1.00	1.00	0.50	1.00	2.00	2
−77.25	42.75	50	33	10	7	1.50	1.50	1.00	2.00	3.00	2
−76.75	42.75	50	29	26	5	1.50	2.00	1.00	2.00	3.00	2
−76.25	42.75	69	8	22	0	1.50	2.50	2.00	3.00	3.00	3
−75.75	42.75	69	8	22	0	1.50	2.50	2.00	3.00	3.00	3
−75.25	42.75	35	15	50	0	1.50	2.50	2.00	3.00	3.50	3
−74.75	42.75	15	10	75	0	3.00	3.00	3.50	5.00	4.00	4
−74.25	42.75	10	10	80	0	3.00	3.00	3.50	5.00	4.00	4
−80.25	42.25	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−79.75	42.25	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−79.25	42.25	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−78.75	42.25	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−78.25	42.25	80	0	0	20	1.00	1.00	0.00	1.00	3.00	2
−77.75	42.25	70	5	5	20	1.00	1.00	0.50	1.00	3.00	2
−77.25	42.25	40	45	12	3	1.50	2.00	1.00	2.00	3.00	2
−76.75	42.25	40	45	20	5	1.50	2.25	1.50	2.00	3.00	2
−76.25	42.25	85	0	15	0	1.50	1.50	2.00	2.50	3.00	3
−75.75	42.25	75	20	10	0	2.00	1.50	2.50	3.50	3.00	3
−75.25	42.25	35	15	50	0	1.50	2.50	2.50	4.00	3.50	3
−74.75	42.25	20	10	70	0	3.00	3.00	3.50	4.50	4.00	4
−74.25	42.25	10	10	80	0	3.00	3.00	4.00	5.00	4.00	4
−73.75	42.25	5	5	90	0	3.00	3.00	4.00	5.00	4.00	4
−80.25	41.75	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−79.75	41.75	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−79.25	41.75	90	0	0	10	1.00	1.00	0.00	1.00	2.00	1
−78.75	41.75	90	0	0	10	1.00	1.00	0.00	1.00	3.00	1

−78.25	41.75	80	0	0	20	1.00	1.00	0.00	1.00	3.00	2
−77.75	41.75	70	5	5	20	1.00	1.00	0.50	1.00	3.00	2
−77.25	41.75	70	4	26	0	2.00	2.50	1.00	2.00	3.00	2
−76.75	41.75	70	4	26	0	2.00	2.50	1.00	2.00	3.00	2
−76.25	41.75	69	8	22	0	1.50	2.50	2.00	3.00	3.00	3
−75.75	41.75	69	8	22	0	1.50	2.50	2.00	3.00	3.00	3
−75.25	41.75	20	10	70	0	3.00	3.00	3.50	4.00	4.00	4
−74.75	41.75	10	10	80	0	3.00	3.00	4.00	5.00	4.00	4
−74.25	41.75	5	5	90	0	3.00	3.00	4.00	5.00	4.00	4
−77.25	40.25	50	35	15	0	1.50	1.00	2.00	2.00	3.00	2
−78.75	39.75	20	75	5	0	1.00	2.00	1.00	2.00	3.00	
−78.25	39.75	50	35	15	0					3.00	
−79.75	39.25	85	10	0	5					1.00	
−79.25	39.25	65	30	5	0	1.00	1.50	0.00	1.00	2.00	
−78.75	39.25	57	38	5	0					3.00	
−78.25	39.25	50	35	15	0					3.00	
−79.75	38.75	65	30	5	0				1.00	2.00	
−79.25	38.75	57	38	5	0				1.00	3.00	
−78.75	38.75	50	35	15	0	1.10	1.50	0.00	1.00	3.00	
−80.25	38.25	65	30	5	0					2.00	
−79.75	38.25	57	38	5	0	1.50			1.00	3.00	
−79.25	38.25	50	35	15	0					3.00	
−80.75	37.75	85	10	0	5					1.00	
−80.25	37.75	75	22	0	3					2.00	
−79.75	37.75	57	38	5	0	2.00				3.00	
−79.25	37.75	50	35	15	0					4.00	
−81.25	37.25	75	22	0	3					2.00	
−80.75	37.25	57	38	5	0	2.00				3.00	
−80.25	37.25	20	40	40	0	2.50	2.25	0.00	2.00	3.00	
−79.75	37.25	20	40	40	0					3.00	
−81.75	36.75	57	38	5	0					3.00	

Table 6. Data used in reconstructing environmental base maps for the *linguiformis* Zone.

Longitude	Latitude	% Mud	% Silt	% Sand	% ls	Bedding	Substrate	Water depth	Environ	Ichno	Oxygen	Biofacies
−78.75	42.75	73	13	4	10	1.00	1.50	0.00	0.0	1.0	2.0	1
−78.25	42.75	30	60	5	5	1.00	2.00	1.00	2.0	2.0	2.5	2
−77.75	42.75	25	60	20	5	2.20	2.25	1.25	3.5	3.0	2.5	2
−77.25	42.75	24	28	52	0	2.00	2.50	1.50	2.0	2.0	3.0	3
−76.75	42.75	69	3	43	0	2.00	2.50	1.50	1.0	1.0	3.0	4
−76.25	42.75	40	0	60	0	2.00	2.50	2.50	4.0	4.0	3.0	4
−75.75	42.75	15	10	75	0	3.00	3.00	4.00	5.0	5.0	4.0	5
−75.25	42.75	10	10	80	0	3.00	3.00	4.00	5.0	5.0	4.0	5
−74.75	42.75	5	5	90	0	3.00	3.00	4.00	5.0	5.0	4.0	5
−74.25	42.75	3	2	95	0	3.00	3.00	4.00	5.0	5.0	4.0	5
−80.25	42.25	85	7	0	8	1.00	1.00	0.00	0.0	1.0	2.0	1
−79.75	42.25	85	7	0	8	1.00	1.00	0.00	0.0	1.0	2.0	1
−79.25	42.25	85	7	0	8	1.00	1.00	0.00	0.0	1.0	2.0	1
−78.75	42.25	73	13	4	10	1.10	1.00	0.00	1.0	2.0	2.0	2
−78.25	42.25	70	10	5	15	1.05	1.00	1.00	1.5	2.0	2.0	2
−77.75	42.25	40	35	25	0	1.50	1.50	1.25	2.0	2.5	2.5	2
−77.25	42.25	20	40	40	0	2.00	2.25	1.50	2.5	2.0	3.0	3
−76.75	42.25	40	5	55	0	2.00	2.50	1.50	2.0	2.0	3.0	4
−76.25	42.25	40	0	60	0	2.00	2.50	2.50	4.0	4.0	4.0	4
−75.75	42.25	15	10	75	0	3.00	3.00	4.00	5.0	5.0	4.0	5
−80.25	41.75	85	7	0	8	1.00	1.00	0.00	0.0	1.0	2.0	1
−79.75	41.75	85	7	0	8	1.00	1.00	0.00	0.0	1.0	2.0	1
−79.25	41.75	85	7	0	8	1.00	1.00	0.00	0.0	1.0	2.0	1

−78.75	41.75	73	13	4	10	1.10	1.00	0.00	1.5	2.0	2.0	2
−78.25	41.75	77	8	15	0	1.50	1.00	1.25	1.0	2.0	2.5	2
−77.75	41.75	77	8	15	0	1.50	1.00	1.50	1.0	2.0	2.5	2
−77.25	41.75	38	4	52	0	2.00	2.50	1.50	2.0	2.0	3.0	3
−76.75	41.75	69	3	43	0	2.00	2.50	1.50	3.0	3.0	3.0	4
−76.25	41.75	40	0	60	0	2.00	2.50	2.50	3.5	3.5	4.0	4
−75.75	41.75	5	20	75	0	3.00	3.00	4.00	4.5	5.0	4.0	5
−76.25	41.25	45	40	13	2	1.00	2.00	0.00	0.5	1.0	3.0	
−75.25	41.25	15	82	3	0	1.50	2.00	0.00	1.0	1.0	2.5	
−74.75	41.25	8	90	2	0	1.50	2.00	0.00	2.0	2.0	3.0	
−78.25	40.75	30	45	25	2	1.00	2.25	1.00	3.0	3.0	3.0	
−77.75	40.75	35	50	15	0	2.00	2.00	1.00	2.5	2.0	3.0	
−77.25	40.75	39	51	10	0	1.50	2.50	0.00	0.5	1.0	3.5	
−76.75	40.75	36	50	14	0	1.00	1.50	0.00	0.5	1.0	3.0	
−76.25	40.75	15	79	5	1	1.00	1.50	0.00	0.5	1.0	3.5	
−75.75	40.75	10	82	8	0	1.00	2.00	0.00	1.0	1.0	3.0	
−75.25	40.75	8	82	10	0	1.50	2.00	0.00	1.0	1.0	3.0	
−78.75	40.25	25	20	55	0	1.00	2.25	0.00	0.5	1.0	3.0	
−78.25	40.25	25	20	55	0	1.00	2.50	0.00	0.5	1.0	3.5	
−77.25	40.25	60	30	10	0	1.50	1.00	1.50	1.0	1.0	3.5	
−76.75	40.25	70	20	1	0	1.50	1.00	0.00	2.0	2.0	3.5	
−76.25	40.25	39	56	5	0	1.50	1.50	0.00	2.0	2.0	3.0	
−78.75	39.75	80	18	2	0	1.00	1.50	1.00	2.5	3.0	3.0	
−78.25	39.75	80	10	10	0	1.00	1.00	1.00	2.5	2.0	3.0	
−79.25	39.25	5	25	70	0	1.00	3.00	2.00	4.0	3.0	3.0	4

For example, a grid box in which deposits attributable to middle-shelf (value 2) and inner-shelf (value 3) environments are present are coded with a value of 2.5 for that parameter. Intermediate coding is an effective coding strategy for incorporating environmental variability within the system in a repeatable and an objective manner. This method is analogous to analyses of the modern biota that utilize time-averaged data, such as mean annual temperature, as environmental variables (Anderson et al., 2003). Additionally, because contour interpolation was used to create grid surfaces for modeling, intermediate, noninteger values are useful data in the analysis.

Once the complete set of stratigraphic and environmental parameters was assembled and coded, the data were imported into ArcView 3.2 (ESRI, 1999) for creation of environmental coverages. The data were imported as an event theme and converted to an ArcView shapefile. Using the Spatial Analyst extension of ArcView 3.2 (ESRI, 1999), an interpolated grid surface was constructed for each environmental variable in each time slice. The interpolation was accomplished at a grid size of 0.03° under an inverse distance weight interpolation procedure using a fixed radius of 75 km at the second power. The radius value was set so that interpolations would include the center of all bounding grid boxes for increased continuity and follows standard contouring protocol (Davis, 2002). An example of an interpolated surface output is presented in Figure 2.

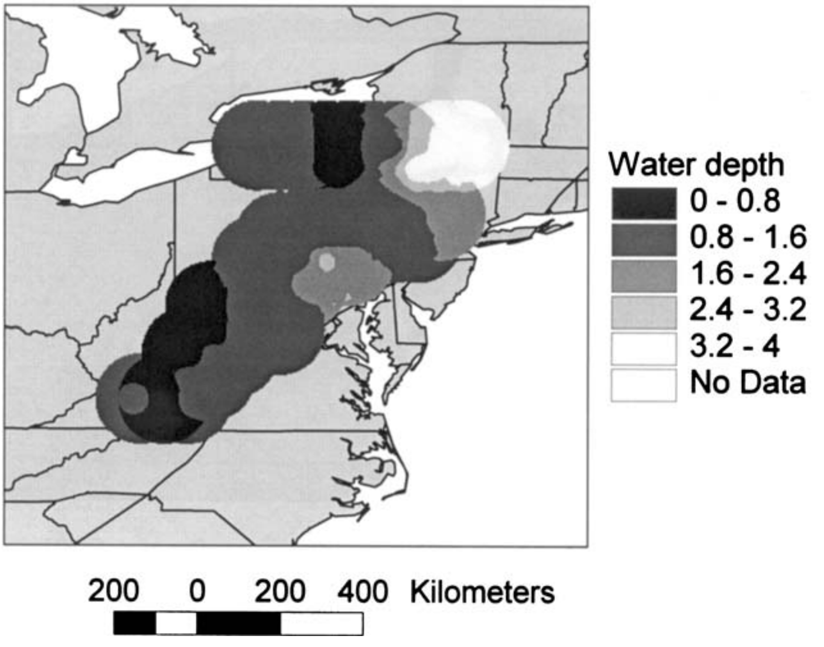

Figure 2. An example of an interpolated environmental layer surface showing water depth in the Lower *varcus* Zone. The numeric values pertain to the coded water depth values in Table 3. Note that water depth shallows to the east nearing the Acadian Highlands and deepens to the west into the Appalachian Foreland Basin. The deeper water region in western New York corresponds to a tectonic basin feature, the Rome Trough (Saverese et al., 1986).

2.4. Distribution modeling

2.4.1. Choice of modeling system

Numerous statistical methods exist for analyzing and predicting the geographic distributions of species, including multiple regression, logistic regression, and genetic algorithms. Multiple regression analysis is a useful method for handling multifactor data and has been used widely in studies that attempt to predict percent cover (e.g. Haltuch et al., 2000). Multiple regression requires assumptions of multivariate normality and equal variance–covariance matrices, however, that are not likely to be met with the data available in palaeontological studies. Logistic regression is free from the requirement of multivariate normality and predicts a dichotomous dependent variable; logistic regression, however, requires that absence data represent true absences, not undersampling (Buchan and Padilla, 2000). This is an unacceptable assumption for palaeontological data where sampling is typically neither statistical nor uniform and species occurrences represent only a subset of a species range due to the limited availability of outcrops available for study. In addition, both multiple linear regression and logistic regression are associated with high error rates and limited ability to accurately predict occurrences (Goodwin et al., 1998; Haltuch et al., 2000; Chong et al., 2001).

Genetic algorithms provide an alternative to standard regression modeling by including several algorithms in an iterative, artificial-intelligence-based approach. This approach automates decision-making by repeatedly analyzing a series of local rules that combine categorical, range-type, and logistic rules to obtain higher significance levels than global rules, such as those applied in regression modeling (Stockwell and Peters, 1999; Stockwell and Peterson, 2002). In addition to maximizing the significance of the prediction, genetic algorithms also strive to achieve predictive accuracy, which is a weakness of the other methods mentioned above (Peterson and Vieglas, 2001). Genetic algorithms are particularly effective for analyzing museum data sets that are assembled by sampling that was neither uniform nor designed for statistical tests, and where environmental data consist of poorly structured domains (Stockwell and Peterson, 2002). The specific genetic algorithm that has been designed for use with biological occurrence data is GARP. GARP is designed to predict species ranges based on the fundamental niche, which is reconstructed from environmental data (Peterson and Vieglas, 2001). The GARP system has been tested extensively and has been shown to achieve high accuracy with low numbers of species occurrence data, even when there are as few as five environmental parameters (Peterson and Cohoon, 1999; Peterson, 2001; Stockwell and Peterson, 2002; Anderson et al., 2003).

2.4.2. GARP implementation

All modeling analyses in this study used DesktopGarp 1.1.4 developed by R. Scachetti-Pereira (www.lifemapper.org/desktopgarp). GARP works as in iterative process of rule selection, evaluation, testing, and incorporation or rejection (Stockwell and Peters, 1999). The species occurrence data points are divided equally into training and test points. The training data set is randomly sampled to create 1250 presence and background (absence) data points. A local rule is generated randomly from a set of possibilities (e.g. logistic regression, logit, atomic), applied to the training data, and tested with an internal test. In each iteration, predictive accuracy is assessed with 1250 points resampled from the test data set and 1250 points randomly sampled from the study region as a whole. The genetic component of the algorithm consists of mutating rules that include point mutations, deletions, and crossovers followed by an assessment of whether the mutation resulted in increased accuracy. The program uses the change in predictive accuracy from the prior iteration to determine whether a particular rule should be incorporated in the model or discarded (Stockwell and Peters, 1999). The algorithm continues until results converge on earlier models or after 1000 iterations.

