

Late Holocene ostracod faunal assemblages from Freshwater Pond, Barbuda

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Abstract

Enhanced rates of environmental change pose a significant threat to freshwater organisms within the Caribbean. Given the pivotal role that these organisms play in supporting ecosystem function, it has become increasingly necessary to understand how they will respond to future changes. This study provides an in-depth analysis of how ostracod populations from Freshwater Pond in Barbuda have responded to environmental changes in the past. This was done through the use of multiple proxies that were used to infer past changes in lake hydrology and primary productivity. The results indicated that both lake hydrology and primary production varied significantly over the past few hundred years. The ostracod populations also varied quite significantly and the overall assemblage was divided into three distinct biostratigraphic zones (FWP 1 -FWP 3). Based on the correlation between these zones and the observed fluctuations in the proxy records, it is inferred that variations in primary production were the dominant environmental control on the ostracod fauna with lake hydrology playing a secondary role.

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1. Introduction

1.1. Background

The amplified rate and extent of environmental change in recent years have given increased urgency and relevance to understanding how ecosystems will respond in the near future (Willis & MacDonald, 2011). This is particularly necessary given the pivotal role that ecosystem services and functions play in supporting the well-being and quality of life on earth (Guo et al., 2010; Haines-Young & Potschin, 2010). However, projecting these changes is quite difficult given that our present environment is a transient condition that has resulted from an entire spectrum of both natural and anthropogenic factors interacting in space and time. Therefore, garnering a better understanding of how the environment may change in the future, requires a perspective that can only be obtained from a better knowledge of the past. Given that the historical instrumental record is too short to capture the natural long-term variability of the environment, most evidence of past environmental change is obtained from natural archives which have preserved a wealth of information about former conditions (Swetnam et al., 1999). From these archives, it is possible to reconstruct the environmental conditions of particular intervals in the past with great clarity and in considerable detail. Through the interpretation of these archives, we are better able to understand how the complex coupled systems of the physical environment interact, which allows us to identify linkages among them and ultimately enables causes and effects to be isolated and assessed. Identifying these linkages allows for a greater understanding of how ecological systems have evolved in the past, which is of critical importance in anticipating and planning for future environmental changes.

The expansive list of literature that currently exists has provided a wealth of high-quality long-term data that has drastically improved our understanding of past environmental changes on a global scale. In spite of this, there is still a large knowledge gap that exists in specific regions due to the sparse geographic distribution of past environmental reconstructions. Generally, studies have been concentrated in regions where research institutions are most abundant which leaves many geographical areas underrepresented. Therefore, some of the most vulnerable regions that are already experiencing the consequences of a changing environment are not sufficiently researched. As a result, it poses a major limitation since it is necessary to gain an understanding of variability at various locations to facilitate confident predictions of future environmental changes. Without locally grounded data, country-specific variability cannot be considered, thereby causing challenges when policy and practice responses are implemented. For these reasons, there is a pressing need for additional research to be undertaken in geographical regions that have not been studied using paleoenvironmental techniques. In particular, it is especially important to garner a better understanding of how ecosystems and individual species function and change over time given the impact of environmental changes on human practices.

1.2. Fundamentals of palaeoecology

As the name suggests, palaeoecology represents a multidisciplinary branch of science which focuses on investigating patterns and processes of past ecosystems, often under environmental conditions that were different from the present day (Gaillard, 1998; Rull, 2010). The information presented by these investigations provides a context for understanding past interactions and community structure, significantly improving our current understanding of

contemporary ecological systems (Davidson et al., 2018; Goodenough & Webb, 2022; Nieto-Lugilde et al., 2021). Paleocological evidence can take many forms, including but not limited to individual fossils, fossil assemblages, sediment organic/inorganic geochemistry, the isotopic composition of fossils and sediments, and sediment lithology (Birks, 2008). These naturally occurring indicators of environmental variability that are used to reconstruct past ecosystems are called proxies. The major philosophical concepts that underpin each of these proxy methods are rooted in the principle of uniformitarianism, which is the assumption that the same processes that operate in our present environment have always operated in the past (Scott, 1963; Wilson, 1967). Therefore, in palaeoecology, this concept is used to make inferences about ancient organisms and environments based on analogies found in the present. Like in all other scientific inquiries, this concept is supported by the central rule of parsimony which suggests that the simplest explanation of an observation is likely to be the most plausible (Beck, 1943). For example, long-term patterns of community change can be inferred from a fossilized species that has similar morphological features to an extant species with known ecological preferences. Given the enormous amount of attention that the field has received in recent years, it is safe to say that this simplistic approach to understanding past ecosystems has been extremely successful. With that being said, as global environmental change continues, paleoecology now provides an essential guide to understanding how Earth's ecosystems will adapt (Seddon et al., 2013).

1.3. Lacustrine Ostracods as indicators of the past

Paleoecological studies based on the interpretation of lacustrine sediments is a technique with a long historical background. (Burge et al., 2017; Smol, 1993) Often found fossilized within these sediments are small bivalved crustaceans known as ostracods. To date, there are over 2,330 extant species of non-marine ostracods, which makes them one of the most abundantly found microorganisms in lacustrine systems (Meisch et al., 2019). Due to their high diversity and wide range of habitat preferences, ostracods play a central role in reconstructing past environments and assessing how ecosystems respond to environmental changes (Boomer et al., 2003; Ruiz et al., 2013). Specifically, each species has a unique set of ecological preferences which inform modern analogues for use in palaeoecological studies. These analogues can then be used to make inferences about a range of environmental variables including past precipitation, temperature, productivity and salinity which can be correlated to form a climatic signature (De Deckker, 2002; Horne et al., 2012). Additionally, a variety of additional habitat factors like water volume, retention time, water transparency, and the extent of aquatic macrophyte cover significantly impact their abundance (Boomer & Eisenhauer, 2002). As such, ostracods are well known as multiproxy organisms and their application to paleoecological studies has become increasingly common and sophisticated in recent decades.

