ANALYSIS OF GRAPTOLITE BIOTOPE AFFINITY THROUGH THE LATE ORDOVICIAN MASS EXTINCTION

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Abstract

The Late Ordovician Mass Extinction (LOME) was the result of a combination of factors, including changes in sea surface temperature, sea level, and ventilation of the oceans, among others. These factors resulted in restricted habitable areas and changes within the habitats themselves. We can investigate these changes using a Bayesian analysis of graptolite species occurrence data from 47 study sites (mainly paleotropical localities but also mid to high latitude locales, including the North African margin of Gondwana) in an effort to estimate the biotope affinities of 79 graptolite species and the water depths at the study sites. During the *Paraorthograptus pacificus* Biozone, preceding the HICE, the graptolites examined behaved as expected, with the temperate regions containing mostly epipelagic neograptine species, and the tropical diplograptine species inhabiting both shallow and deep localities. The biotope affinities of the surviving graptolites in the succeeding *Metabolograptus extraordinarius* Biozone, however, exhibit a profound shift in the biotope affinities of the surviving graptolites. Eighteen percent were reassigned from epipelagic to mesopelagic biotopes, i.e., to a more restricted depth designation. We suggest that the changing oceanic conditions altered the distribution of the resources that these particular graptolites relied upon. As those resources became more restricted and localized to deeper water sites, epipelagic graptolites that previously occurred in on-shore sites moved to more offshore locations, and possibly to greater depths in the water column, thus behaving as mesopelagic taxa.

Background

- Peak in LOME glacial activity resulted in glacial accumulations on every landmass[6], producing a fall in sea level of ~70-100m[2,3,4].
- The epicontinental seas drained and shelf habitats became restricted[5,7,9].
- The LOME is characterized by the extinction of the low-latitude, tropical Diplograptina species[8] and the immigration of high-latitude, temperate Neograptina[5,7,9].
- The mesopelagic zone, located below the surface mixed layer, was a zone of relatively high productivity and diversity fueled by nutrient upwelling at the shelf margins[1,9].
- The epipelagic species inhabited the overlying surface-mixed layer, where productivity was more dominantly sunlight driven[1,9].
- Changing circulation patterns and ventilation of the ocean were a driving factor in the extinction of mesopelagic taxa[1,9].
- Changing sea level and loss of shelf habitats displaced shallow water, epipelagic species into more offshore locations.