Prior to running complete analyses on all species within the database, a jackknifing procedure was performed to determine the suitability of the 11 reconstructed environmental variables for species range prediction. This procedure has been used previously to test the efficacy of environmental layers (e.g. Peterson et al., 2002; Stockwell and Peterson, 2002). Environmental jackknife analysis was accomplished by implementing the "all combinations of selected layers" option within GARP. The environmental jackknife procedure was performed for all included species with greater than ten unique occurrence points within the Lower *varcus* Zone. These taxa are: *Athyris spiriferoides* (Eaton), *Cariniferella carinata* (Hall), *Palaeoneilo constricta* (Conrad), and *Spinatrypa spinosa* (Hall). The errors in terms of omission and commission values were assessed for each environmental layer using multiple linear regression in Minitab 14 (Minitab Inc., 2003). In this context, multiple linear regression is used to assess whether the inclusion of each environmental layer increases amount of error, measured as omission and commission, which is a distinctly different application than that discussed above (Davis, 2002). Multiple linear regression analysis was performed for each species individually and for each conodont zone with species pooled. Each species had a unique set of environmental factors that were significantly correlated with high omission and commission values; however, no factor was significantly associated with error in all four species. For *Athyris spiriferoides*, error was associated with limestone percent; error in *Cariniferella carinata* was associated with silt percent; for *Palaeoneilo constricta*, error was associated with limestone percent, mud percent, and oxygenation variables; and error in *Spinatrypa spinosa* was related to limestone percent. To characterize further how various environmental layers contributed to errors, the niche of each species was predicted using 100 replications when the layers significantly associated with error were removed and with all environmental layers included. The resulting error between these two experiments for each species was compared using a *t*-test and including a Dunn–Šidák correction to account for multiple comparisons (Sokal and Rolfe, 1995) in Minitab 14. In all cases, there was no significant difference in error between species models run with all environmental layers and those with the potentially error-inducing layers removed. Each of the environmental variables was therefore considered informative, and species niche for range predictions were reconstructed using all environmental variables.

Within this analysis, species ranges were predicted by running 200 replicate models of each species ecological niche at a convergence level of 0.01. All environmental variables (Table 3) were included within the analysis as justified above. The best subset selection option was invoked, and the ten best species predictions under an omission threshold of 10% and a commission threshold of 50% were retained following standard protocol (A.T. Peterson, pers. comm. 2004). Range prediction maps were output as Arc/Info Grids and imported into ArcView 3.2 for analysis. Within ArcView Spatial Analyst, the ten best subset outcomes were summed to provide a distribution model for each species (e.g. Fig. 3).

2.5. Determining robustness of GARP models

The GARP models were compared with other predictions of species distribution to determine the robustness of GARP distribution predictions. GARP range predictions are based on a set of five to 50 rules developed using a variety of methods (e.g. logit, regression, etc.), and these rules are not included with the model output. The complexity of the GARP rule-set means that direct statistical comparison of predicted species ranges to environmental base layers is not readily available, and untangling the precise effect of a single environmental layer on the final species range prediction is a complex problem. An alternative approach was thus taken: predicted species ranges were compared with previously published descriptions of expected species occurrences (e.g. Bowen et al., 1974; McGhee, 1976; McGhee and Sutton, 1981, 1983; Sutton et al., 1970; Sutton and McGhee, 1985). Predicted ranges within the *linguiformis* Zone were compared with ranges expected based on the community palaeoecology studies of McGhee and Sutton (1981) and with those reconstructed by digitizing a polygon to enclose points by Rode and Lieberman (2004) (Table 7). Because the geographic range reconstruction undertaken by Rode and Lieberman (2004) encompasses a greater geographic area, comparisons between GIS- and

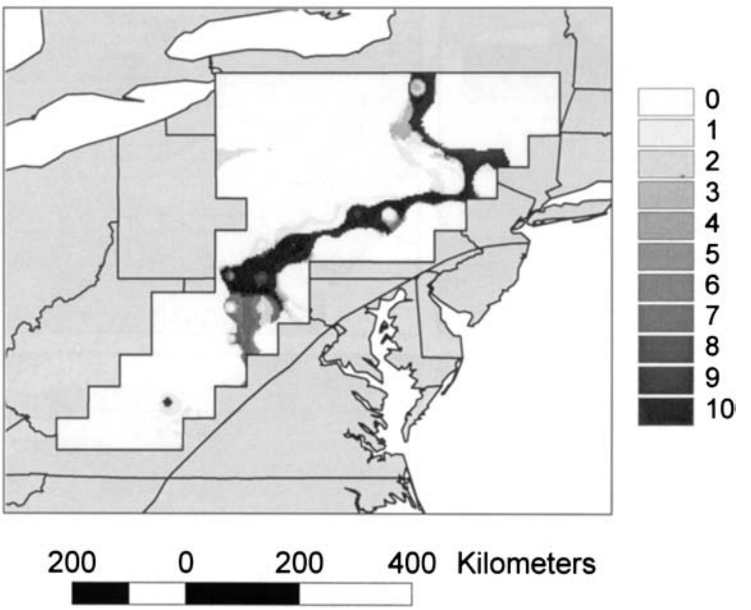

Figure 3. An example of a predicted species range map: *Leptodesma spinerigum* (Conrad) during the Lower *varcus* Zone. Darker shades indicate an increased number the ten best subset maps predict *L. spinerigum* to occur at a location. Comparison with Fig. 2 indicates that the range of *L. spinerigum* partially, though not precisely, follows the general trend of the Givetian shoreline.

Table 7. Comparison of differences in species ranges predicted by GIS bounding-polygon reconstruction and GARP.

Species	GIS (km^2)	GARP (km^2)	Conodont zone
Cariniferella carinata	8,700	39,700	Lower *varcus*
Cypricardella bellistriata	39,700	25,800	Lower *varcus*
Cyrtospirifer chemungensis	2,000	4,200	*linguiformis*
Praewaagenoconcha speciosa	17,000	53,500	*linguiformis*
Spinatrypa spinosa	5,900	20,300	*linguiformis*

GARP-modeled ranges were restricted to species endemic to roughly the northern part of the Appalachian Basin (Devonian outcrop belts in Maryland, New York, Pennsylvania, Virginia, and West Virginia).

2.6. Examination of species survival with environment

Statistical analyses were conducted to assess the effects of distribution changes on species survival during the Late Devonian biodiversity crisis. The areal extent of each species range was calculated in ArcView by summing the areas common to six or more of the ten best subset predictions following the method of Peterson et al. (2002). Since the total geographic area modeled within each conodont zone was different (Fig. 1), these values are reported in Table 8 as both raw numbers and as percentages of the total geographic area within the modeling limits of each conodont zone. A comparison of species range and species survival suggested a relationship may exist, because species that survive tend to have larger geographic ranges (Table 9). The relationship between the area of species' ranges and species survival was investigated statistically using an ANOVA including a Dunn–Šidák correction to account for multiple comparisons (Tables 10–13). In addition, ranges of species that crossed two time intervals were compared to determine the amount of expansion or reduction in geographic distribution (Table 14).

3. Results and discussion

3.1. Comparison of outputs with other predictions

The GARP models were developed for 10 species in the Lower *varcus* Zone, nine species in the *punctata* Zone, and 20 species in the *linguiformis* Zone (Table 2). Each of these models produced a unique species range based on the 11 environmental parameters considered. Comparison of the *linguiformis* Zone predictions with the community palaeoecology established by McGhee and Sutton (1981) provides the most direct comparison with previously published descriptions of expected species occurrences and is used as a case study to test the robustness of the GARP predictions as the data sets underlying the two distribution models are distinct.

McGhee and Sutton (1981) established three community types based on brachiopod and bivalve species in the Java Formation of New York and Foreknobs Formation of West

Table 8. Geographic ranges predicted from GARP modeling with status of species analyzed by relevant conodont zone. Species are designated survivors (Y) if they persisted through the biodiversity crisis and into the Famennian and victims (N) if they did not.

Species	Area (km^2)	Coverage (%)	Survivor	Conodont zone
Ambocoelia gregaria	27,100	19.4	Y	*linguiformis*
Ambocoelia umbonata	9,500	6.8	Y	*linguiformis*
Athyris angelica	42,400	30.4	Y	*linguiformis*
Athyris cora	21,600	11.6	N	Lower *varcus*
Athyris spiriferoides	39,700	21.3	N	Lower *varcus*
Cariniferella carinata	7,300	5.2	N	*linguiformis*
Cariniferella carinata	39,700	21.3	N	Lower *varcus*
Cariniferella tioga	6,000	4.4	N	*linguiformis*
Cupularostrum contracta	42,700	30.6	Y	*linguiformis*
Cupularostrum exima	24,000	17.2	Y	*linguiformis*
Cupularostrum exima	5,900	5.1	Y	*punctata*
Cypricardella bellistriata	25,700	13.8	N	Lower *varcus*
Cyrtospirifer chemungensis	7,200	5.1	N	*linguiformis*
Douvillina cayuta	6,600	4.7	N	*linguiformis*
Eoschizodus chemungensis	31,100	26.5	N	*punctata*
Floweria chemungensis	40,000	28.6	Y	*linguiformis*
Floweria parva	31,400	22.5	N	*linguiformis*
Goniophora chemungensis	7,300	6.2	Y	*punctata*
Grammysia elliptica	34,500	29.4	Y	*punctata*
Leptodesma nitida	14,100	12.0	N	*punctata*
Leptodesma spinerigum	39,200	28.1	Y	*linguiformis*
Leptodesma spinerigum	23,400	12.5	Y	Lower *varcus*
Mucrospirifer mucronatus	16,300	8.8	N	Lower *varcus*
Nervostrophia nervosa	4,800	3.5	N	*linguiformis*
Palaeoneilo constricta	5,300	4.5	Y	*punctata*
Paleoneilo constricta	39,300	21.1	Y	Lower *varcus*
Paracyclas lirata	31,500	16.9	N	Lower *varcus*
Praewaagenoconcha speciosa	53,500	38.3	Y	*linguiformis*
Praewaagenoconcha speciosa	8,500	7.3	Y	*punctata*
Productella rectispina	22,900	16.4	Y	*linguiformis*
Pseudatrypa devoniana	40,600	29.1	N	*linguiformis*
Ptychopteria chemungensis	1,800	1.5	N	*punctata*
Schizophoria impressa	40,200	28.9	Y	*linguiformis*
Spinatrypa spinosa	20,300	14.6	N	*linguiformis*
Spinatrypa spinosa	32,900	17.6	N	Lower *varcus*
Spinocyrtia granulosa	11,900	6.4	N	Lower *varcus*
Strophonella hybrida	26,600	19.1	N	*linguiformis*
Tylothyris mesacostalis	29,100	20.9	Y	*linguiformis*
Tylothyris mesacostalis	12,400	10.6	Y	*punctata*

Virginia. Five species were included both in McGhee and Sutton's (1981) community analysis and this analysis: *Ambocoelia gregaria* (Hall); *Athyris angelica* (Hall); *Floweria chemungensis* (Conrad); *Leptodesma spinerigum* (Conrad); and *Tylothyris mesacostalis* (Hall). McGhee and Sutton (1981) characterized *Ambocoelia gregaria* and *Athyris angelica* as

Table 9. Size of geographic range (km^2) versus species survival through the crisis interval for species during the conodont zones considered.

		Survivors	Victims
Lower *varcus*	31.3×10^3	24.7×10^3	
punctata		12.3×10^3	15.6×10^3
linguiformis		33.7×10^3	16.7×10^3
Total		26.7×10^3	20.9×10^3

Table 10. ANOVA table showing analysis of geographic range versus survival through the Late Devonian biodiversity crisis for Lower *varcus* Zone species.

Source	Degrees of freedom	Sum of squares	Mean squares	*F*-value	*P*-value
Survival	1	2.47E + 07	2.47E + 07	0.22	0.648
Error	8	8.79E + 08	1.10E + 08		
Total	9	9.03E + 08			

Table 11. ANOVA table showing analysis of geographic range versus survival through the Late Devonian biodiversity crisis for *punctata* Zone species.

Source	Degrees of freedom	Sum of squares	Mean squares	*F*-value	*P*-value
Survival	1	2.17E + 07	2.17E + 07	0.14	0.715
Error	7	1.05E + 09	1.50E + 08		
Total	8	1.08E + 08			

Table 12. ANOVA table showing analysis of geographic range versus survival through the Late Devonian biodiversity crisis for *linguiformis* Zone species.

Source	Degrees of freedom	Sum of squares	Mean squares	*F*-value	*P*-value
Survival	1	1.42E + 09	1.42E + 09	8.64	0.009
Error	16	2.95E + 09	1.64E + 08		
Total	17	4.37E + 09			

Table 13. ANOVA table showing analysis of geographic range versus survival through the Late Devonian biodiversity crisis for all species.

Source	Degrees of freedom	Sum of squares	Mean squares	*F*-value	*P*-value
Survival	1	4.28E + 08	4.28E + 08	2.15	0.151
Error	35	6.97E + 09	1.99E + 08		
Total	36	7.40E + 09			

Table 14. Relative change in geographic range size of species that occurred in two conodont zones based on GARP predicted modeling and its general association with species survival through the crisis interval.

Species	Conodont zones of transition	Relative size of younger range (%)	Survival
Cupularostrum exima	*punctata* to *linguiformis*	379	Y
Praewaagenoconcha speciosa	*punctata* to *linguiformis*	526	Y
Tylothyris mesacostalis	*punctata* to *linguiformis*	197	Y
Cariniferella carinata	*varcus* to *linguiformis*	24	N
Leptodesma spinerigum	*varcus* to *linguiformis*	224	Y
Spinatrypa spinosa	*varcus* to *linguiformis*	83	N
Palaeoneilo constricta	*varcus* to *punctata*	21	Y

dominant members of the open-shelf setting, *Tylothyris mesacostalis* and *Floweria chemungensis* as key members of the outer-platform community, and *Leptodesma spinerigum* as a dominant species within the inner-platform and nearshore settings. These predictions are borne out by the GARP predictions (Fig. 4): *Athyris angelica* and *Ambocoelia gregaria* occupy the most basinward positions, whereas *Leptodesma spinerigum* is predicted to occupy a more nearshore setting, and *Tylothyris mesacostalis* and *Floweria chemungensis* are most frequently predicted to occur in a central, middle-shelf setting. McGhee and Sutton (1981) noted that whereas these five species are characteristic of specific depositional settings, their ranges often extend into adjacent settings. This is also illustrated in the results from the GARP models. For example, although *Athyris angelica* occurs throughout the basinal setting, this species also commonly occurs in the outer shelf and in some areas of the middle- or inner-shelf setting (Fig. 4b). The GARP models also illustrate that whereas species ranges follow depositional setting in part, a one-to-one correlation does not exist, indicating the importance of additional environmental factors in determining the fundamental or realized niche of each species.

Comparison of species ranges predicted from community analyses of McGhee and Sutton (1981) with species distributions predicted by GARP shows that GARP modeling is a robust way in which to predict species ranges. GARP modeling shows a high level of predictive accuracy with known species occurrences and expected palaeoecology and appears to be a viable approach for reconstructing the ranges of fossil species in shallow marine ecosystems.