Though it is possible to gain a great deal of information from the abundance of different ostracod species, several other techniques have been utilized to gain insights into past environments. In this way, numerous studies have analysed the chemical composition of ostracod valves to derive additional information about the environment in which they existed. This technique is based on the fact that the geochemical characteristics of the water in which they live are reflected in the ostracod's calcitic valves and can be measured and interpreted as proxies of the past. In each species, the organism moults up to nine times before reaching maturity, in which case it produces a new calcite shell each time. Therefore, given that each

shell will reflect the conditions of the host water during the period it was formed ostracod valves have the potential to provide very high-resolution information about past environmental changes. In particular, the calcitic valves of ostracods reflect the trace-element chemistry and stable isotope composition of their host waters (Holmes & Chivas, 2002; Holmes, 1996). In lakes, the oxygen isotope composition of the water is primarily influenced by changes in the hydrological regime of the lake, often caused by changes in the ratio of precipitation to evaporation (Decrouy et al., 2011; Holmes & De Deckker, 2012). The ostracod shell carbon isotope composition is often used to estimate changes in the primary productivity within a lake system, with increased $\delta^{13}\text{C}$ values indicating higher productivity (Keatings et al., 2002). However, carbon isotopic signatures are generally recognized as the result of more complicated processes compared to oxygen isotopic signatures. In particular, there are several issues that arise when interpreting both isotopic signatures from ostracod shells because their exact controls vary between waterbodies (Holmes and De Deckker, 2012). This highlights the complexity of interpreting isotopic signatures derived from ostracod shells and underscores the significance of understanding the dominant drivers of the lake's isotopic composition prior to making a palaeoenvironmental inference.

1.4. Project objective

Despite significant advances in recent decades, paleoenvironmental methods are still not widely applied in many geographical regions. Specifically, there have been relatively few texts explicitly concerned with reconstructions within the Lesser Antillean arc of small islands in the Caribbean. Therefore, the region still lacks a coherent network of reliable quantitative data about past environments, which makes research in this area extremely valuable. To effectively address this discrepancy, this project will be based on a sediment sequence recovered from Freshwater Pond, Barbuda with the primary aim of assessing the response of the ostracod faunal assemblage to fluctuations in lake hydrology and productivity that have occurred over the past few hundred years. This assessment is necessary given the importance of understanding ecological responses to environmental changes given the vital connections between plants, animals and their surroundings. Previous studies focused on ostracods have also indicated that they are extremely useful indicators of ecosystem health, biodiversity and environmental change. As such, the locally grounded data that is provided by this study is not only valuable because of its scientific merit but also because of its societal relevance.

2. Location of Study

2.1. Geographical Setting

Barbuda is a low-lying island comprised of Pleistocene and Recent limestones with a total area of 161 km² of which approximately one-fifth is covered by shallow lagoons (Brasier & Mather, 1975). The island forms the northernmost part of the Easter Caribbean archipelago collectively known as the Lesser Antilles, which separates the Caribbean Sea from the tropical Atlantic Ocean. Physiographically the island has very little topographical variation and can be divided into two regions: (i) an elevated limestone plateau to the east known as 'The Highlands' and (ii) a lowland area to the west, parts of which are only a metre above mean sea level (Brasier & Mather, 1975; Donovan et al., 2014). Climatologically, Barbuda is characterised by a seasonal sub-tropical maritime climate with minimal variations in average temperatures throughout the year, and a distinctive bimodal precipitation structure that is typical of most islands in the region (Angeles et al., 2010). Nevertheless, annual precipitation on the island is comparatively low due to the lack of orographic rainfall which is a consequence of the low-lying topography. Owing to its geology and climatic features, this island is susceptible to a diverse range of environmental perturbations which makes it an ideal location for paleoenvironmental investigation.

2.2. Site Description

Freshwater Pond is a permanent inland lake situated on the Codrington Limestone Group in the southern region of Barbuda (Burn et al., 2016) (Figure 1). It is assumed to have originated in the late Holocene as a result of rising eustatic sea levels which was followed by the development of a freshwater lens (Brasier and Donahue, 1985). Given that outflow in the lake is restricted, it can be classified as a hydrologically closed basin that experiences seasonal changes in shape, character and surface water levels in response to variations in both precipitation and evaporation. Consequently, during the wetter months, the lake freshens and increases in both its size and biological productivity. Conversely, during the drier months, the lake contracts as a result of increased evaporation which creates a brackish lake environment. As a result, lake water salinity fluctuates between fresh to slightly brackish throughout the year. Therefore, Freshwater Pond can be classified as an oligo-mesohaline lake system which supports a thriving community of fresh to brackish water organisms inclusive of ostracods which are the primary subjects of this study.