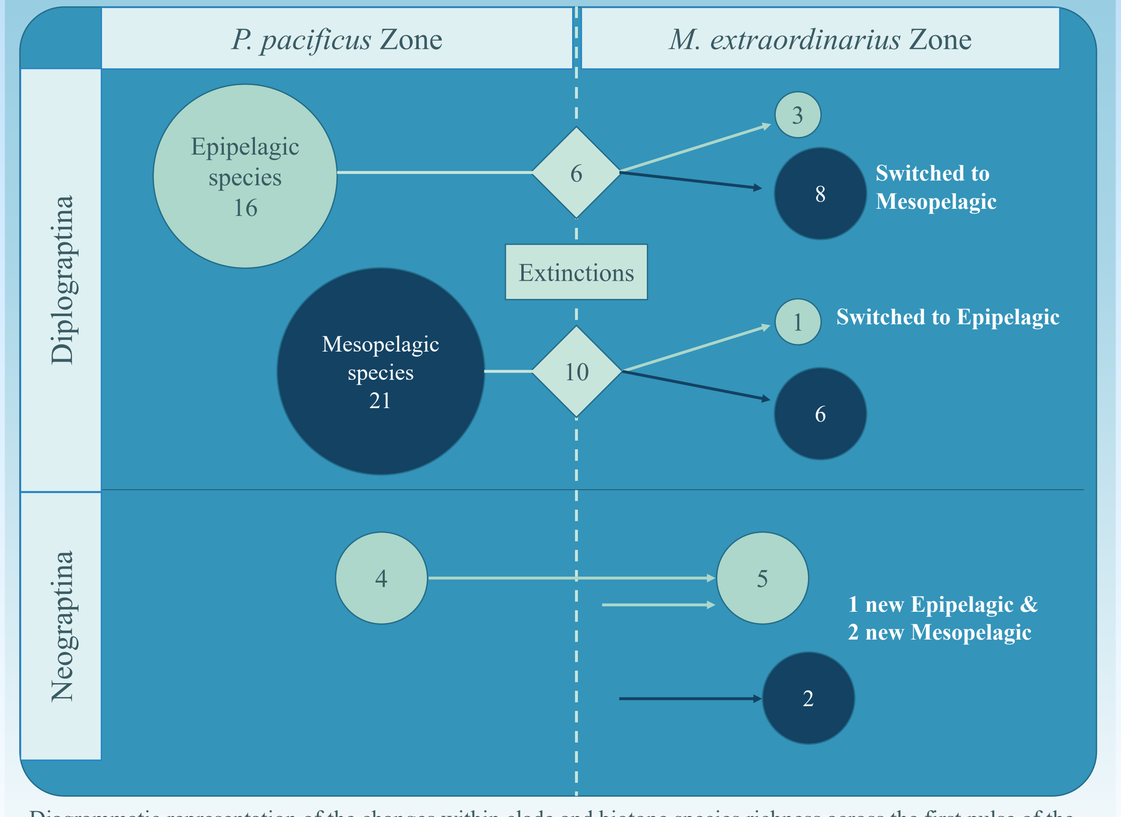
Data & Methods

- The graptolite presence data comes from 47 global geologic sections containing species from the *Paraorthograptus pacificus* and *Metabolograptus extraordinarius* biozones
- The *pacificus* biozone localities consist of 232 horizons and 75 species
- The *extraordinarius* biozone localities contain 59 horizons and 32 species
- Log likelihood functions of probability of observing a species at each depth category (mesopelagic or epipelagic) used to determine Bayesian a priori biotope affinities
- Likelihood function of species being mesopelagic[6]:
  $$L_i(M) = P_i(D|M)^{Ni(D)} \times (1 - P_i(D|M))^{(N(D)-Ni(D))} \times P_e^{Ni(S)} \times (1 - P_e)^{(N(S)-Ni(S))}$$
- Likelihood function of species being epipelagic[6]:
  $$L_i(E) = P_i(E)^{Ni(D)} \times (1 - P_i(E))^{(N(D)-Ni(D))} \times P_i(E)^{Ni(S)} \times (1 - P_i(E))^{(N(S)-Ni(S))}$$
- Explanation of terms in the Table (right)
- MCMC approach applied to determine Bayesian posterior values of species biotope
- Sensitivity analysis conducted by randomizing the species presence data across the possible sections and reconducting analyses 100 times

Results

- From the *P. pacificus* biozone to the *M. extraordinarius* biozone, 48% of mesopelagic species and 30% of epipelagic species have gone extinct
- Compared to the *P. pacificus* biozone, the species within the *M. extraordinarius* biozone are predominately mesopelagic (50% of all taxa compared to 29%)
- Through both biozones, neograptine taxa remained predominately epipelagic
- Thirty-three percent of the Diplograptina that survived into the *M. extraordinarius* biozone changed from epipelagic to mesopelagic
- Sensitivity analysis shows robustness of the model: there is a 0.0-2.0% chance of a species being randomly assigned to the mesopelagic biotope
- Due to the overall deepening conditions, the epipelagic graptolites from the *P. pacificus* biozone likely moved to more offshore locations, appearing to behave as mesopelagic species

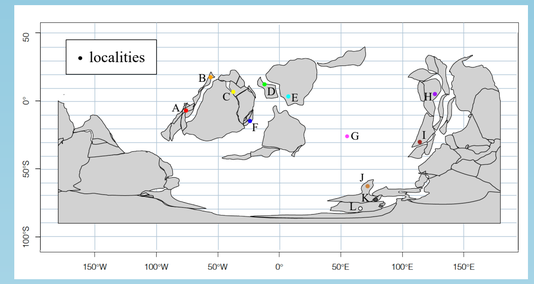
During the Late Ordovician Mass Extinction, the Diplograptine taxa predominately occupy the mesopelagic biotope, with 33% changing from an epipelagic biotope.



Diagrammatic representation of the changes within clade and biotope species richness across the first pulse of the LOME with inferred biotope assignments.

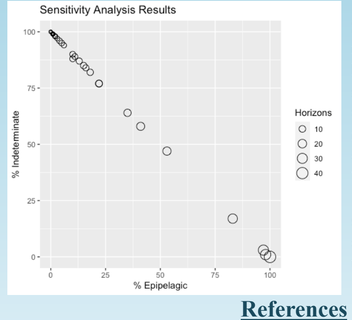
Additional Methods

Terms	Definition
E	epipelagic
M	mesopelagic
N(D)	number of deep horizons where species could be recovered
N(S)	number of shallow horizons where species could be recovered
Ni(D)	number of deep sites where taxon is observed
Ni(S)	number of shallow sites where taxon is observed
Pi(D|E)	probability taxon occurs at deep site if it is epipelagic
Pi(D|M)	probability taxon occurs at deep site if it is mesopelagic
Pi(E)	equal probability of finding epipelagic taxa at shallow & deep sites



Global paleo-reconstruction of all localities. A: 3 sites, B: 3 sites, C: 4 sites, D: 7 sites, E: 6 sites, F: 2 sites, G: 7 sites, H: 6 sites, I: 1 site, J: 1 site, K: 1 site, L: 1 site. Map generated using the chronosphere R package[6].

Additional Results



Sensitivity analysis results, represented as percentage of how often each species was assigned to each biotope. Circle size represents the total number of horizons or occurrences of each species. The mesopelagic biotope is not included in this graph because species were assigned to this category a maximum of 2% of the total analyses.

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