3.2. Comparison of GARP and GIS enclosure ranges

Ranges of Devonian brachiopod and bivalve species have previously been modeled using GIS (Rode and Lieberman, 2004, 2005). This technique essentially involves enclosing known species occurrences during a conodont zone interval within a polygon. Detailed descriptions of this method are published elsewhere (Rode and Lieberman, 2004) and are not repeated herein. The method by which species occurrence points are enclosed within a minimum area polygon has the potential to both under- and over-predict species ranges. Under-prediction is expected typically, since all localities where a species lived will

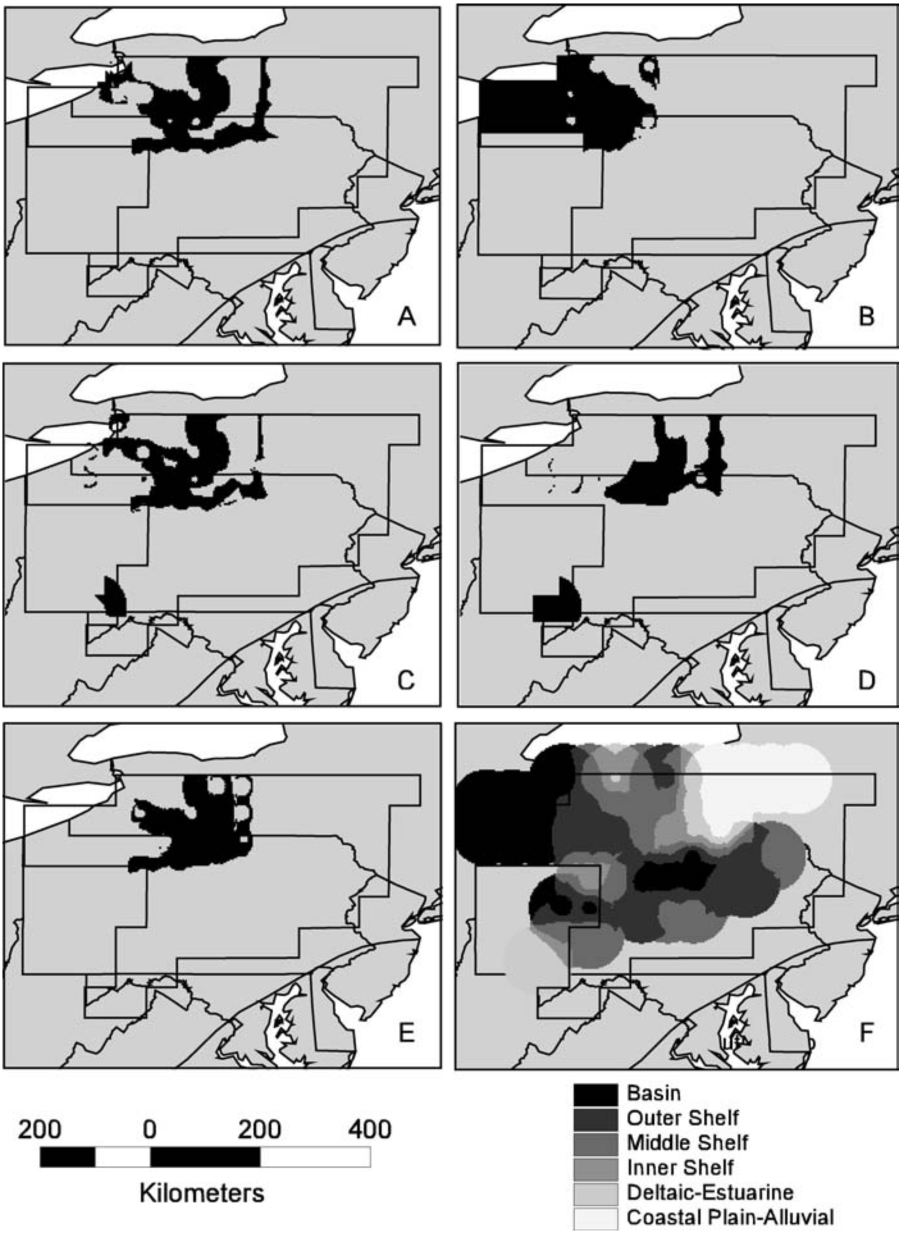

Figure 4. GARP prediction maps. The area shown in black indicates the part of the modeled region, bounded by the line, in which all of the best subset maps predict the species to occur. (A) *Ambocoelia gregaria* (Hall), (B) *Athyris angelica* (Hall), (C) *Floweria chemungensis* (Conrad), (D) *Leptodesma spinerigum* (Conrad), (E) *Tylothryris mesacostalis* (Hall). (F) Interpolated surface grid indicating depositional environment, the key parameter examined in McGhee and Sutton (1981), and one of the eleven parameters examined within this analysis. Circular holes within the reconstructed ranges indicate a lack of environmental data at a particular site, which prevents accurate prediction in that part of the range.

necessarily not be present within the data set. Over-prediction can occur when a bounding polygon includes areas that would have been inhospitable to the species due to local changes in shoreline, sediment influx, or other environmental conditions.

The GARP distribution models produced herein were compared with the minimum area polygon ranges reconstructed using GIS by Rode and Lieberman (2004) to further characterize the general utility of the GARP method for fossil invertebrates. Because the GIS data sets of Rode and Lieberman (2004) included some geographic areas outside the study area of this project, only species whose range occurs entirely within the northern Appalachian Basin were used for comparison. It is important to note, however, that the same data set discussed above is the data source for both these studies, so the two studies are directly comparable. Two species from the Lower *varcus* and three species from the *linguiformis* Zones were examined (Table 14) and side-by-side comparisons of species range predictions are shown in Figure 5.

In most pairwise comparisons of polygon enclosure and GARP prediction models, the ranges are roughly consistent between the two outputs. Commonly, though not always, the GARP-predicted range encompasses the entire polygon enclosure range and predicts species to occur in additional areas adjacent to the polygon range (i.e. Fig. 5A,B; E,F; G,H; I,J for: *Cariniferella carinata* (Hall), *Cyrtospirifer chemungensis* (Hall), *Praewaagenoconcha speciosa* (Hall), and *Spinatypra spinosa* (Hall), respectively). Often the predicted ranges compare quite closely with the polygon ranges, e.g. in *Cyrtospirifer chemungensis* (Fig. 5E,F), which may suggest both that GARP is accurately predicting known ranges, and that the method of collection of data for the GIS polygon enclosure ranges may be sufficient to reasonably capture the actual species range. The distribution of *Cypricardella bellistriata* (Conrad) differs from the general pattern described above; instead of the GARP prediction encompassing a greater area than the polygon reconstruction, it includes a smaller area (Fig. 5C,D). Comparison of the two range reconstructions indicates that the preferred habitat of *C. bellistriata* is discontinuous within the polygon enclosure. This indicates that when species ecological preferences result in discontinuous populations, polygon enclosure ranges will over-predict species ranges, whereas the predictive approach produces a more accurate representation of the area a species can successfully colonize. The GARP modeling algorithm seems to estimate species ranges successfully, and does not appear to suffer from significant under- or over-prediction errors when compared with GIS constructed species occurrence enclosure ranges. Because the GARP algorithm-predicted species ranges are based on a rule-set that has been trained on the data and contains both internal and external tests, it should be expected to produce more refined estimates of species range than GIS enclosure models. In fact, predicted ranges that exceed the known species occurrence-bounding polygon provide testable hypotheses for future work in assessing the boundaries of species ranges, predicting ranges of species groups and boundaries of community types, and also determining the quality of the fossil record.

3.3. Quantifying geographic range change and species survival

The size of a species geographic range has previously been shown to be related to species survival during the Late Devonian biodiversity crisis interval (Rode and Lieberman, 2004). Rode and Lieberman (2004) determined this relationship using species ranges estimated

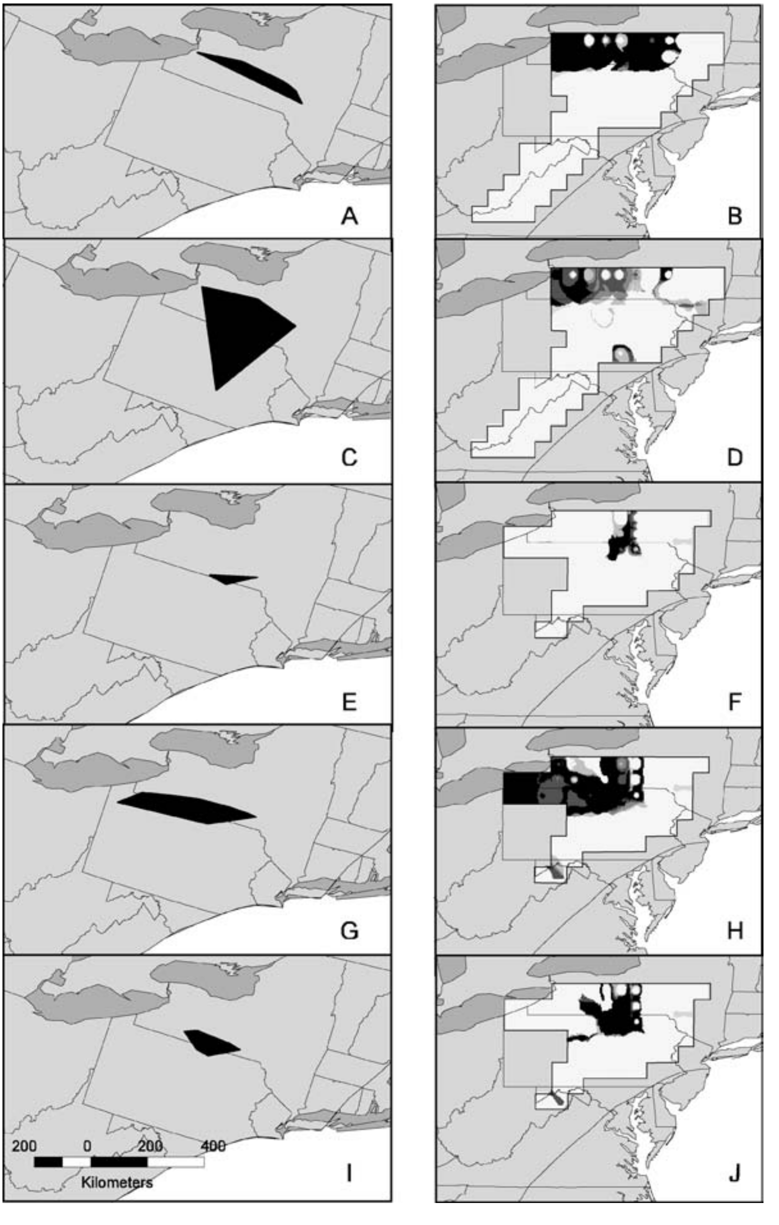

Figure 5. Comparison of GIS polygon enclosure range reconstructions and GARP distribution predictions. (A) Polygon enclosure range and (B) GARP prediction range for *Cariniferella carinata* (Hall) during the *varcus* Zone; (C) Polygon enclosure range and (D) GARP prediction range for *Cypricardella bellistriata* (Conrad) during the *varcus* Zone; (E) Polygon enclosure range and (F) GARP prediction range for *Cyrtospirifer chemungensis* (Hall) during the *linguiformis* Zone; (G) Polygon enclosure range and (H) GARP prediction range for *Praewaagenoconcha speciosa* (Hall) during the *linguiformis* Zone; (I) Polygon enclosure range and (J) GARP prediction range for *Spinatrypa spinosa* (Hall) during the *linguiformis* Zone. Circular holes within the reconstructed ranges indicate a lack of environmental data at a particular site, which prevents accurate prediction in that portion of the range.

by the bounding-polygon method. Because it was noted that GARP range predictions, although often congruent with GIS range reconstructions, can differ in size and geographic area from polygon inclusion reconstructions, it is worth investigating the further resiliency of these results. Thus, the areal changes within the range of a single species between conodont zones based on GARP modeling were quantified (Table 14). There are seven species whose ranges could be predicted for two conodont zones, and of these, four species exhibited range increases and three exhibited range decreases. Range expansions appear to be the result of species colonizing additional habitat, and are not just attributable to habitat tracking. For example, in the *linguiformis* Zone, the increased range of *Leptodesma spinerigum* (Fig. 6C,D) and *Praewaagenoconcha speciosa* (Fig. 6E,F) cannot be explained by habitat tracking, because the east-west breadth, hence the number of environments occupied, increased. Range contractions, when they occurred, resulted from a species becoming restricted to a subset of its prior range. An example of this for *Cariniferella carinata* is shown in Figure 6A,B. In this case, although the ancestral population of *C. carinata* occupied a wide array of environments in the Lower *varcus* Zone, *linguiformis* Zone populations were restricted to a very narrow geographic area.

Again, based on GARP modeling, and matching the results from Rode and Lieberman (2004) based on GIS, a correlation may exist between changes in species distribution and survival through the biodiversity crisis interval and into the Famennian (Table 14). Of the seven species whose ranges were predicted in two different time slices, all species that undergo range expansion into the *linguiformis* Zone persisted through the biodiversity crisis. None of the species with ranges contracting from the Lower *varcus* into the *linguiformis* Zones survive into the Famennian. Not only range expansion, but also the timing of range expansion and the areas that species expanded into, may have controlled species survival during the Late Devonian as the range of *Palaeoneilo constricta* contracts between the Lower *varcus* and *punctata* Zones, but it survives the biodiversity crisis. Perhaps expansion or contraction during the *linguiformis* Zone may be crucial, although there were too few data to consider this statistically. This may indicate that range size and range expansion may be parameters that were critical for surviving this particular biodiversity crisis, although not as critical for species survival during the adjacent background intervals.

To further examine the effect timing and geographic range had on survival, ANOVAs were computed to compare the mean ranges of species that persisted into the Famennian with species that became extinct by the end of the Frasnian. Each species was characterized as a survivor if it persisted into the Famennian or a victim if it did not; the geographic range was calculated for each species per stage; conodont zones were analyzed separately and together to determine whether species that survived the crisis had statistically larger ranges and whether the survival advantage was constant or varied across time. The differences between survivor and victim species ranges were not statistically different in either the *punctata* or the Lower *varcus* zones (Tables 10, 11); in fact, during the *punctata* zone, the average geographic range of species that became extinct was higher than for survivor species, although not significantly so (Tables 8, 10). In addition, the ANOVA in which species extant in all conodont zones were pooled together also did not indicate significant survival differences by geographic range (Table 13). A significant size difference was recovered for the *linguiformis* Zone, however ($p = 0.002$) (Table 12). The significance of this result remained even after compensating for multiple analyses using the Dunn–Šidák

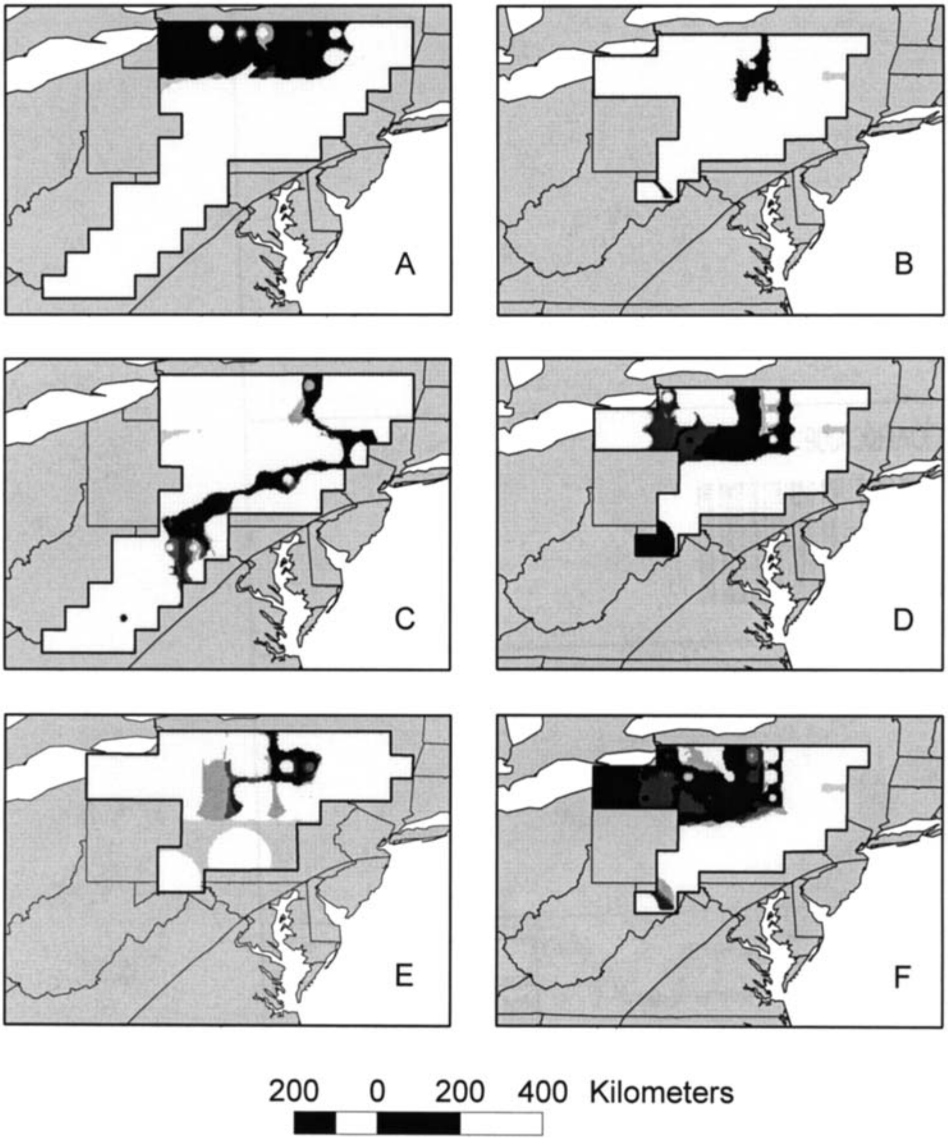

Figure 6. Comparison of the geographic ranges predicted by GARP modeling for species that occurred in two of the relevant conodont zones. (A) Lower *varcus* Zone and (B) *linguiformis* Zone distribution of *Cariniferella carinata* (Hall); (C) Lower *varcus* Zone and (D) *linguiformis* Zone distribution of *Leptodesma spinerigum* (Conrad); (E) *punctata* Zone and (F) *linguiformis* Zone distribution of *Praewaagenoconcha speciosa* (Hall).

correction (Sokal and Rolfe, 1995). This indicates that species with larger geographic ranges during the *linguiformis* Zone were more successful during the crisis interval than those with smaller ranges. It is also important to note that geographic range prior to the crisis interval (i.e. in the *punctata* or Lower *varcus* Zones) and larger geographic range overall (as shown by the analysis of pooled species) did not confer a significant survival advantage during the biodiversity crisis interval.