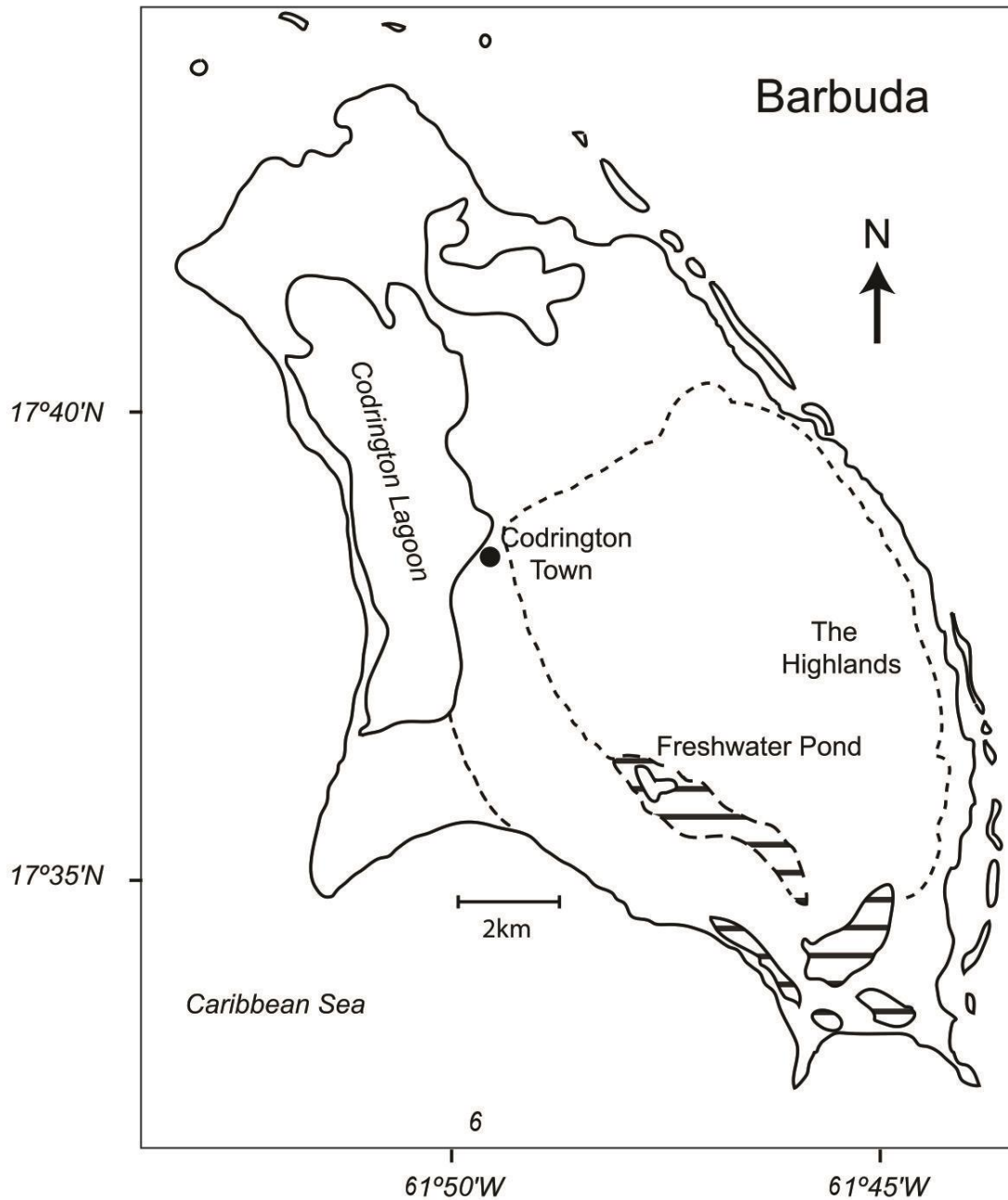


Figure 1: Map of Barbuda showing the study site Freshwater Pond. (Source: Burn et al., 2016)

2.3. Previous work at Freshwater Pond

Like many other lake systems in the Caribbean, Freshwater Pond has not been the subject of many paleoenvironmental studies. To date, there has only been one published paleoclimatic record which utilized a sediment sequence recovered from the lake. This seminal work produced by Burn et al., 2016 significantly contributed to the current understanding of long-term changes in hydrological variability in Barbuda and the Caribbean region as a whole, which is an area that has long been hampered by the absence of high-resolution paleoclimatic archives. Additionally, this work provides essential information about the evolution of the study site and the ecology of species that are found there which will drastically improve the accuracy of this research project.

In order to effectively investigate past changes in climatic variability, Burn et al., 2016 employed a multiproxy methodological approach which utilized both stable isotope and biostratigraphic analyses of the microfossils found throughout the recovered sediment core. Specifically, they analysed episodic fluctuations in freshwater ostracod and gastropod shell accumulation as well as variations in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ derived from ostracod shells. Results from the conducted analyses identified five biostratigraphic zones (FP1-FP5) and suggest that variations in ostracod populations within the sediment record are primarily controlled by changes in the local precipitation and evaporation ratio. However, considering that the Freshwater Pond sediment record documents the evolution of a new ecosystem, it is likely that internal ecosystem dynamics also played a substantial role in shaping observed biological assemblages. It is therefore necessary to provide a more in-depth analysis of observed changes in faunal assemblages over time in order to identify the factors that are responsible for shaping them. As such, this dissertation seeks to conduct a similar investigation with a greater focus on investigating the relationship between ostracod faunal assemblages and past fluctuations in lake hydrology and primary productivity within the lake.