4. Conclusions

The results presented above suggest that GARP models provide both robust and useful characterizations of species ranges. The general congruence between GARP predictions and the palaeobiological understanding of species ranges supports the accuracy of the predicted ranges. In addition, both the expansion and refinement of ranges available with GARP versus GIS polygon enclosures further supports the utility of this technique.

4.1. Implications for understanding the Late Devonian biodiversity crisis

Both changes in species geographic ranges and the sizes of species ranges impact species survivorship through the Late Devonian biodiversity crisis interval. The timing of range changes is critical in conferring a survival advantage. Both a broad range during the terminal Frasnian *linguiformis* Zone and an increasing range entering that interval are related to survival into the Famennian. Based on this analysis, neither a large range nor expansion events prior to the *linguiformis* Zone, however, appear to have enhanced species survival. Species extant in the middle Frasnian *punctata* Zone that persisted into the Famennian, in fact, tended to have slightly smaller ranges (although not statistically significantly so) than their counterparts that did not survive the biodiversity crisis. Likewise, broad Lower *varcus* Zone species ranges conferred no advantage to species during the crisis. Moreover, differences in range size were not statistically associated with survival when species of all time periods were pooled, which further underscores the unique importance of large ranges during the *linguiformis* Zone for surviving the biodiversity crisis interval.

The Late Devonian biodiversity crisis has been attributed to a set of five pulses of extinction: one immediately prior to the *linguiformis* Zone in the Late *rhenana* Zone, three at the end of the *linguiformis* Zone, and one in the following Early *crepida* Zone (McGhee, 2001). Of the three time slices examined in this analysis, only the *linguiformis* Zone interval occurs within the biodiversity crisis window. The Lower *varcus* and *punctata* zones preceded the crisis interval by approximately 14.2 and 3.8 million years, respectively (Tucker et al., 1998). The Late Devonian extinction was a temporally protracted event (e.g. McGhee, 1989, 1996). The results of this study indicate that the effects of geographic range on species survival did not extend as far back as the middle Frasnian *punctata* Zone. An important component of the biodiversity crisis, however, was a decline in speciation rates (McGhee, 1989, 1996), and the affects of geographic range on speciation rate may have operated earlier in the Frasnian (Rode, 2004; Rode and Lieberman, 2003, 2004).

4.2. Further applicability

The results presented herein indicate that ecological niche modeling methods such as GARP may be robust tools for predicting the geographic ranges of fossil taxa. The design of the algorithm, which permits *ad hoc* sampling readily available from museum collections, and the use of a relatively limited number of environmental coverages at a relatively coarse spatial scale (km versus meters), is ideally suited for handling fossil data in areas where the stratigraphy and sedimentology are well known and densely sampled. The success of modeling species ranges within this study suggests this method may be more broadly applicable to other palaeontological regions and time periods where extensive museum collections and fine-scale sedimentological data exist.

The level of analytical rigor of species range prediction achieved using GARP could be used as a tool to achieve a number of palaeontological or sedimentological goals. Range prediction maps could be consulted when creating search strategies for new field sites targeted for the collection of specific species. Combining range predictions for several species may allow the investigation of community patterns based on niche parameters, including the long-term stability of species associations, coordinated stasis, or Gleasonian versus Clementsian communities within specific environments or portions of time. In addition, comparison of species ranges within an evolutionary framework may permit the identification of speciation by vicariance, dispersal, or geodispersal (e.g. Wiley and Mayden, 1985; Lieberman, 2000). Resource partitioning or competitive exclusion could also potentially be examined (e.g. Anderson et al., 2002). Thus, this is potentially a new and valuable technique that can be applied to the study of the fossil record.

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Appendix 1.1. Raw environmental base data for the Lower *varcus* Zone

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style /thickness	Substrate type	Water depth
–78.75	42.75	Ludlowville: Wanakah Sh; med grey, soft, fossilif. Shale & shaly mudstone	55	20	0	25	ls concretions, fossils in tempestite layers	Thin	Muddy	Photic zone below SWB to above SWB for ls
–78.25	42.75	Ludlowville: Wanakah Sh; dk grey sh, ls, calcareous grey sh, encrinte	50	30	0	20	Tempestite shell layers	Thin	Muddy	Below SWB to near normal WB
–77.75	42.75	Ludlowville: Wanakah, grey fissile shale	70	0	0	30	Burried bottom ls assemblage	Thin	Muddy	SWB to normal WB for ls (20–25 m), below SWB for sh (100-150 m)
–77.25	42.75	Ludlowville: Wanakah, black shale	70	15	0	15	Shell beds	Thin	Muddy	Below SWB
–76.75	42.75	Ludlowville: Wanakah, black shale, micritic ls	80	10	0	10	Shell beds	Thin	Muddy	Below SWB
–76.25	42.75	Ludlowville: Otisco Sh, Ivy Pt. Siltst.; siltstone, ls, concretions, mudst	60	20	0	20	Individual HCS, laminated mudstone	Thin to moderate	Muddy to sandy	Below SWB to lower shoreface
–75.75	42.75	Ludlowville: upper, undif, micacous siltst, silty sh, sandy siltst	30	60	0	10	Laminated and ripple laminated	Thin to moderate	Silty	Below SWB to just above SWB
–75.25	42.75	Ludlowville to Panther Mtn sst	15	10	75	0				

–74.75	42.75	Panther Mtn sst, Ashokan Fm., med grain graywacke sst, olive brown mudst, dk shale	20	0	80	0	Fluvial & tidal influences; channel sands; x-beds to laminated	Thick	Sandy	Intertidal to subaerial
–74.25	42.75	Panther to Plattekill Fm. coarse sst, red-grey sh, siltst, mudst	20	10	70	0	x-beds, channel fill	Thick	Sandy	Subaerially exposed
–73.75	42.75	No outcrop								
–80.25	42.25	No outcrop								
–79.75	42.25	No outcrop								
–79.25	42.25	No outcrop								
–78.75	42.25	No outcrop								
–78.25	42.25	No outcrop								
–77.75	42.25	No outcrop								
–77.25	42.25	No outcrop								
–76.75	42.25	No outcrop								
–76.25	42.25	No outcrop								
–75.75	42.25	No outcrop								
–75.25	42.25	Plattekill Fm. coarse sst, red-grey sh, siltst, mudst	20	10	70	0	x-beds, channel fill	Thick	Sandy	Subaeriall exposed
–74.75	42.25	No outcrop								
–74.25	42.25	No outcrop								
–73.75	42.25	No outcrop								
–80.25	41.75	No outcrop								
–79.75	41.75	No outcrop								
–79.25	41.75	No outcrop								
–78.75	41.75	No outcrop								
–78.25	41.75	No outcrop								

Appendix 1.1. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style /thickness	Substrate type	Water depth
–77.75	41.75	No outcrop								
–77.25	41.75	No outcrop								
–76.75	41.75	No outcrop								
–76.25	41.75	No outcrop								
–75.75	41.75	No outcrop								
–75.25	41.75	No outcrop								
–74.75	41.75	No outcrop								
–74.25	41.75	No outcrop								
–80.25	41.25	No outcrop								
–79.75	41.25	No outcrop								
–79.25	41.25	No outcrop								
–78.75	41.25	No outcrop								
–78.25	41.25	No outcrop								
–77.75	41.25	No outcrop								
–77.25	41.25	Millsboro Shale and Mahantango; black shale to siltstone	90	10	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–76.75	41.25	Millsboro Shale and Mahantango; black shale to siltstone	80	20	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–76.25	41.25	Millsboro Shale and Mahantango; black shale to siltstone to fine sst.	63	35	2	0	Laminated beds, ripple forms, a few HCS	Thin to moderate	Muddy to silty	Below SWB to above SWB
–75.75	41.25	Mahantango; mudstone to siltstone a few fine sst	43	47	10	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above SWB

–75.25	41.25	Mahantango; mudstone to fine sst (more mudst)	52	44	4	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to sandy	Below SWB to lower shoreface
–74.75	41.25	Mahantango; siltstone to fine sst (more sst)	20	28	52	0	HCS, amalgamated or single, sto-rm facies only	Moderate to thick	Silty to sandy	At SWB to upper Shoreface
–78.25	40.75	Millsboro Shale and Mahantango; black shale to siltstone	80	20	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–77.75	40.75	Millsboro Shale and Mahantango; black shale to siltstone to fine sst.	57	40	3	0	Laminated beds, ripple forms, a few HCS	Thin to moderate	Muddy to silty	Below SWB to above SWB
–77.25	40.75	Mahantango; SWB mudstone to siltstone a few fine sst	62	25	13	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above
–76.75	40.75	Mahantango; mudstone to fine sst (more mudst)	27	40	33	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Tuddy to sandy	Below SWB to lower shoreface
–76.25	40.75	Mahantango; mudstone to fine sst (more mudst)	21	47	32	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to sandy	Below SWB to lower shoreface
–75.75	40.75	Mahantango; mudstone to fine sst (more mudst)	14	46	40	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to sandy	Below SWB to lower shoreface
–75.25	40.75	Mahantango; mudstone to	10	53	37	0	Laminated beds, a few HCS,	Thin (mainly) to moderate	Muddy to sandy	Below SWB to lower shoreface

Appendix 1.1. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style /thickness	Substrate type	Water depth
		fine sst (more mudst)					storm facies			
–78.75	40.25	Mahantango & Millsboro; Blk sh, mudst, few sltst.	48	52	0	0	Laminated beds, ripple forms, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above SWB
–78.25	40.25	Mahantango; mudstone to siltstone a few fine sst	36	50	14	0	Laminated beds, massive siltstone, a few HCS, storm facies	Thin (mainly) storm facies	Muddy to silty	Below to just above SWB
–77.75	40.25	Mahantango; mudstone to siltstone a few fine sst	28	50	22	0	Laminated beds, massive siltstone, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to fine sandy	Below SWB to lower shoreface
–77.25	40.25	Mahantango; siltstone to coarse sst	15	41	44	0	Amalgamated HCS, TXB, channel sands, mud draped ripples	Moderate to thick	Sandy	At SWB, upper shoreface to intertidal
–76.75	40.25	Mahantango; fine to coarse sst	0	6	94	0	Amalgamated HCS, TXB, channel sands, mud draped ripples	Moderate to thick	Sandy	Above SWB, upper shoreface to intertidal
–76.25	40.25	Mahantango, none					None	None	Subaerially exposed	Subaerially exposed

–75.75	40.25	Mahantango, none					None	None	Subaerially exposed	Subaerially exposed
–78.75	39.75	Mahantango; mudstone to siltstone a few fine sst	33	50	17	0	Laminated beds, massive siltstone, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above SWB
–78.25	39.75	Mahantango; mudstone to siltstone a few fine sst	25	50	25	0	Laminated beds, massive siltstone, a few HCS, storm facies	Thin (mainly) to moderate	Silty	Just above SWB
–77.75	39.75	Mahantango; mudstone, fine to coarse sst	15	43	42	0	Amalgamated HCS, TXB, channel sands, mud draped ripples	Few thin, mostly moderate to thick	Muddy to sandy (mostly)	At SWB to upper shoreface to intertidal
–79.75	39.25	Millsboro Shale; black shale	100	0	0	0	Laminated	Thin	Muddy	Well below SWB
–79.25	39.25	Millsboro Shale and Mahantango; black shale to siltstone	75	25	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–78.75	39.25	Mahantango; mudstone to siltstone a few fine sst	31	50	19	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above SWB
–78.25	39.25	Mahantango; mudstone to fine sst (more mudst)	25	50	25	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Silty	Just above SWB
–77.75	39.25	No outcrop								

Appendix 1.1. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style /thickness	Substrate type	Water depth
–79.75	38.75	Millsboro Shale; black shale	100	0	0	0	Laminated	Thin	Muddy	Well below SWB
–79.25	38.75	Millsboro Shale and Mahantango; black shale to siltstone	77	23	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–78.75	38.75	Mahantango; mudstone to siltstone a few fine sst	35	50	15	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above SWB
–78.25	38.75	Mahantango; mudstone to fine sst (more mudst)	21	50	29	0	Laminated beds, ripple forms, single and amalgamated HCS	Thin (mainly) to moderate	Silty	Just above SWB
–80.25	38.25	Millsboro Shale; black shale	100	0	0	0	Laminated	Thin	Muddy	Well below SWB
–79.75	38.25	Millsboro Shale and Mahantango; black shale to siltstone	87	13	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–79.25	38.25	Mahantango; mudstone to fine sst (more mudst)	46	40	14	0	Laminated beds, ripple forms, single and amalgamated HCS	Thin (mainly) to moderate	Muddy to sandy	Well below SWB to lower shoreface
–78.75	38.25	No outcrop								
–80.75	37.75	No outcrop								

–80.25	37.75	Millsboro Shale and Mahantango; black shale to siltstone	66	32	2	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–79.75	37.75	Mahantango; mudstone to fine sst (more mudst)	34	50	16	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to sandy	Below SWB to lower shoreface
–79.25	37.75	no outcrop								
–81.25	37.25	Millsboro Shale and Mahantango; black shale to siltstone	75	25	0	0	Laminated and storm-derived ripples	Thin to moderate	Muddy to silty	Below to just at SWB
–80.75	37.25	Mahantango; mudstone with a few siltstone to v. fine sst	38	62	0	0	Laminated beds, ripple forms	Thin	Muddy	Below SWB
–80.25	37.25	Mahantango; mudstone to siltstone a few fine sst	39	50	11	0	Laminated beds, a few HCS, storm facies	Thin (mainly) to moderate	Muddy to silty	Below to just above SWB
–79.75	37.25	No outcrop								
–81.75	36.75	No outcrop								

Appendix 1.1. Raw environmental base data for the Lower *varcus* Zone.

Longitude	Latitude	Depositional environment	Ichnofacies/bioturbation	Oxygenation	Biofacies	Reference
–78.75	42.75	Outer to middle shelf	*Cruziana* and *Zoophycus*	Normal marine	*Ambocoelia, Athyris,* and normal marine	Oliver and Klapper, 1981; Miller, 1986; Wygart, 1996; Batt, 1999
–78.25	42.75	outer to middle shelf		Normal marine		Batt, 1999
–77.75	42.75	Deep to distal shelf	*Zoophycus*, lots of bioturbation	Normal marine	*Ambocoelia, Palaeoneilo, Chonetids*	Oliver and Klapper, 1981; Savarese et al., 1986; Batt, 1999
–77.25	42.75	Shelf to basin	*Zoophycus*	Dysaerobic	Dysaerobic	Batt, 1999
–76.75	42.75	Basin	*Zoophycus*	Dysaerobic	Dysaerobic	Batt, 1999
–76.25	42.75	Shelf	*Zoophycus*, lots of bioturbation	Normal marine	Corals	Brett et al., 1986; Brett and Baird, 1994; Mayer, 1994
–75.75	42.75	Middle shelf		Normal marine	*Cypricardella, Ambocoelia, Tropidoleptus*	Oliver and Klapper, 1981
–75.25	42.75					
–74.75	42.75	Tidal to estuarine		Subaerial	Nonmarine	Ver Straeten and Brett, 1999
–74.25	42.75	Alluvial fan & coastal plain		Subaerial	Nonmarine	Ver Straeten and Brett, 1999
–73.75	42.75					
–80.25	42.25					
–79.75	42.25					
–79.25	42.25					
–78.75	42.25					
–78.25	42.25					
–77.75	42.25					
–77.25	42.25					

–76.75	42.25					
–76.25	42.25					
–75.75	42.25					
–75.25	42.25	Alluvial fan & coastal plain		Subaerial	Nonmarine	Ver Straeten and Brett, 1999
–74.75	42.25					
–74.25	42.25					
–73.75	42.25					
–80.25	41.75					
–79.75	41.75					
–79.25	41.75					
–78.75	41.75					
–78.25	41.75					
–77.75	41.75					
–77.25	41.75					
–76.75	41.75					
–76.25	41.75					
–75.75	41.75					
–75.25	41.75					
–74.75	41.75					
–74.25	41.75					
–80.25	41.25					
–79.75	41.25					
–79.25	41.25					
–78.75	41.25					
–78.25	41.25					
–77.75	41.25					
–77.25	41.25	Deep to outer shelf	*Cruziana*; slight to intense	Dysaerobic	Anoxic to open marine	Prave et al., 1996: inferred
–76.75	41.25	Deep to outer shelf	*Cruziana*; slight to intense	Dysaerobic	Anoxic to open marine	Prave et al., 1996: inferred
–76.25	41.25	Outer shelf to middle shelf	*Cruziana*; bioturbation common	Nn	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred

Appendix 1.1. (*Continued*)

Longitude	Latitude	Depositional environment	Ichnofacies/bioturbation	Oxygenation	Biofacies	Reference
–75.75	41.25	Outer shelf to middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred
–75.25	41.25	Outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Prave et al., 1996: inferred
–74.75	41.25	Middle shelf to inner shelf/shoreface	*Cruziana* and *Skolithos*	Normal marine	Open marine to abraded brach valves	Prave et al., 1996: section
–78.25	40.75	Deep to outer shelf	*Cruziana*; slight to intense	Normal marine	Anoxic to open marine	Prave et al., 1996: inferred
–77.75	40.75	Outer shelf to middle shelf	*Cruziana*; bioturbation common	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred
–77.25	40.75	Outer shelf to middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred
–76.75	40.75	Outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Prave et al., 1996: inferred; Faill et al., 1973: section
–76.25	40.75	Outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Prave et al., 1996: inferred
–75.75	40.75	Outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Prave et al., 1996: section
–75.25	40.75	Outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Prave et al., 1996: inferred
–78.75	40.25	Basin, outer shelf	*Cruziana*	Dysaerobic	Open marine & anoxic	Prave et al., 1996: inferred; Dennison and Hasson, 1976: section

–78.25	40.25	Outer shelf to middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred; Dennison and Hasson, 1976: section
–77.75	40.25	Outer shelf to inner shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred; Dennison and Hasson, 1976: section
–77.25	40.25	Middle platform to prograding tidal delta	*Skolithos*	Normal marine	Thick shelled brachs, mainly abraded	Prave et al., 1996: section
–76.75	40.25	Inner platform to prograding tidal delta	*Skolithos*	Normal marine	Thick shelled brachs, mainly abraded	Prave et al., 1996: section
–76.25	40.25	Coastal plain	subaerially exposed	Subaerial	Subaerially exposed	Prave et al., 1996: inferred
–75.75	40.25	Coastal plain	subaerially exposed	Subaerial	Subaerially exposed	Prave et al., 1996: inferred
–78.75	39.75	Outer shelf to middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: inferred; Dennison and Hasson, 1976: section
–78.25	39.75	Middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Prave et al., 1996: section; Dennsion et al., 1979: section
–77.75	39.75	Middle platform to prograding tidal delta	*Cruziana* (some) and *Skolithos*	Normal marine	Open marine to thick shelled brachs, mainly abraded	Prave et al., 1996: inferred
–79.75	39.25	Deep shelf	?	Anaerobic	Anoxic	Dennison and Hasson, 1976: inferred
–79.25	39.25	Deep to outer shelf	*Cruziana;* slight to intense	Dysaerobic	Anoxic to open marine	Dennison and Hasson, 1976: inferred
–78.75	39.25	Outer shelf to middle shelf	*Cruziana;* slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Dennison and Hasson, 1976: inferred
–78.25	39.25	Outer shelf to middle shelf	*Cruziana;* slight to intense		Open marine: brachs, coral, crinoids; bryo and mollusks rare	Dennison and Hasson, 1976: inferred

Appendix 1.1. (*Continued*)

Longitude	Latitude	Depositional environment	Ichnofacies/bioturbation	Oxygenation	Biofacies	Reference
–77.75	39.25					
–79.75	38.75	Deep shelf	?		Anoxic	Dennison and Hasson, 1976, inferred
–79.25	38.75	Deep to outer shelf	*Cruziana*; slight to intense	Anaerobic	anoxic to open marine	Dennison and Hasson, 1976, inferred
–78.75	38.75	Middle shelf	*Cruziana*; slight to intense	Dysaerobic	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Dennison and Hasson, 1976, inferred
–78.25	38.75	Outer shelf to middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Dennison and Hasson, 1976: inferred
–80.25	38.25	Deep shelf	?	Anaerobic	Anoxic	Dennison and Hasson, 1976: inferred
–79.75	38.25	Deep to outer shelf	*Cruziana*; slight to intense	Dysaerobic	Anoxic to open marine	Dennison and Hasson, 1976: inferred; Hasson and Dennison, 1979, text
–79.25	38.25	Deep outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Dennison and Hasson, 1976: inferred

–78.75	38.25					
–80.75	37.75					
–80.25	37.75	Deep to outer shelf	*Cruziana;* slight to intense	Dysaerobic	Anoxic to open marine	Dennison and Hasson, 1976: inferred
–79.75	37.75	Outer shelf to inner shelf/shoreface	*Cruziana* and some *Skolithos*	Normal marine	Open marine to abraded brach valves	Dennison and Hasson, 1976: inferred
–79.25	37.75					
–81.25	37.25	Deep to outer shelf	*Cruziana*; slight to intense	Dysaerobic	Anoxic to open marine	Dennison and Hasson, 1976: inferred
–80.75	37.25	Outer shelf	*Cruziana*; bioturbation common	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Dennison and Hasson, 1976: inferred
–80.25	37.25	Outer shelf to middle shelf	*Cruziana*; slight to intense	Normal marine	Open marine: brachs, coral, crinoids; bryo and mollusks rare	Dennison and Hasson, 1976: inferred
–79.75	37.25					
–81.75	36.75					

Appendix 1.2. Raw environmental base data for the *punctata* Zone.

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style / thickness	Substrate type	Water depth
–78.75	42.75	Cashaqua Sh: light to dark gray shale w/concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below wave base
–78.25	42.75	Cashaqua Sh: olive gray mudst 80% w/concretions 20%	80	0	0	20	Concretions horizons	Thin	Muddy	Below wave base
–77.75	42.75	Cashaqua Sh: gray-green sh, mdst, concretions	70	5	5	20	Concretions	Thin	Muddy	Below wave base to shallow basin
–77.25	42.75	Cashaqua (1/2) Rock Stream Fm (1/2); blue-gray calc siltstone and shale	50	33	10	7	Rare shallow current ripples; isolated turbidite flows; bioturbated	Thin to moderate	Muddy to silty	Above or near SWB
–76.75	42.75	Cashaqua/ Rock Stream Fm. Olive grey shale, 40% silt/sand, 60% mud	50	29	26	5	Rare shallow current ripples	Thin to moderate	Silty	Above or near SWB
–76.25	42.75	Glen Aubrey	69	8	22	0	Rare shallow current ripples, HCS, scours	Thin to moderate	Muddy and sandy	Above or near FWWB
–75.75	42.75	Glen Aubrey	69	8	22	0	Rare shallow current ripples, HCS, scours	Thin to moderate	Muddy and sandy	Above or near FWWB
–75.25	42.75	Glen Aubrey/Walton	35	15	50	0	rare shallow current ripples	Thin to moderate	Muddy and sandy	Above or near FWWB

–74.75	42.75	Walton	15	10	75	0	Bar complexes, fluvial sedimentation	Thick	Sandy	Above FWWB to subaerial
–74.25	42.75	Walton	10	10	80	0	Bar complexes, fluvial sedimentation	Thick	Sandy	Above FWWB to subaerial
–73.75	42.75	Eroded								
–80.25	42.25	Cashaqua Sh. Gray shale with lst concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–79.75	42.25	Cashaqua Sh. Gray shale with lst concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–79.25	42.25	Cashaqua Sh. Gray shale with lst concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–78.75	42.25	Cashaqua Sh: light to dark gray shale w/concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–78.25	42.25	Cashaqua Sh: olive gray mudst 80% w/concretions 20%	80	0	0	20	Concretions horizons	Thin	Muddy	Below SWB
–77.75	42.25	Cashaqua Sh: gray-green sh, mdst, concretions	70	5	5	20	Concretions	Thin	Muddy	Below wave to near SWB basin
–77.25	42.25	Cashaqua (1/2) Rock Stream Fm (1/2); blue-gray calc siltst and shale	40	45	12	3	x-beds, isolated turbidites, bioturbated	Thin to moderate	Silty	Above or near SWB
–76.75	42.25	Cashaqua/Rock Stream olive gray sh, 40% silt/s and, 60% mud	40	45	20	5	Rare shallow current ripples, x-beds, concretions	Thin to moderate	Silty to sandy	Above SWB to near FWWB

Appendix 1.2. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style / thickness	Substrate type	Water depth
–76.25	42.25	Glen Aubrey mudst interbed w/silst thinner sh or sst	85	0	15	0	Groove casts, cross lamination, cuspate ripples	Thin to moderate	Muddy to silty	At or below FWWB, 30 to 120' of water
–75.75	42.25	Glen Aubrey, green shale, silst, sst	75	20	10	0	HCS, scours, wave ripples	moderate	Muddy to silty	At FWWB to intertidal
–75.25	42.25	Glen Aubrey/Walton	35	15	50	0	Rare shallow current ripples, HCS, scours	Thin to moderate	Muddy and sandy	Above or near FWWB
–74.75	42.25	Walton Fm. red shale and coarse sst	20	10	70	0	Tidal indicators, x-beds, shallow channels	Thick	Sandy	Intertidal to subaerial
–74.25	42.25	Walton Fm. red shale and sst; red and gray (Onteora sst)	10	10	80	0	Fluvial system, x-beds, slickensides	Thick	Sandy	Subaerial
–73.75	42.25	Walton Fm. red shale and sst	5	5	90	0	Fluvial system	Thick	Sandy	Subaerial
–80.25	41.75	Cashaqua Sh. Gray shale with lst concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–79.75	41.75	Cashaqua Sh. Gray shale with lst concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–79.25	41.75	Cashaqua Sh. Gray shale with lst concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB
–78.75	41.75	Cashaqua Sh: light to dark gray shale w/concretions	90	0	0	10	Concretions horizons	Thin	Muddy	Below SWB

–78.25	41.75	Cashaqua Sh: olive gray mudst 80% w/concretions 20%	80	0	0	20	Concretions horizons	Thin	Muddy	Below SWB
–77.75	41.75	Cashaqua Sh: gray-green sh, mdst, concretions	70	5	5	20	Concretions	Thin	Muddy	Below wave to near SWB basin
–77.25	41.75	Rock Stream; sst, mudst	70	4	26	0	Current and wave ripples; moderate ripples	Moderate	Muddy and sandy	above SWB but below FWWB
–76.75	41.75	Rock Stream; sst, mudst	70	4	26	0	Current and wave ripples; moderate ripples	Moderate	Muddy and sandy	Above SWB but below FWWB
–76.25	41.75	Glen Aubrey mudst interbed w/silst thinner sh or sst	69	8	22	0	Rare shallow current ripples, HCS, scours	Thin to moderate	Muddy to sandy	At or below FWWB, 30 to 120’ of water
–75.75	41.75	Glen Aubrey mudst interbed w/silst thinner sh or sst	69	8	22	0	Rare shallow current ripples, HCS, scours	Thin to moderate	Muddy to sandy	At or below FWWB, 30 to 120’ of water
–75.25	41.75	Walton Fm. red shale and sst	20	10	70	0	Tidal indicators	Thick	Sandy	Intertidal to subaerial
–74.75	41.75	Walton Fm. red shale and sst	10	10	80	0	Fluvial system	Thick	Sandy	Subaerial
–74.25	41.75	Walton Fm. red shale and sst	5	5	90	0	Fluvial system	Thick	Sandy	Subaerial
–80.25	41.25	No outcrop								
–79.75	41.25	No outcrop								
–79.25	41.25	No outcrop								
–78.75	41.25	No outcrop								
–78.25	41.25	No outcrop								
–77.75	41.25	No outcrop								
–77.25	41.25	No outcrop								
–76.75	41.25	No outcrop								

Appendix 1.2. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style / thickness	Substrate type	Water depth
–76.25	41.25	Subaerial redbeds								
–75.75	41.25	Subaerial redbeds								
–75.25	41.25	Subaerial redbeds								
–74.75	41.25	Eroded								
–78.25	40.75	Marine sh, siltst, sst								
–77.75	40.75	Marine sh, siltst, sst								
–77.25	40.75	Subaerial redbeds								
–76.75	40.75	Subaerial redbeds								
–76.25	40.75	Subaerial redbeds								
–75.75	40.75	Subaerial redbeds								
–75.25	40.75	Subaerial redbeds								
–78.75	40.25	Marine sh, siltst, sst								
–78.25	40.25	Marine sh, siltst, sst								
–77.75	40.25	Subaerial redbeds								
–77.25	40.25	Trimmers Rock Fm., siltstone to silty shale within sst beds and Redbeds	50	35	15	0	Graded beds, flute casts, ball and pillow	Thin to moderate	Muddy	Moderate
–76.75	40.25	Subaerial redbeds								
–76.25	40.25	Eroded								
–75.75	40.25	Eroded								
–78.75	39.75	Bralier Fm., gray silst and silty shale	20	75	5	0	Flute casts	Thin	Silty	Below FWWB and near SWB

−78.25	39.75	Trimmers Rock Fm. equivalent, siltstone to silty shale within sst beds	50	35	15	0				
−77.75	39.75	Catskill, non-marine red beds								
−79.75	39.25	Chatanooga, black shale	85	10	0	5				
−79.25	39.25	"Portage" or Brallier, grey silty shale and siltst	65	30	5	0	Thickly laminated shales w/siltstone interbeds	Thin	Muddy to silty	Below SWB
−78.75	39.25	Brallier Fm., gray silst and silty shale	57	38	5	0				
−78.25	39.25	"Chemung" or Trimmers Rock equivalent, silstone with shale and sst	50	35	15	0				
−77.75	39.25	Catskill, non-marine red beds								
−79.75	38.75	"Portage" or Brallier, grey silty shale and siltst	65	30	5	0				
−79.25	38.75	Brallier Fm., gray silst and silty shale	57	38	5	0				
−78.75	38.75	"Chemung" or Trimmers Rock equivalent, silstone with shale and sst	50	35	15	0	Poorly sorted siltstone, thickly aminated	Thin (90%) to moderate (10%)	Muddy to silty	Below SWB
−78.25	38.75	Catskill, non-marine red beds								

Appendix 1.2. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style / thickness	Substrate type	Water depth
–80.25	38.25	"Portage" or Brallier, grey silty shale and siltst	65	30	5	0				
–79.75	38.25	Brallier Fm., gray silst and silty shale	57	38	5	0		Siltstone		
–79.25	38.25	"Chemung" or Trimmers Rock equivalent, silstone with shale and sst	50	35	15	0				
–78.75	38.25	Catskill, non-marine red beds								
–80.75	37.75	Chatanooga, black shale	85	10	0	5				
–80.25	37.75	Dark shale basinal of Brallier	75	22	0	3				
–79.75	37.75	Brallier Fm., gray silst and silty shale	57	38	5	0		Moderate		
–79.25	37.75	"Chemung" or Trimmers Rock	50	35	15	0				

		equivalent, silstone with shale and sst								
−81.25	37.25	Dark shale basinal of Brallier	75	22	0	3				
−80.75	37.25	Brallier Fm., gray silst and silty shale	57	38	5	0		Moderate		
−80.25	37.25	Brallier Fm., gray silst and silty shale	20	40	40	0	x-beds, lenticular-irregular beds, coursening upward, TXB, Bouma seq	Mod to thick	Sandy and silty	Below FWWB
−79.75	37.25	Brallier Fm., gray silst and silty shale	20	40	40	0				
−81.75	36.75	Brallier Fm., gray silst and silty shale	57	38	5	0				

Appendix 1.2. Raw environmental base data for the *punctata* Zone.