2. Methods

This study was carried out on a 51cm long sediment core that was recovered from Freshwater Pond, Barbuda in June 2013 as part of a recently completed NERC-funded project titled Neotropics1k. As such, core retrieval/splitting, lithological descriptions, radiocarbon dating, stable isotope and loss on ignition analysis were previously conducted on the sediments of Freshwater Pond by Professor Jonathan Holmes and Rachel Gwynn and are used in this study as unpublished data. For the purpose of this study, additional ostracod faunal assemblage and grain size analysis were conducted using resampled material. SEM photographs were also taken of exceptionally preserved ostracod specimens that were identified in the resampled sediment sections.

2.1. Core Splitting/ Sediment description

The core was split lengthwise to separate the sediments in half using a core splitter at the PCRG. All laboratory analysis was conducted on one half of the core, while the other half was stored for archival purposes. After splitting, a macroscopic analysis of the core was conducted in order to identify down-core differences in sediment colour and stratigraphy. The Troels-Smith classification system was used to ensure consistency in the stratigraphic descriptions while the Munsell colour chart was used to standardize the characterization of sediment colours.

2.2. Loss on Ignition

Sequential loss on ignition analysis used to calculate the organic and carbonate percentages of the lake sediments from FWP followed the method proposed by Dean, 1974. Thus, the 1cm³ sediment samples were dried overnight at 110°C to remove pore water content. To prevent any moisture from entering the samples, they were cooled to room temperature with a desiccator and weighed with a digital balance. Using the equation below, the percentage of water content was calculated.

$$((W_{wet} + LOI_{110}) - W_{wet}) * 100$$

The dried sediment samples were burned for four (4) hours at 550°C, then cooled to room temperature and weighed again to determine their organic content. Using the equation below, the percentage of organic matter content was calculated.

$$((LOI_{110} - LOI_{550}) / W_{dry}) * 100$$

Once they were weighed the samples were burned again for two (2) hours at 950°C, then cooled to room temperature and weighed to determine their carbonate content. Using the equation below, the percentage of carbonate content was calculated.

$$((LOI_{550} - LOI_{950}) / W_{dry} * 100) * 1.36$$

2.3. Stable Isotopes

Individual ostracod valves were used to illustrate downcore variations in the stable isotope composition of the FWP sediment core. The valves used for the analysis were comprised solely of adult specimens of *Heterocypris punctata* which was one of the most dominant species that had a sufficient number of well-preserved valves observed throughout the core. The specimens were carefully picked from the coarse fraction of the subsampled stratigraphic sections using a paintbrush and a binocular microscope. After picking, each valve was cleaned and then examined for impurities. The valves were then analysed using a mass spectrometer at the Bloomsbury Environmental Isotope Facility (BEIF).

2.4. Ostracod Faunal Analysis

In order to characterize changes in the ostracod faunal assemblage from FWP, a section of the sediment core was subsampled at continuous 1 cm intervals. Although there is no specific amount of sediment required for this analysis, to ensure that each sample was properly represented this study utilized sediment volumes of 1cm³. After subsampling, the individual sediment sections were placed into 100ml flasks and stirred then left overnight in 1ml of distilled water. The following day the deflocculated sediments were gently wet-sieved using a 125- μ m sieve. The coarse fraction was recovered and placed in an oven where it dried overnight. The dried sediment was then placed in a 10ml glass tube to be used for picking. From each sample, at least 100 ostracod valves were picked and placed on a micropaleontological slide. The valves were only picked if they were well-preserved and sufficiently whole to allow identification. Once all the samples were picked, the total number of each species was counted and then converted into a percentage. The percentages were then used to create a stratigraphic plot in MATLAB. A hierarchical cluster analysis was used to identify biostratigraphic units based on the ostracod assemblage data. Photographs taken with a scanning electron microscope were used to identify the morphological characteristics of each species which aided in their identification. Taxonomic information on individual species and ecological interpretations of the delimited assemblages were based on the results of numerous studies.

2.5. Particle size

Downcore variations in particle size distribution from the FWP sediment core were identified through laser diffraction analysis of all 51 sediment sections using the Malvern Mastersizer 2000. The analysis was conducted using the fine fraction (<125 μ m) of the resampled sediment sections that were sieved for the ostracod faunal analysis. Once the samples were sieved and the coarse fraction was secured for the faunal analysis, the wet sediment was poured into a 125ml plastic bottle where it was stored until the time of analysis. In preparation for analysis, the samples were not pre-treated because sieving would have already removed bonding agents. Therefore, the analytical procedure began with the plastic bottles being vigorously shaken to create suspension prior to pipetting into the Hydro 2000MU pump, which ensured that the analysed material was representative of the entire sediment section. For the purpose of this study, the chosen dispersant was undistilled tap water which controlled the distribution of the sediment and ensured that the particles were delivered to the measurement cell in a stable state of dispersion. Based on the observed characteristics of the FWP sediments, an average obscuration of 5% was maintained for each sample to avoid multiple scattering. Each sample was analysed by four successive laser diffraction runs of 12 seconds and the average was

automatically calculated and reported on the Malvern Mastersizer 2000 software. Before accepting a grain size analysis, results were first order inspected with the software to check for any anomalous results that could be attributed to air bubbles, machine spikes or other operational errors. Once all samples were analysed the data was exported and the summary statistics were calculated using the particle size analysis software GradiStatV9.1. All graphical measures in this study utilized the Folk and Ward method of classification.