Longitude	Latitude	Depositional environment	Ichnofacies/ bioturbation	Oxygenation	Biofacies	Reference
–78.75	42.75	Distal slope	?		Ammonites, conodonts	Over et al., 1999; Oliver and Klapper, 1981; Sutton et al., 1970; Sutton, 1963; Sutton and McGhee, 1985
–78.25	42.75	Distal slope	Some		Naples fauna	Kirchgasser, 1983; Sutton et al., 1970; Sutton, 1960
–77.75	42.75	Dstal slope	High in middle, lower on top and bottom		Middle-bivalves & plants, other bivalves and	Kirchgasser et al., 1994; Sutton et al., 1970; Sutton, 1960 gastropods
–77.25	42.75	Outer shelf, distal platform	?	Good	***Rhipidomella***; bivalves, gast, ceph, brachs, arths, fish	Sutton and McGhee, 1985
–76.75	42.75	Outer shelf, distal platform	?	Good	***Rhipidomella***; bivalves, gast, ceph, brachs, arths, fish	Adams et al., 1956; Sutton et al., 1970; Sutton and McGhee, 1985; Sutton, 1960
–76.25	42.75	Inner shelf	?		***Cypricardella***	Sutton and McGhee, 1985; Sutton et al., 1970; Sutton, 1960
–75.75	42.75	Inner shelf	?		***Cypricardella***	Sutton and McGhee, 1985; Sutton et al., 1970; Sutton, 1960
–75.25	42.75	Inner shelf	?		***Cypricardella***	Sutton and McGhee, 1985; Sutton et al., 1970
–74.75	42.75	Alluvial plain	?	Subaerial		Sutton et al., 1970; Woodrow, 1985
–74.25	42.75	Alluvial plain	?	Subaerial		Sutton et al., 1970; Woodrow, 1985
–73.75	42.75					Sutton et al., 1970

–80.25	42.25	Distal slope		Mod	Ammonites, conodonts	Sutton et al., 1970
–79.75	42.25	Distal slope		Mod	Molluscan	Tesmer, 1966; Sutton et al., 1970
–79.25	42.25	Distal slope		Mod	Molluscan	Tesmer, 1966; Sutton et al., 1970
–78.75	42.25	Distal slope	?		Ammonites, conodonts	Tesmer, 1966; Sutton et al., 1970
–78.25	42.25	Distal slope	Some		Naples fauna	Sutton et al., 1970
–77.75	42.25	Distal slope	High in middle, lower on top and bottom		Middle-bivalves & plants, other bivalves and gastropods	Sutton et al., 1970
–77.25	42.25	Outer shelf, distal platform		Good	***Rhipidomella***; bivalves, ceph, gast; rare brachs, arths, fish	Sutton et al., 1970; Sutton, 1960
–76.75	42.25	Outer shelf	?	Good	***Rhipidomella***; bivalves, ceph, gast; rare brachs, arths, fish	Sutton and McGhee, 1985; Sutton et al., 1970; Sutton, 1960
–76.25	42.25	Prodelta, distal platform, and open shelf	Tracks, trails, burrows	Good	***Cypricardella***; Productella, *Ambocoelia, Chonetes, Leptodesma,*	Bowen et al., 1970; Sutton et al., 1970; Sutton and McGhee, 1985; Bishuk et al., 1991
–75.75	42.25	Tidal flat/marsh, prodelta, delta platform			***Cypricardella***	Krajewski and Williams, 1971; Sutton et al., 1970; Sutton and McGhee, 1985
–75.25	42.25	Inner shelf to subaerial	?		***Cyrpricardella***	Krajewski and Williams, 1971; Sutton et al., 1970; Sutton and McGhee, 1985
–74.75	42.25	Tidal flat to alluvial plain		Subaerial	Plant roots and stems	Fletcher, 1962; Woodrow, 1985; Krajewski and Williams, 1971; Sutton et al., 1970; Bridge and Dingman, 1981

Appendix 1.2. (*Continued*)

Longitude	Latitude	Depositional environment	Ichnofacies/ bioturbation	Oxygenation	Biofacies	Reference
–74.25	42.25	Alluvial plain		Subaerial		Fletcher, 1962; Woodrow, 1985; Krajewski and Williams, 1971; Sutton et al., 1970
–73.75	42.25	Alluvial plain		Subaerial		Inferred
–80.25	41.75	Distal slope		Mod	Ammonites, conodonts	Inferred
–79.75	41.75	Distal slope		Mod	Molluscan	Inferred
–79.25	41.75	Distal slope		Mod	Molluscan	Inferred
–78.75	41.75	Distal slope	?		Ammonites, conodonts	Inferred
–78.25	41.75	Distal slope	Some		Naples fauna	Inferred
–77.75	41.75	Distal slope	High in middle, lower on top and bottom		Middle-bivalves & plants, other bivalves and gastropods	Inferred
–77.25	41.75	Outer shelf			***Rhipidomella***	Krajewski and Williams, 1971; Sutton et al., 1970; Sutton and McGhee, 1985
–76.75	41.75	Outer shelf			***Rhipidomella***	Krajewski and Williams, 1971; Sutton et al., 1970; Sutton and McGhee, 1985
–76.25	41.75	Inner shelf	Tracks, trails, burrows		***Cypricardella***	Krajewski and Williams, 1971; Sutton et al., 1970; Sutton and McGhee, 1985
–75.75	41.75	Inner shelf	Tracks, trails, burrows		***Cypricardella***	Krajewski and Williams, 1971; Sutton et al., 1970; Sutton and McGhee, 1985

–75.25	41.75	Tidal flat	Krajewski and Williams, 1971; Sutton et al., 1970; Woodrow, 1985
–74.75	41.75	Alluvial plain	Krajewski and Williams, 1971; Sutton et al., 1970; Woodrow, 1985
–74.25	41.75	Alluvial plain	Krajewski and Williams, 1971; Sutton et al., 1970; Woodrow, 1985
–80.25	41.25		
–79.75	41.25		
–79.25	41.25		
–78.75	41.25		
–78.25	41.25		
–77.75	41.25		
–77.25	41.25		
–76.75	41.25		
–76.25	41.25		
–75.75	41.25		
–75.25	41.25		
–74.75	41.25		
–78.25	40.75		
–77.75	40.75		
–77.25	40.75		
–76.75	40.75		
–76.25	40.75		
–75.75	40.75		
–75.25	40.75		
–78.75	40.25		

Appendix 1.2. (*Continued*)

Longitude	Latitude	Depositional environment	Ichnofacies/ bioturbation	Oxygenation	Biofacies	Reference
–78.25	40.25					
–77.75	40.25					
–77.25	40.25	Shelf, turbidite flows	Low overall, higher in intervals		Crinoids, brachs, bivalves, gast in siltst.	
–76.75	40.25					
–76.25	40.25					
–75.75	40.25					
–78.75	39.75	Turbidite basin		Good		Dennison et al., 1979
–78.25	39.75					
–77.75	39.75					Dennison, 1985
–79.75	39.25					Dennison, 1985
–79.25	39.25	Turbidite basin				Dennison, 1985; Dennison et al., 1979
–78.75	39.25					Dennison, 1985
–78.25	39.25					Dennison, 1985
–77.75	39.25					Dennison, 1985
–79.75	38.75	Turbidite basin				Dennison, 1985; Dennison et al., 1979
–79.25	38.75	Turbidite basin				Dennison, 1985; Dennison et al., 1979

–78.75	38.75	Turbidite basin			Dennison, 1985
–78.25	38.75				Dennison, 1985
–80.25	38.25				Dennison, 1985
–79.75	38.25	Turbidite basin			Dennison, 1985; Dennison et al., 1979
–79.25	38.25				Dennison, 1985; Dennison et al., 1979
–78.75	38.25				Dennison, 1985; Dennison et al., 1979
–80.75	37.75				Dennison, 1985
–80.25	37.75				Dennison, 1985
–79.75	37.75				Dennison, 1985; Lundegard et al., 1985
–79.25	37.75				Dennison, 1985
–81.25	37.25				
–80.75	37.25				Lundegard et al., 1985
–80.25	37.25	Delta front, turbidite slopes	Low, vertical burrows	Good	Lundegard et al., 1985
–79.75	37.25				
–81.75	36.75				Lundegard et al., 1985

Appendix 1.3. Raw environmental base data for the *linguiformis* Zone.

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style/ thickness	Substrate type	Water depth
–78.75	42.75	Hanover Fm; 10% calc., grey sh 75%, siltst 15%, few sst	73	13	4	10	Distal turbidites, concretions	Thin 90% to moderate 10%	Muddy to silty	Below SWB
–78.25	42.75	Wiscoy Fm & Hanover; grey sh 30%, silst 60%, sst 5%, lst 5%	30	60	5	5	Turbidites (more proximal), calc. concretions	Thin 50% to moderate 50%	Mainly silty	Near to above SWB
–77.75	42.75	Wiscoy Fm; calc silst 20%, fine sst 60%, gray shale 20%, thin lst 5%	25	60	20	5	No HCS	Silst = massive; moderate 80% to thick 20%	Silty to sandy	Above SWB to near or above FWWB
–77.25	42.75	Wiscoy; grey to green, sst 52%; mudst 24%, sh 14%, siltst 4%	24	28	52	0	x-beds, current ripples	Moderate	Muddy and sandy	Above SWB to below FWWB
–76.75	42.75	Wiscoy; sst 43%; mudst 18%, sh 51%, siltst3%	69	3	43	0	Current ripples	Moderate	Muddy and sandy	Above SWB to below FWWB
–76.25	42.75	Manfield Sh and sst; 40% sh, 60% sst	40	0	60	0	x-bedding, parting lineation, oscillation ripples, load casts	Thin to thick	Muddy and sandy	Above FWWB to subtidal
–75.75	42.75	Slide Mountain; Catskill Facies, sst, redbeds	15	10	75	0	Thick x-beds, shallow channels	Thick	Sandy	Subaerial to fluvial

–75.25	42.75	Slide Mountain; Catskill Facies, sst, redbeds	10	10	80	0	Thick x-beds, shallow channels	Thick	Sandy	Subaerial to fluvial
–74.75	42.75	Slide Mountain; Catskill Facies, sst, redbeds	5	5	90	0	Thick x-beds, shallow channels	Thick	Sandy	Subaerial to fluvial
–74.25	42.75	Slide Mountain; Catskill Facies, sst, redbeds	3	2	95	0	Thick x-beds, shallow channels	Thick	Sandy	Subaerial to fluvial
–73.75	42.75	eroded								
–80.25	42.25	Hanover Sh; grey sh w/ dk grey sh and silst and lst	85	7	0	8	Calcareous nodules	Thin	Muddy	Below SWB
–79.75	42.25	Hanover Sh; grey sh w/ dk grey sh and silst and lst	85	7	0	8	Calcareous nodules	Thin	Muddy	Below SWB
–79.25	42.25	Hanover Sh; grey sh w/ dk grey sh and silst and lst	85	7	0	8	Calcareous nodules	Thin	Muddy	Below SWB
–78.75	42.25	Hanover Sh; grey sh w/ dk grey sh and silst and lst	73	13	4	10	Distal turbidities, concretions	Thin (90%), moderate (10%)	Muddy	Below SWB
–78.25	42.25	Hanover (type section); med gray to med green-gr calc sh and mudrock	70	10	5	15	lst concretions	Thin 95% to moderate 5%	Muddy	Below SWB to above SWB
–77.75	42.25	Wiscoy and Hanover, shale, siltst, sandst	40	35	25	0	Flute casts, cuspidate ripples, turbidite deposits	Thin to moderate	Muddy to silty	Below SWB to near FWWB

Appendix 1.3. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style/ thickness	Substrate type	Water depth
–77.25	42.25	Wiscoy; med-dk gray and dk green-gray silst and fine sst	20	40	40	0	HCS, bed rolls	Moderate	Silty to sandy	Above SWB to below FWWB
–76.75	42.25	Wiscoy	40	5	55	0	Groove and flute casts	Moderate	Muddy to sandy	Above SWB to below FWWB
–76.25	42.25	Manfield Sh and sst; 40% sh, 60% sst	40	0	60	0	x-bedding, parting lineat-ion, oscillation ri-pples, load casts	Thin to thick	Muddy and sandy	Above FWWB to subtidal
–75.75	42.25	Slide Mountain; Catskill Facies, sst, redbeds	15	10	75	0	Thick x-beds, shallow channels	Thick	Sandy	Subaerial to fluvial
–75.25	42.25	eroded								
–74.75	42.25	eroded								
–74.25	42.25	eroded								
–73.75	42.25	eroded								
–80.25	41.75	Hanover Sh; grey sh w/ dk grey sh and silst and lst	85	7	0	8	Calcareous nodules	Thin	Muddy	Below SWB
–79.75	41.75	Hanover Sh; grey sh w/ dk grey sh and silst and lst	85	7	0	8	Calcareous nodules	Thin	Muddy	Below SWB
–79.25	41.75	Hanover Sh; grey sh w/ dk grey sh and silst and lst	85	7	0	8	Calcareous nodules	Thin	Muddy	Below SWB

–78.75	41.75	Hanover Sh; grey sh w/ dk grey sh and silst and lst	73	13	4	10	Distal turbidites, concretions	Thin (90%), moderate (10%)	Muddy	Below SWB
–78.25	41.75	Hanover-Wiscoy; sst 15%; mudst 18%; sh 59%, silst 8%	77	8	15	0		Thin to moderate	Muddy	Above SWB and below FWWB
–77.75	41.75	Hanover-Wiscoy; sst 15%; mudst 18%; sh 59%, silst 8%	77	8	15	0		Thin to moderate	Muddy	Above SWB and below FWWB
–77.25	41.75	Wiscoy; sst 52%; mudst 24%, sh 14%, siltst 4%	38	4	52	0	Current ripples	Moderate	Muddy and sandy	Above SWB to below FWWB
–76.75	41.75	Wiscoy; sst 43%; mudst 18%, sh 51%, siltst3%	69	3	43	0	Current ripples	Moderate	Muddy and sandy	Above SWB to below FWWB
–76.25	41.75	Manfield Sh and sst; 40% sh, 60% sst	40	0	60	0	x-bedding, parting lineation, oscillation ripp-les, load casts	Thin to thick	Muddy and sandy	Above FWWB to subaerial
–75.75	41.75	Slide Mountain, red siltstone 40, sst 60%	5	20	75	0	Trough cross beds, ripples	Thick	Sandy	Above FWWB to subaerial
–75.25	41.75	Eroded								
–74.75	41.75	Eroded								
–74.25	41.75	Eroded								
–80.25	41.25	Eroded								
–79.75	41.25	Eroded								
–79.25	41.25	Eroded								
–78.75	41.25	Eroded								
–78.25	41.25	Eroded								
–77.75	41.25	Eroded								
–77.25	41.25									
–76.75	41.25									

Appendix 1.3. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style/ thickness	Substrate type	Water depth
–76.25	41.25	Trimmers Rock Fm, silty sh, sst, siltst, gray, olive-green, brown	45	40	13	2	x-beds, laminated, load structures	Thin	Silty	Below SWB
–75.75	41.25									
–75.25	41.25	Trimmers Rock, type I, coarse sst to fine; lt to dk gray	15	82	3	0	Load casts, eroded bases	Thin to moderate	Silty	Below SWB
–74.75	41.25	Trimmers Rock, type I, coarse sst to fine; mod to light gray	8	90	2	0	Load casts, few x-beds, planar, graded beds to massive	Thin to moderate	Silty	Below SWB
–78.25	40.75	Trimmers Rock, Type I, dk. Brown, red, lt. Grey silty shale facies	30	45	25	2	x-beds, load casts, pillows, HCS	Thin	Silty to sandy	Within SWB
–77.75	40.75	Trimmers Rock, silty sh and sst	35	50	15	0	x-beds, flaser bedding, wavy beds, HCS	Thin to thick	Silty	Within SWB
–77.25	40.75	Trimmers Rock Fm, Type I (80%), type II (20%), grey, olive, red, sst and mudst	39	51	10	0	Cross beds, load casts, some is	Thin to moderate	Muddy and sandy	Below SWB

–76.75	40.75	Trimmers Rock, Type I and II, green-olive	36	50	14	0	x-beds, load casts, scour bases	Thin	Muddy to silty	Below SWB
–76.25	40.75	Trimmers Rk/Catskill, Type I sst and sh, lt. Gray, olive, & lt. Brown	15	79	5	1	Load structures, laminated	Thin	Muddy to silty	Below SWB
–75.75	40.75	Trimmers Rock, silty sh and sst	10	82	8	0	Fining upward	Thin	Silty	Below SWB
–75.25	40.75	Trimmer Rock, silty and silty sh, few sst	8	82	10	0	Bouma sequences, load structures, etc.	Thin to moderate	Silty	Below SWB
–78.75	40.25	Trimmers Rock, siltst to shale and sst	25	20	55	0		Thin	Silty to sandy	Below SWB
–78.25	40.25	Trimmers Rock, Type I, green/red/ lt.gray shale and sst	25	20	55	0	x-beds, loads	Thin	Sandy and muddy	Below SWB
–77.75	40.25									
–77.25	40.25	Trimmers Rock Fm., dk to lt olive, brn, red,siltst to silty sh, top= green shale	60	30	10	0	Load casts, graded beds, flute casts	Thin to moderate	Muddy	Between SWB and FWWB
–76.75	40.25	Trimmer Rock Fm, sst to shale, red, olive, lt brown, gray	70	20	1	0	Load casts, snowballs	Thin to moderate	Muddy	Below SWB
–76.25	40.25	Trimmers Rock Fm, shales to type I sst	39	56	5	0	x-beds, load casts, eroded base, laminated beds	Thin to moderate	Muddy to silty	Below SWB

Appendix 1.3. (*Continued*)

Longitude	Latitude	Grain size/rock type	% Mud	% Silt	% Sand	% ls	Sedimentary structures	Bedding style/ thickness	Substrate type	Water depth
–75.75	40.25									
–78.75	39.75	Foreknobs Fm: Pound sst./Trimmer Rock, siltst-sh	80	18	2	0	HCS	Thin	Muddy to silty	Within SWB
–78.25	39.75	Trimmers Rock, lt gray, brown, green sh and sst, Types I and II	80	10	10	0	Load casts, x-beds	Thin	Muddy	Within SWB
–77.75	39.75									
–79.75	39.25									
–79.25	39.25	Foreknobs Fm: Pound sst.; yellow-gray sst	5	25	70	0	Cross beds	Thick	Sandy	Above SWB to intertidal zone
–78.75	39.25	Foreknobs Fm: Pound sst.; yellow-gray sst					Cross beds	Thick	Sandy	Above SWB to intertidal zone
–78.25	39.25	Foreknobs Fm: Pound sst.; yellow-gray sst					Cross beds	Thick	Sandy	Above SWB to intertidal zone
–77.75	39.25	exposed								
–79.75	38.75	Chemung								

–79.25	38.75	Foreknobs Fm: Pound sst.; fine to med yellow-gray sst	Cross beds	Thick	Sandy	Above SWB to intertidal zone
–78.75	38.75	exposed				
–78.25	38.75	exposed				
–80.25	38.25	Brallier				
–79.75	38.25	Foreknobs Fm: Pound sst.; yellow-gray sst	Cross beds	Thick	Sandy	Above SWB to intertidal zone
–79.25	38.25	Foreknobs Fm: Pound sst.; yellow-gray sst	Cross beds	Thick	Sandy	Above SWB to intertidal zone
–78.75	38.25	exposed				
–80.75	37.75	"Portage" gray shale				
–80.25	37.75	Brallier silst				
–79.75	37.75	Chemung				
–79.25	37.75	Catstill				
–81.25	37.25	"Portage" gray shale				
–80.75	37.25	"Portage" gray shale				
–80.25	37.25	Brallier				
–79.75	37.25	Chemung				

Appendix 1.3. Raw environmental base data for the *linguiformis* Zone.

Longitude	Latitude	Depositional environment	Ichnofacies/ bioturbation	Oxygenation	Biofacies	Reference
–78.75	42.75	Proximal basin	Gutter casts, escape burrows		Gast, carb. plants, crinoids, pterioids, ammonites, cephalopods	Jacobi and Smith, 1999; Over, 1997; Sutton and McGhee, 1985; deWitt, 1960; Smith and Jacobi, 2000; Pepper and deWitt, 1950
–78.25	42.75	Shelf to lower shoreface	*Skolithos* to offshore		*Ambocoelia, Cariniferella*	Jacobi and Smith, 1999; Over, 1997 Sutton and McGhee, 1985
–77.75	42.75	Lower shoreface to lagoon	*Skolithos; Arenicolites/ Teichichnus*		Fossils scarce, *Ambocoelia, Cariniferella*	Jacobi and Smith, 1999; Over, 1997; Sutton and McGhee, 1985
–77.25	42.75	Middle shelf			*Tylothyris-Schizophoria*	McGhee and Sutton, 1981
–76.75	42.75	Inner shelf			*Cyrtospirifer-Douvillina*	McGhee and Sutton, 1981
–76.25	42.75	Nearshore marine, estuary, lagoon, distributary mouth bar	Tracks and trails		*Cyrtospirifer-Douvillina*	inferred
–75.75	42.75	Alluvial fans	Root traces	Subaerial		Woodrow, 1985
–75.25	42.75	Alluvial fans	Root traces	Subaerial		Woodrow, 1985
–74.75	42.75	Alluvial fans	Root traces	Subaerial		Woodrow, 1985
–74.25	42.75	Alluvial fans	Root traces	Subaerial		Woodrow, 1985
–73.75	42.75					
–80.25	42.25	Proximal basin	Low	Low	Conodonts and ammonites	inferred
–79.75	42.25	Proximal basin	Low	Low	Conodonts and ammonites	inferred
–79.25	42.25	Proximal basin	Low	Low	Conodonts and ammonites	Jacobi and Smith, 1999; Metzger et al., 1974; Tesmer, 1974; Leighton, 2000; McGhee and Sutton, 1981

–78.75	42.25	Shelf to lower shelf	*Skolithos* to offshore		*Ambocoelia, Cariniferella*	Jacobi and Smith, 1999; Metzger et al., 1974; Tesmer, 1974; Leighton, 2000; McGhee and Sutton, 1981
–78.25	42.25	Shelf, slope, and basin	*Cruziana*		Ammonites, *Ambocoelia, Cariniferella*	Smith and Jacobi, 2000; Jacobi and Smith, 1999; Tesmer, 1974; Leighton, 2000; McGhee and Sutton, 1981
–77.75	42.25	Distal slope, open shelf, inner platform to lower shoreface	*Cruziana/Skolithos*		Brachs, gast, bivalves, *Ambocoelia, Cariniferella*	deWitt, 1960; McGhee and Sutton, 1981; Leighton, 2000; Jacobi and Smith, 1999; Metzger et al., 1974
–77.25	42.25	Nearshore to inner platform; open shelf, prodelta, inner & outer platform	*Zoophycus/Skolithos*		Rugose corals, *Tylothyris-Schizophoria*	deWitt, 1960; McGhee and Sutton, 1981; Leighton, 2000; Jacobi and Smith, 1999; Metzger et al., 1974
–76.75	42.25	Middle shelf			*Cyrtospirifer-Douvillina*, *Tylothyris-Schizophoria*	Woodrow, 1985
–76.25	42.25	Nearshore marine, estuary, lagoon, distributary mouth bar	Tracks and trails		*Cyrtospirifer-Douvillina*	
–75.75	42.25	Alluvial fans	Root traces	Subaerial		Krajecski and Williams, 1971; Woodrow, 1985

Appendix 1.3. (*Continued*)

Longitude	Latitude	Depositional environment	Ichnofacies/ bioturbation	Oxygenation	Biofacies	Reference
–75.25	42.25					Krajewski and Williams, 1971
–74.75	42.25					Krajewski and Williams, 1971
–74.25	42.25					Krajewski and Williams, 1971
–73.75	42.25					Krajewski and Williams, 1971
–80.25	41.75	Proximal basin	Low	Low	Conodonts and ammonites	inferred
–79.75	41.75	Proximal basin	Low	Low	Conodonts and ammonites	inferred
–79.25	41.75	Proximal basin	Low	Low	Conodonts and ammonites	inferred
–78.75	41.75	Shelf to lower shelf	*Skolithos* to offshore		*Ambocoelia, Cariniferella*	inferred
–78.25	41.75	Outer shelf	*Cruziana*		*Ambocoelia-Cariniferella*	McGhee and Sutton, 1981
–77.75	41.75	Outer shelf	*Cruziana*		*Ambocoelia-Cariniferella*	McGhee and Sutton, 1981
–77.25	41.75	Middle shelf			*Tylothyris-Schizophoria*	McGhee and Sutton, 1981
–76.75	41.75	Inner shelf			*Cyrtospirifer-Douvillina*	McGhee and Sutton, 1981
–76.25	41.75	Inner shelf, nearshore marine, estuary, lagoon, distributary mouth bar	Tracks and trails		*Cyrtospirifer-Douvillina*	McGhee and Sutton, 1981
–75.75	41.75	Beach, tidal flat	Some burrows in red siltst		None	Krajewski and Williams, 1971; Woodrow, 1985
–75.25	41.75					Krajewski and Williams, 1971
–74.75	41.75					Krajewski and Williams, 1971
–74.25	41.75					Krajewski and Williams, 1971
–80.25	41.25					Krajewski and Williams, 1971

–79.75	41.25					Krajewski and Williams, 1971
–79.25	41.25					
–78.75	41.25					
–78.25	41.25					
–77.75	41.25					
–77.25	41.25					
–76.75	41.25					
–76.25	41.25	Distal slope to proximal basin floor	Some		Isolated	Frakes, 1964
–75.75	41.25					Schultz, 1974
–75.25	41.25	Shelf slope	Common	Good	Isolated fossils	Frakes, 1964; Schultz, 1974
–74.75	41.25	Turbidites stacked, shelf slope	Common	Good	Isolated fossils	Frakes, 1964; Schultz, 1974
–78.25	40.75	Shallow marine, prodelta, subtidal		Good		Frakes, 1964; Rahmanian, 1979; Williams and Slingerland, 1985
–77.75	40.75	Shallow marine, subtidal, shelf	Common			Rahmanian, 1979; Williams and Slingerland, 1985
–77.25	40.75	Shelf slope to basin floor	Common		Sparse fossils	Frakes, 1964
–76.75	40.75	Shelf slope to basin floor	Common		Sparse fossils	Frakes, 1964
–76.25	40.75	Basinal or distal slope	Common		Sparse fossils	Frakes, 1964; Schultz, 1974
–75.75	40.75	Slope	Common		In lenses	Frakes, 1964; Schultz, 1974
–75.25	40.75	Slope				Frakes, 1964; Schultz, 1974
–78.75	40.25	Slope to basin				Rahmanian, 1979
–78.25	40.25	Distal slope and basinal floor				Frakes, 1964; Rahmanian, 1979

Appendix 1.3. (*Continued*)

Longitude	Latitude	Depositional environment	Ichnofacies/ bioturbation	Oxygenation	Biofacies	Reference
–77.75	40.25					
–77.25	40.25	Shelf, turbidite flows	Overall low, higher in intervals	High	Crinoid columnals, brachs & bivalves, gastropods	Frakes, 1964
–76.75	40.25	Platform slope	Common		Sparse fossils	Frakes, 1964
–76.25	40.25	Platform slope	Common		Sparse fossils	Frakes, 1964
–75.75	40.25					
–78.75	39.75	Shallow marine to beach, prodelta, slope				Rahmanian, 1979, Dennison, 1979
–78.25	39.75	Shallow marine to distal platfrom				Frakes, 1964; Rahmanian, 1979
–77.75	39.75					
–79.75	39.25					
–79.25	39.25	Nearshore bar sands	*Skolithos*	High	*Cyrtospirifer-Camarotoechia*; crinoids, brach, plant stems	McGhee, 1976; McGhee and Sutton, 1981; Dennison et al., 1979
–78.75	39.25	Nearshore bar sands	*Skolithos*	High	*Cyrtospirifer-Camarotoechia*	McGhee, 1976; McGhee and Sutton, 1981; Dennison, et al., 1979
–78.25	39.25	Nearshore bar sands	*Skolithos*	High	*Cyrtospirifer-Camarotoechia*	McGhee, 1976; McGhee and Sutton, 1981
–77.75	39.25					
–79.75	38.75					Dennison, 1985

–79.25	38.75	Nearshore bar sands	*Skolithos*	High	*Cyrtospirifer-Camarotoechia, Schizophoria, Atrypa*	McGhee, 1976; McGhee and Sutton, 1981; Dennison, et al., 1979; Dennison, 1985
–78.75	38.75					Dennison, 1985
–78.25	38.75					Dennison, 1985
–80.25	38.25					Dennison, 1985
–79.75	38.25	Nearshore bar sands	*Skolithos*	High	*Cyrtospirifer-Camarotoechia*	McGhee, 1976; McGhee and Sutton, 1981; Dennison, et al., 1979; Dennison, 1985
–79.25	38.25	Nearshore bar sands	*Skolithos*	High	*Cyrtospirifer-Camarotoechia*	McGhee, 1976; McGhee and Sutton, 1981; Dennison, 1985
–78.75	38.25					Dennison, 1985
–80.75	37.75					Dennison, 1985
–80.25	37.75					Dennison, 1985
–79.75	37.75					Dennison, 1985
–79.25	37.75					Dennison, 1985
–81.25	37.25					Dennison, 1985
–80.75	37.25					Dennison, 1985
–80.25	37.25					Dennison, 1985
–79.75	37.25					Dennison, 1985

Appendix 2. Species occurrence data used in the GARP modeling analysis.

Appendix 2.1 Occurrence data points of species extant during the Lower *varcus* Zone.

Species	Longitude	Latitude
Athyris cora	–76.42	42.71
Athyris cora	–76.11	42.80
Athyris cora	–75.92	42.82
Athyris cora	–75.53	42.82
Athyris cora	–78.78	42.65
Athyris cora	–75.91	42.88
Athyris spiriferiodes	–77.30	42.88
Athyris spiriferiodes	–77.90	42.77
Athyris spiriferiodes	–76.53	42.55
Athyris spiriferiodes	–77.90	42.77
Athyris spiriferiodes	–77.44	42.23
Athyris spiriferiodes	–78.88	42.75
Athyris spiriferiodes	–78.67	42.77
Athyris spiriferiodes	–78.37	42.88
Athyris spiriferiodes	–78.52	42.85
Athyris spiriferiodes	–78.23	42.90
Athyris spiriferiodes	–76.58	42.97
Athyris spiriferiodes	–78.20	42.15
Athyris spiriferiodes	–74.77	42.60
Athyris spiriferiodes	–75.53	42.82
Athyris spiriferiodes	–77.30	42.88
Athyris spiriferiodes	–76.90	40.34
Cariniferella carinata	–77.30	42.88
Cariniferella carinata	–78.37	42.88
Cariniferella carinata	–74.86	42.38
Cariniferella carinata	–75.88	42.77
Cariniferella carinata	–76.53	42.55
Cariniferella carinata	–77.90	42.77
Cariniferella carinata	–77.28	42.83
Cariniferella carinata	–76.27	42.17
Cariniferella carinata	–75.74	42.71
Cariniferella carinata	–78.88	42.75
Cariniferella carinata	–83.73	42.77
Cariniferella carinata	–78.77	42.88
Cariniferella carinata	–78.35	42.90
Cariniferella carinata	–78.23	42.90
Cariniferella carinata	–78.10	42.92
Cariniferella carinata	–78.28	42.92
Cariniferella carinata	–76.55	42.53
Cariniferella carinata	–75.18	42.62
Cariniferella carinata	–78.83	42.70
Cariniferella carinata	–75.53	42.72
Cariniferella carinata	–77.30	42.88

Appendix 2.1 (*Continued*)

Species	Longitude	Latitude
Cypricardella bellistriata	–75.18	42.62
Cypricardella bellistriata	–78.67	42.77
Cypricardella bellistriata	–76.74	42.95
Cypricardella bellistriata	–76.95	40.47
Leptodesma (Leiopteria) spinerigum	–75.25	42.81
Leptodesma (Leiopteria) spinerigum	–78.73	39.67
Leptodesma (Leiopteria) spinerigum	–75.92	42.82
Leptodesma (Leiopteria) spinerigum	–75.52	42.53
Leptodesma (Leiopteria) spinerigum	–75.62	42.82
Mucrospirifer mucronatus	–78.10	42.92
Mucrospirifer mucronatus	–74.86	42.38
Mucrospirifer mucronatus	–77.90	42.77
Mucrospirifer mucronatus	–77.28	42.83
Mucrospirifer mucronatus	–78.77	42.88
Mucrospirifer mucronatus	–78.23	42.90
Mucrospirifer mucronatus	–78.10	42.92
Mucrospirifer mucronatus	–78.10	42.92
Mucrospirifer mucronatus	–78.97	42.72
Palaeoneilo constricta	–78.76	39.61
Palaeoneilo constricta	–78.54	39.52
Palaeoneilo constricta	–78.73	39.67
Palaeoneilo constricta	–75.50	42.64
Palaeoneilo constricta	–75.57	42.69
Palaeoneilo constricta	–77.02	42.76
Palaeoneilo constricta	–78.78	42.65
Palaeoneilo constricta	–74.31	42.67
Palaeoneilo constricta	–76.42	42.71
Palaeoneilo constricta	–75.62	42.82
Palaeoneilo constricta	–76.74	42.95
Palaeoneilo constricta	–78.44	40.39
Palaeoneilo constricta	–76.95	40.47
Paracyclas lirata	–74.77	42.60
Paracyclas lirata	–78.09	39.68
Paracyclas lirata	–74.86	42.38
Paracyclas lirata	–75.18	42.48
Paracyclas lirata	–75.09	42.53
Paracyclas lirata	–74.86	42.38
Paracyclas lirata	–75.53	42.82
Paracyclas lirata	–78.04	39.86
Paracyclas lirata	–76.95	40.47
Spinatrypa spinosa	–74.77	42.60
Spinatrypa spinosa	–77.77	42.73
Spinatrypa spinosa	–78.67	42.77
Spinatrypa spinosa	–76.53	42.01
Spinatrypa spinosa	–75.09	42.53

Appendix 2.1 (*Continued*)

Species	Longitude	Latitude
Spinatrypa spinosa	–76.42	42.71
Spinatrypa spinosa	–76.11	42.80
Spinatrypa spinosa	–76.05	42.83
Spinatrypa spinosa	–76.53	42.55
Spinatrypa spinosa	–76.42	42.71
Spinatrypa spinosa	–78.97	42.72
Spinatrypa spinosa	–77.90	42.77
Spinatrypa spinosa	–77.90	42.77
Spinatrypa spinosa	–78.81	42.77
Spinatrypa spinosa	–75.43	42.80
Spinatrypa spinosa	–78.18	43.00
Spinocyrtia granulosa	–78.78	42.65
Spinocyrtia granulosa	–78.97	42.72
Spinocyrtia granulosa	–77.03	42.75
Spinocyrtia granulosa	–78.67	42.77
Spinocyrtia granulosa	–78.98	42.81
Spinocyrtia granulosa	–78.37	42.88
Spinocyrtia granulosa	–78.78	42.65

Appendix 2.2 Occurrence data points of species extant during the *punctata* Zone.