2.6. SEM

Scanning electron microscope (SEM) photographs were taken of 51 gold-sputtered specimens consisting of ostracods (50), ooids (4), a rupia seed (1), and a charophyte oospore (1). The photographs were taken using a Jeol JSM-6480LV high-performance, Variable Pressure Analytical Scanning Electron Microscope at the UCL Earth Sciences SEM Laboratory

3. Results

3.1. Sediment Description

According to the macroscopic analysis of FWP's 51 cm long sediment core, five major lithostratigraphic units can be distinguished (Figure 2). The sediment is largely characterized by calcareous muds that are rich in both macro and micro fossils including ostracods, gastropods, and charophyte oospores which can be observed throughout the core. The lowermost 4 cm of the core is comprised of mottled clays and contains trace amounts of organic material as well as relatively uniform gravel-sized ooids.

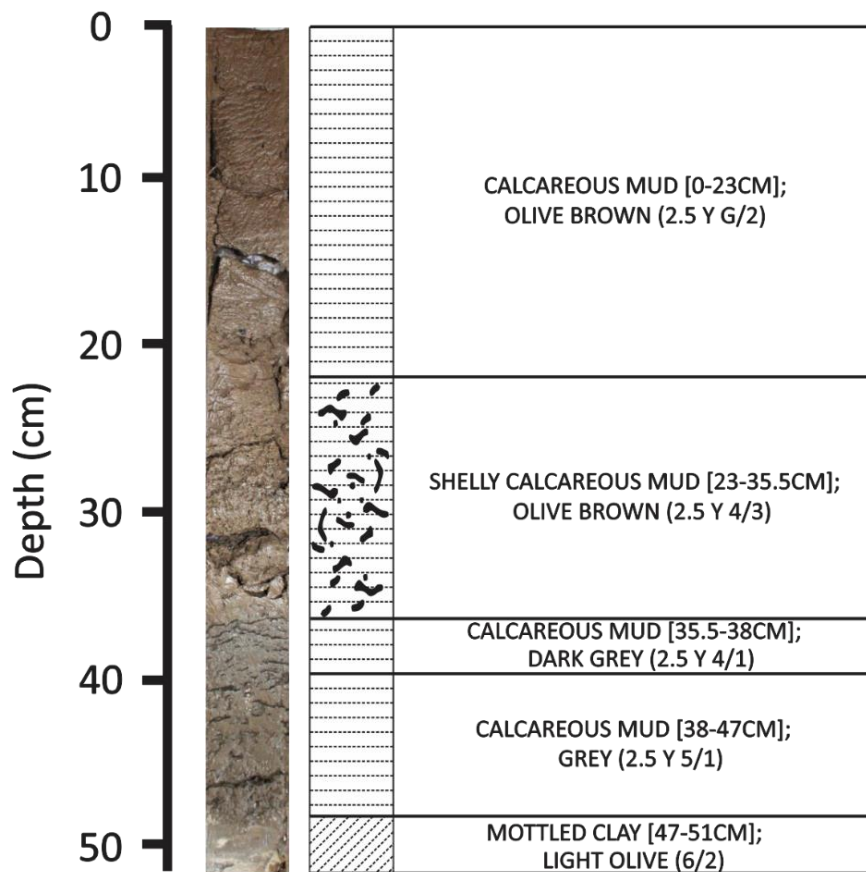


Figure 2 Core lithology for sediment core FWP from Freshwater Pond, Barbuda.

The units can be subdivided into: (1) a distinct olive-brown calcareous muddy-sand layer with a diffused lower boundary (0-23cm), which transitions into (2) a shelly calcareous mud with inclusions of organic and carbonate fragments (23-35.5cm). This unit has a sharp lower boundary, with two underlying variations of calcareous mud which are distinguished based on their differences in colour. Additionally, the lowermost layer of calcareous mud is interspersed with medium sand inclusions and shell fragments. A fairly sharp boundary transitions to the lowermost light grey unit which has white-mottled clay inclusions.

3.2. Sedimentation rate and age model

Based on ^{14}C dates derived from *Ruppia* seeds, the 51cm long FWP sediment core spans a 653-year period extending from 1360 to 2013 (Figure 3). The average sedimentation rate was relatively low throughout this period at 0.17 cm/yr. However, sedimentation accumulation gradually increased over time from an average of 0.08 cm/year in the 1400s to 0.50 cm/yr in the 2000s. Most notably there was an abrupt increase in sediment accumulation around 1980 with a peak value of 1cm/yr occurring in 2007.

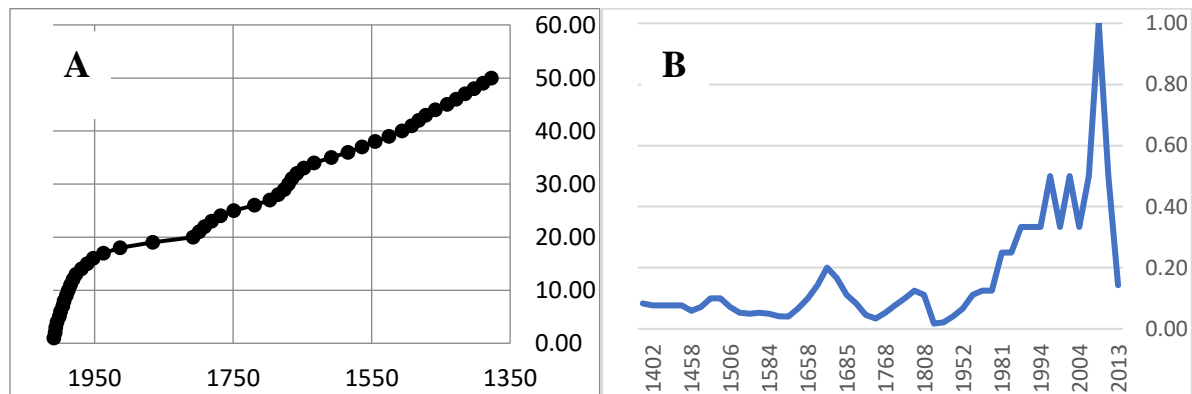


Figure 3: (A) Age model and (B) sedimentation rates from core FWP.

3.3. Particle size

Textural analysis of the FWP sediment samples was carried out to qualitatively characterize downcore variations in grain size attributes. With regards to the grain size distribution patterns, the results indicate that all 51 sediment samples from FWP are classified as unimodal. Specifically, there is only one observed mode on the frequency curve which is very finely skewed (negative) and a single straight line on the main body of the cumulative curve (Figure 4). Given that the frequency distribution curve of sediment grain size directly reflects the grain size character (Xiang et al., 2006), it is inferred that there has been one dominant mode of sediment transport to the lake since its formation.

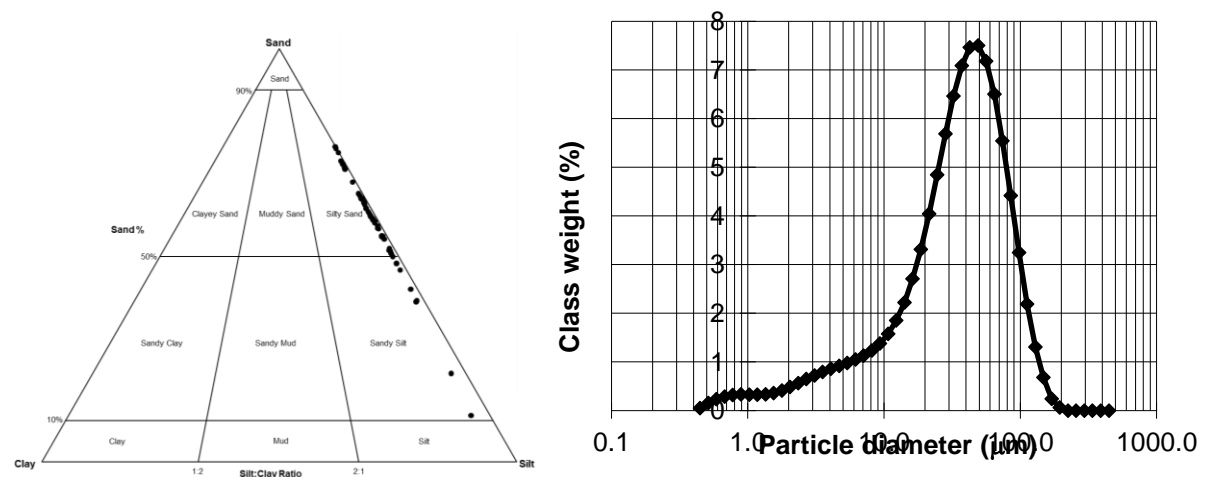


Figure 4: (A) Sand, Silt Clay diagram and (B) frequency distribution curve from core FWP.

Generally, the ternary diagram plot suggests that the vast majority of the analysed samples are texturally classified as silty sand, which is also consistent with the observations made while examining the core lithology. Despite this uniformity in classification, there are notable downcore variations in the proportion of sand, silt and clay fractions which suggests that there were changes in the processes and energy of sediment transport over time. Similarly, statistical measures such as mean grain size, sorting, skewness and kurtosis, exhibit considerable downcore variations which also suggests that there have been changes in the depositional environment over time (Figure 5).

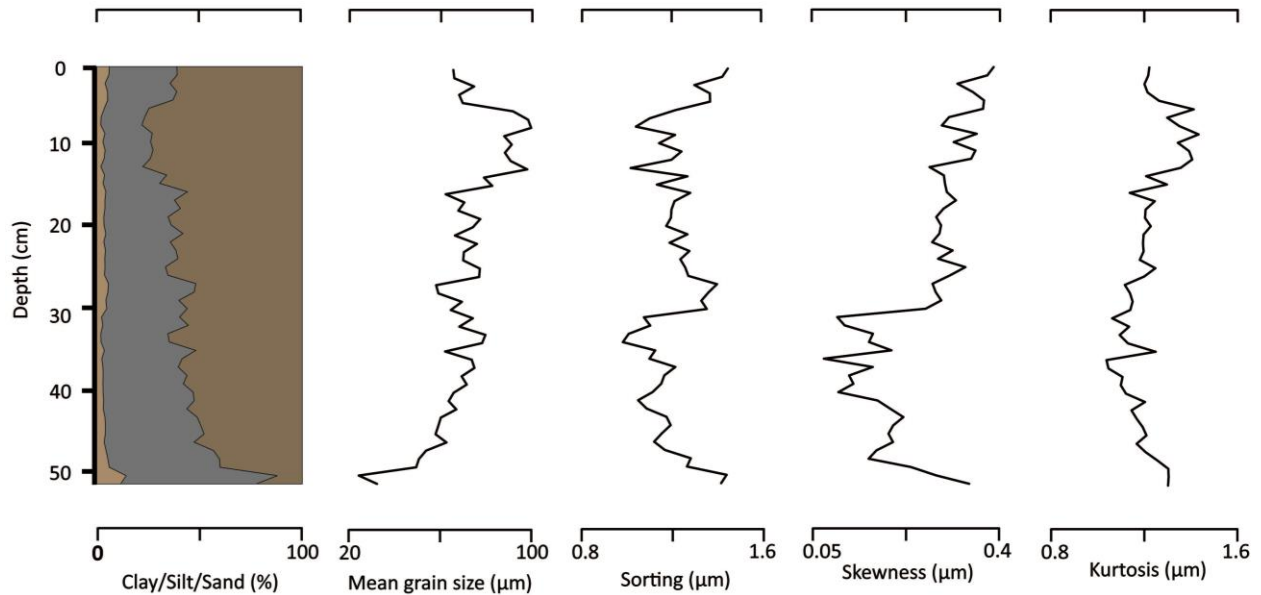


Figure 5: Downcore variations in mean grain size, sorting, skewness and kurtosis from the FWP sediment core.