Species	Longitude	Latitude
Cupularostrum exima	–76.72	42.03
Cupularostrum exima	–76.72	42.03
Cupularostrum exima	–76.42	42.22
Cupularostrum exima	–76.42	42.22
Cupularostrum exima	–75.87	42.33
Cupularostrum exima	–76.30	42.38
Eoschizodus chemungensis	–76.57	42.02
Eoschizodus chemungensis	–77.98	42.17
Eoschizodus chemungensis	–75.54	42.31
Eoschizodus chemungensis	–75.54	42.31
Eoschizodus chemungensis	–75.31	42.33
Goniophora chemungensis	–76.73	42.02
Goniophora chemungensis	–76.57	42.02
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–76.72	42.03
Goniophora chemungensis	–75.87	42.33
Goniophora chemungensis	–76.05	42.79
Grammysia elliptica	–76.73	42.03
Grammysia elliptica	–76.72	42.03
Grammysia elliptica	–76.72	42.03
Grammysia elliptica	–76.72	42.03
Grammysia elliptica	–76.72	42.03
Grammysia elliptica	–76.72	42.03
Grammysia elliptica	–78.05	42.27
Grammysia elliptica	–75.57	42.30
Grammysia elliptica	–75.54	42.31
Grammysia elliptica	–75.87	42.33
Grammysia elliptica	–75.50	42.36
Leptodesma (Leioptera) nitida	–76.57	42.02
Leptodesma (Leioptera) nitida	–76.57	42.02
Leptodesma (Leioptera) nitida	–76.72	42.03
Leptodesma (Leioptera) nitida	–76.72	42.03
Leptodesma (Leioptera) nitida	–76.72	42.03
Leptodesma (Leioptera) nitida	–76.72	42.03
Leptodesma (Leioptera) nitida	–76.72	42.03
Leptodesma (Leioptera) nitida	–77.98	42.17
Leptodesma (Leioptera) nitida	–76.42	42.22
Palaeoneilo constricta	–76.57	42.02

Appendix 2.2 (*Continued*)

Species	Longitude	Latitude
Palaeoneilo constricta	–75.87	42.33
Palaeoneilo constricta	–76.40	42.37
Palaeoneilo constricta	–76.03	42.44
Palaeoneilo constricta	–76.37	42.59
Praewaagenoconcha speciosa	–76.57	42.02
Praewaagenoconcha speciosa	–76.72	42.03
Praewaagenoconcha speciosa	–76.72	42.03
Praewaagenoconcha speciosa	–78.03	42.22
Praewaagenoconcha speciosa	–75.57	42.30
Praewaagenoconcha speciosa	–75.87	42.33
Praewaagenoconcha speciosa	–75.87	42.33
Praewaagenoconcha speciosa	–75.87	42.33
Ptychopteria chemungensis	–76.57	42.02
Ptychopteria chemungensis	–76.57	42.02
Ptychopteria chemungensis	–76.57	42.02
Ptychopteria chemungensis	–76.64	42.03
Ptychopteria chemungensis	–76.72	42.03
Ptychopteria chemungensis	–75.87	42.33
Tylothyris mesacostalis	–76.73	42.03
Tylothyris mesacostalis	–76.72	42.03
Tylothyris mesacostalis	–75.54	42.31
Tylothyris mesacostalis	–75.87	42.33
Tylothyris mesacostalis	–75.87	42.33
Tylothyris mesacostalis	–76.36	42.35
Tylothyris mesacostalis	–76.18	42.60

Appendix 2.3 Occurrence data points of species extant during the *linguiformis* Zone.

Species	Longitude	Latitude
Ambocoelia gregaria	–77.50	41.88
Ambocoelia gregaria	–78.19	41.95
Ambocoelia gregaria	–76.92	42.07
Ambocoelia gregaria	–75.82	42.08
Ambocoelia gregaria	–75.93	42.17
Ambocoelia gregaria	–79.11	42.22
Ambocoelia gregaria	–76.61	42.22
Ambocoelia gregaria	–77.79	42.25
Ambocoelia gregaria	–79.10	42.29
Ambocoelia umbonata	–79.16	41.85
Ambocoelia umbonata	–76.27	42.17
Ambocoelia umbonata	–77.67	42.33
Ambocoelia umbonata	–77.55	42.27
Athyris angelica	–80.35	41.73
Athyris angelica	–77.08	41.81
Athyris angelica	–79.16	41.85
Athyris angelica	–78.07	42.22
Athyris angelica	–78.28	42.22
Athyris angelica	–77.77	42.27
Athyris angelica	–77.55	42.27
Athyris angelica	–78.18	42.30
Athyris angelica	–78.13	42.33
Athyris angelica	–77.67	42.33
Athyris angelica	–78.11	42.34
Cariniferella carinata	–77.13	41.91
Cariniferella carinata	–76.62	42.01
Cariniferella carinata	–76.73	42.02
Cariniferella carinata	–76.82	42.05
Cariniferella carinata	–76.81	42.09
Cariniferella carinata	–77.09	42.16
Cariniferella carinata	–76.50	42.25
Cariniferella carinata	–76.36	42.35
Cariniferella tioga	–76.71	41.72
Cariniferella tioga	–76.53	42.01
Cariniferella tioga	–76.53	42.01
Cariniferella tioga	–76.73	42.02
Cariniferella tioga	–77.04	42.15
Cariniferella tioga	–76.92	42.22
Cariniferella tioga	–76.61	42.22
Cariniferella tioga	–76.67	42.23
Cariniferella tioga	–76.50	42.25
Cariniferella tioga	–76.48	42.35
Cupularostrum contracta	–77.08	41.81
Cupularostrum contracta	–77.08	41.81

Appendix 2.3 (*Continued*)

Species	Longitude	Latitude
Cupularostrum contracta	–77.50	41.88
Cupularostrum contracta	–76.82	42.05
Cupularostrum contracta	–79.48	42.08
Cupularostrum contracta	–79.48	42.08
Cupularostrum contracta	–76.81	42.09
Cupularostrum contracta	–78.40	42.23
Cupularostrum contracta	–77.79	42.25
Cupularostrum contracta	–79.57	42.31
Cupularostrum contracta	–77.67	42.33
Cupularostrum exima	–76.71	41.68
Cupularostrum exima	–80.06	41.80
Cupularostrum exima	–79.20	42.02
Cupularostrum exima	–79.10	42.29
Cupularostrum exima	–75.97	42.33
Cyrtospirifer chemungensis	–76.52	41.92
Cyrtospirifer chemungensis	–77.12	42.02
Cyrtospirifer chemungensis	–77.12	42.02
Cyrtospirifer chemungensis	–77.13	42.03
Cyrtospirifer chemungensis	–76.42	42.07
Cyrtospirifer chemungensis	–76.25	42.10
Douvillina cayuta	–76.71	41.68
Douvillina cayuta	–77.08	41.81
Douvillina cayuta	–77.13	41.91
Douvillina cayuta	–77.11	41.96
Douvillina cayuta	–77.13	42.00
Douvillina cayuta	–76.62	42.01
Douvillina cayuta	–76.46	42.01
Douvillina cayuta	–76.37	42.02
Douvillina cayuta	–77.14	42.03
Douvillina cayuta	–76.72	42.03
Douvillina cayuta	–76.87	42.08
Douvillina cayuta	–76.81	42.09
Douvillina cayuta	–76.82	42.17
Douvillina cayuta	–76.61	42.22
Douvillina cayuta	–76.50	42.25
Floweria chemungensis	–79.19	41.83
Floweria chemungensis	–77.12	42.02
Floweria chemungensis	–77.13	42.03
Floweria chemungensis	–76.05	42.17
Floweria chemungensis	–75.93	42.17
Floweria chemungensis	–78.40	42.23
Floweria chemungensis	–77.79	42.25
Floweria parva	–80.33	42.05
Floweria parva	–78.07	42.22
Floweria parva	–78.07	42.22

Appendix 2.3 (*Continued*)

Species	Longitude	Latitude
Floweria parva	–77.55	42.27
Floweria parva	–78.18	42.30
Leptodesma (Leptodesma) spinerigum	–79.41	39.41
Leptodesma (Leptodesma) spinerigum	–78.84	39.63
Leptodesma (Leptodesma) spinerigum	–78.93	39.66
Leptodesma (Leptodesma) spinerigum	–76.71	41.67
Leptodesma (Leptodesma) spinerigum	–77.08	41.81
Leptodesma (Leptodesma) spinerigum	–77.08	41.81
Leptodesma (Leptodesma) spinerigum	–77.13	42.00
Leptodesma (Leptodesma) spinerigum	–76.37	42.02
Leptodesma (Leptodesma) spinerigum	–79.20	42.02
Leptodesma (Leptodesma) spinerigum	–77.14	42.03
Leptodesma (Leptodesma) spinerigum	–76.72	42.03
Leptodesma (Leptodesma) spinerigum	–80.33	42.05
Leptodesma (Leptodesma) spinerigum	–75.82	42.08
Leptodesma (Leptodesma) spinerigum	–77.09	42.16
Nervostrophia nervosa	–76.71	41.67
Nervostrophia nervosa	–76.46	42.01
Nervostrophia nervosa	–76.73	42.02
Nervostrophia nervosa	–76.57	42.02
Nervostrophia nervosa	–76.78	42.03
Nervostrophia nervosa	–76.45	42.04
Nervostrophia nervosa	–76.87	42.08
Nervostrophia nervosa	–76.55	42.20
Nervostrophia nervosa	–76.53	42.32
Praewaagenoconcha speciosa	–80.15	41.64
Praewaagenoconcha speciosa	–77.08	41.81
Praewaagenoconcha speciosa	–77.08	41.81
Praewaagenoconcha speciosa	–77.50	41.88
Praewaagenoconcha speciosa	–77.50	41.88
Praewaagenoconcha speciosa	–77.13	41.91
Praewaagenoconcha speciosa	–79.48	42.07
Praewaagenoconcha speciosa	–76.05	42.17
Praewaagenoconcha speciosa	–78.40	42.23
Praewaagenoconcha speciosa	–77.98	42.25
Praewaagenoconcha speciosa	–77.67	42.33
Praewaagenoconcha speciosa	–76.48	42.35
Productella rectispina	–80.35	41.73
Productella rectispina	–80.06	41.80
Productella rectispina	–77.08	41.81
Productella rectispina	–77.08	41.81
Productella rectispina	–79.16	41.85
Productella rectispina	–76.58	42.02
Productella rectispina	–78.18	42.30
Productella rectispina	–78.18	42.30

Appendix 2.3 (*Continued*)

Species	Longitude	Latitude
Pseudatrypa devoniana	–76.71	41.72
Pseudatrypa devoniana	–80.35	41.73
Pseudatrypa devoniana	–80.06	41.80
Pseudatrypa devoniana	–77.08	41.81
Pseudatrypa devoniana	–77.08	41.81
Pseudatrypa devoniana	–76.57	42.03
Pseudatrypa devoniana	–80.33	42.05
Pseudatrypa devoniana	–78.07	42.22
Pseudatrypa devoniana	–77.77	42.27
Ptychopteria chemungensis	–76.52	41.96
Ptychopteria chemungensis	–76.46	42.01
Ptychopteria chemungensis	–76.53	42.01
Ptychopteria chemungensis	–76.37	42.02
Ptychopteria chemungensis	–76.37	42.02
Ptychopteria chemungensis	–76.40	42.07
Ptychopteria chemungensis	–76.31	42.16
Ptychopteria chemungensis	–76.31	42.16
Ptychopteria chemungensis	–75.53	42.23
Ptychopteria chemungensis	–76.50	42.25
Ptychopteria chemungensis	–76.50	42.25
Schizophoria impressa	–80.35	41.73
Schizophoria impressa	–77.08	41.81
Schizophoria impressa	–77.08	41.81
Schizophoria impressa	–77.14	42.03
Schizophoria impressa	–77.13	42.03
Schizophoria impressa	–76.42	42.07
Schizophoria impressa	–76.49	42.21
Schizophoria impressa	–78.40	42.23
Schizophoria impressa	–77.55	42.27
Schizophoria impressa	–79.72	42.28
Schizophoria impressa	–78.18	42.30
Schizophoria impressa	–75.77	42.33
Schizophoria impressa	–78.11	42.34
Schizophoria impressa	–76.50	42.43
Schizophoria impressa	–76.50	42.44
Spinatrypa spinosa	–77.08	41.81
Spinatrypa spinosa	–77.50	41.88
Spinatrypa spinosa	–76.57	42.02
Spinatrypa spinosa	–77.13	42.05
Spinatrypa spinosa	–76.10	42.17
Spinatrypa spinosa	–78.07	42.22
Spinatrypa spinosa	–76.50	42.25
Spinatrypa spinosa	–77.67	42.33
Strophonella hybrida	–77.08	41.81
Strophonella hybrida	–78.07	42.22

Appendix 2.3 (*Continued*)

Species	Longitude	Latitude
Strophonella hybrida	–77.55	42.27
Strophonella hybrida	–78.02	42.28
Strophonella hybrida	–78.18	42.30
Strophonella hybrida	–79.16	41.85
Tylothyris mesacostalis	–76.71	41.72
Tylothyris mesacostalis	–77.30	41.75
Tylothyris mesacostalis	–77.08	41.81
Tylothyris mesacostalis	–77.10	41.84
Tylothyris mesacostalis	–77.50	41.88
Tylothyris mesacostalis	–77.50	41.88
Tylothyris mesacostalis	–77.13	41.91
Tylothyris mesacostalis	–78.19	41.95
Tylothyris mesacostalis	–76.62	42.01
Tylothyris mesacostalis	–76.46	42.01
Tylothyris mesacostalis	–76.53	42.01
Tylothyris mesacostalis	–76.33	42.02
Tylothyris mesacostalis	–76.64	42.03
Tylothyris mesacostalis	–76.61	42.22
Tylothyris mesacostalis	–75.53	42.23
Tylothyris mesacostalis	–78.40	42.23
Tylothyris mesacostalis	–76.50	42.25
Tylothyris mesacostalis	–77.79	42.25
Tylothyris mesacostalis	–78.16	42.31
Tylothyris mesacostalis	–76.48	42.35
Tylothyris mesacostalis	–76.10	42.17

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