The dominance of clay and silt-sized fractions at the bottom of the core represents a period of low-level lake stands corresponding with the genesis of the lake. This is supported by the observed poor sorting and negative skewness which points to the presence of low-energy currents that led to the erosion and persistence of fine particles. There is then an assumed transition to a more stable depositional environment in the overlying section of the core, characterized by a gradual increase in sand-sized particles and mean grain size. Based on the consistently low sedimentation rate that prevailed throughout most of the core, it is inferred that energy conditions do not heavily influence the depositional environment. Instead, it has been determined that lake size and water level are the most important factors controlling sedimentation deposition rather than only catchment-related changes. Nevertheless, the abrupt increase in sedimentation rate and the subsequent spike in mean grain size near the top of the core suggests that there may have been an external influence on sediment deposition in recent periods. Based on the structure and geographic location of the basin, there is a possibility that shoreline materials eroded by storm-driven waves could have contributed to the accumulation of sediments in the lake during this time. However, the very narrow-ranging sand mode does not support this theory and points to the potential influence of human land management practices around the lake.

3.4. Loss on Ignition and Stable Isotopes

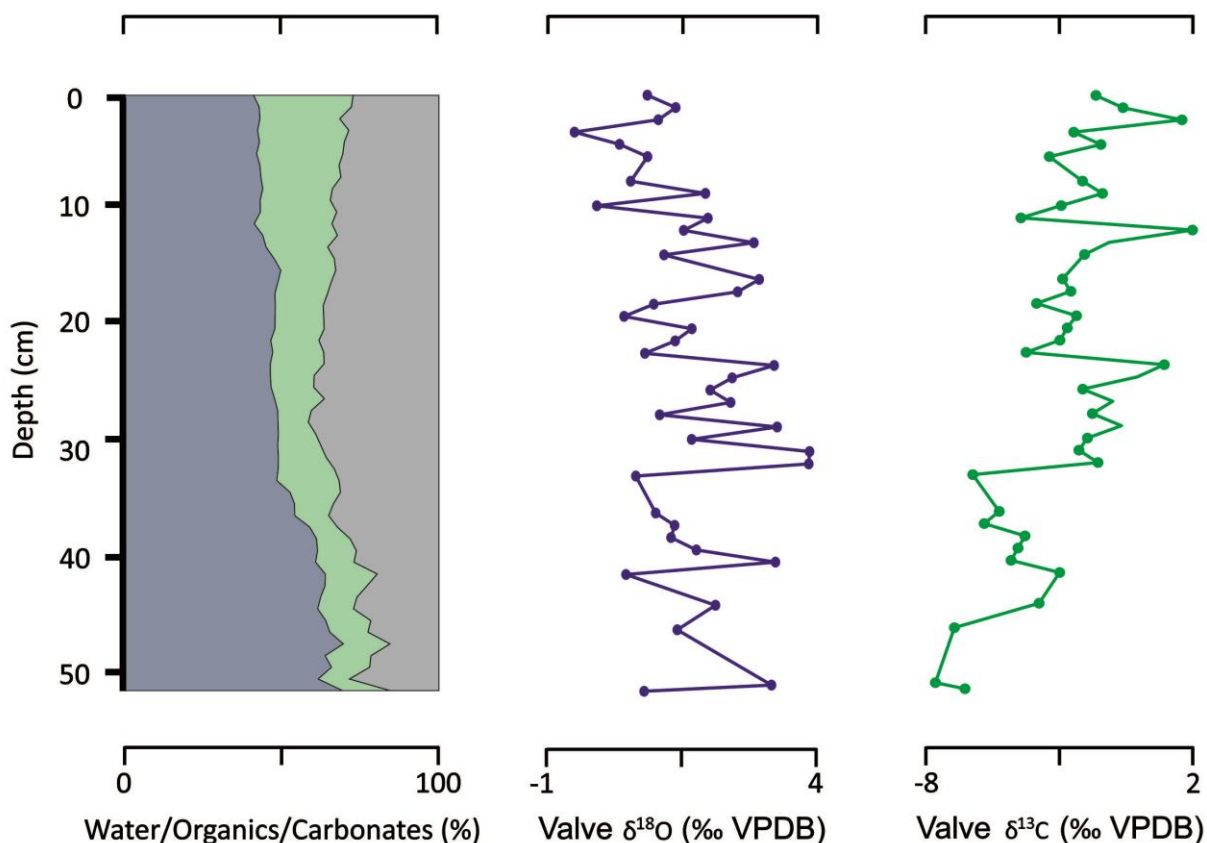


Figure 6: Water, organic matter and carbonate curves determined by loss-on-ignition analysis along with corresponding stable oxygen and carbon isotope measurements derived from fossil valves of the ostracod *Heterocypris punctata*.

3.4.1. Loss on Ignition

Loss on drying analysis revealed a marked decrease in the vertical profile of pore water content from the FWP sediment core (Figure 6). Based on the observed changes it appears as if there are fixed upper and lower limits of water content for Freshwater Pond sediments. Based on observation, it is believed that these limits reflect the structure and natural porosity of the sediments, which are both influenced by the density of organic matter content. In this way, as pore water content decreased there was a synchronous increase in organic matter towards the top of the core where the highest value of 25.24% is recorded. However, this increase was not linear and there were several notable fluctuations with the most significant occurring between 30-40cm. Similarly, the percentage of carbonate material within the core also varied significantly with depth. The lower section (31-51cm) has several abrupt fluctuations which have a general increasing trend that peaks with a value of 41% at approximately 28cm which is associated with the distinct shelly calcareous mud lithostratigraphic layer. Thereafter, carbonate values then gradually decrease towards the top of the core but remained relatively higher (<20%) than the values found in the lowest section of the core.

3.4.2. Stable Isotopes

Stable isotope values derived from the individual valves of *H. punctata* varied significantly throughout the FWP sediment core. The $\delta^{18}\text{O}$ values ranged from -0.5‰ to 3.9‰ with a mean of 1.65‰ and a standard deviation of ± 1.06 . Though the curve is characterized by a number of abrupt fluctuations, the values generally become more negative towards the top of the core. Specifically, the highest values are recorded in the lower 10 cm of the core while the lowest values are found near the sediment surface. Based on the observed trends it can be inferred that there have been significant changes in both short and long-term hydrological dynamics of the basin over time. Comparably, the $\delta^{13}\text{C}$ values also vary quite markedly throughout the core with values ranging from -7.66‰ to 1.98‰ with a mean of -2.78‰ and a standard deviation of ± 2.19 . Apart from the sustained fluctuations, there is a gradual increase in $\delta^{13}\text{C}$ values towards the sediment surface which also suggests both short and long-term changes in organic production. Despite there being a weak correlation ($r^2 = 0.13$) between both profiles, there are a few observable instances of synchronicity. Most notably, the correlation between both profiles is much stronger ($r^2 = 0.63$) between 15 -30cm suggesting a causal relationship between both isotopes. Therefore, it can be inferred that changes in the hydrological dynamics of the basin would have led to similar fluctuations in organic productivity during this period.

3.5. Ostracods

The ostracod fauna from FWP consists of eight (8) distinctive species belonging to six (6) genera, some of which have been extensively described in previous studies in the Caribbean. Specifically, the ostracod species found in the core were *Perissocytheridea cribosa*, *Potamocypris sp. 1*, *Potamocypris sp. 2*, *Heterocypris punctata*, *Chlamydotheca sp.*, *Heterocypris antillensis*, *Cypreideis edentata* and *Cypridopsis vidua*. Interestingly, four (4) of these species have been documented for the first time at FWP which suggests that the ostracod is more diverse than previously assumed. Most notably, the dominant species *Perissocytheridea cribosa* was not previously identified at this site despite being found in every section of the core. Its abundance and exceptional preservation throughout the sediment sequence suggest that there was a methodological inefficiency which led to its exclusion in the previous study. In addition, *Potamocypris sp 1*, *Potamocypris sp 2* and *Heterocypris antillensis* were also not identified.

3.5.1. Ecological Information

Family Cytherideidae

Genus Cyprideis

Species Cyprideis edentata

This species has been previously identified in Barbuda and a range of other aquatic environments throughout the Caribbean (Keyser & Schöning, 2000; Medley et al., 2007; Palmer et al., 2020). Its widespread distribution in the region is due to its euryhaline and eurythermal nature which allows it to adapt to a broad range of salinities and temperatures. This is necessary given that salinity conditions in coastal Caribbean environments can fluctuate

between freshwater conditions in wetter periods to hypersaline conditions during prolonged dry spells. However, despite its ability to tolerate a range of environmental conditions, *C.edentata* has a documented preference for shallow, oligo-mesohaline environments with muddy to mixed mud-sand substrate (Sandberg, 1964).

Cyprididae (Family)

Cyprinotinae (Subfamily)

Heterocypris (Genus)

Heterocypris punctata (Species)

Across the Caribbean, *Heterocypris punctata* has generally been identified in warm oligo-mesohaline waters of coastal lagoons (Broodbakker, 1982; Broodbakker, 1983). In this way, the salinities of 2–7‰ and temperatures between 17-32°C have previously been reported as the optimal range for this species. As a nektobenthic species, substrate type has also been highlighted as an important factor controlling the distribution of this species given that it has been most abundant in muddy environments. Although, there is evidence that it lives in the littoral zones of Central American freshwater lakes amid dense stands of aquatic macrophytes (Perez et al., 2011).

Cytherideidae (Family)

Perissocytheridea (Genus)

Perissocytheridea cribrosa (Species)

This brackish-water species is a typical colonizer of coastal lagoons and mangroves throughout the Caribbean (Keyser 1977; Martens, 1998). Remarkably, the species has a reported salinity tolerance range of 5–48‰ and can live in aquatic environments with temperatures ranging from 16-34 °C. In spite of its ability to tolerate a wide range of environmental conditions, *Perissocytherida cribrosa* is often found amongst other euryhaline genera and has a preference for polyhaline waters with high conductivity and a sandy-mud substrate (Palmer et al., 2020).

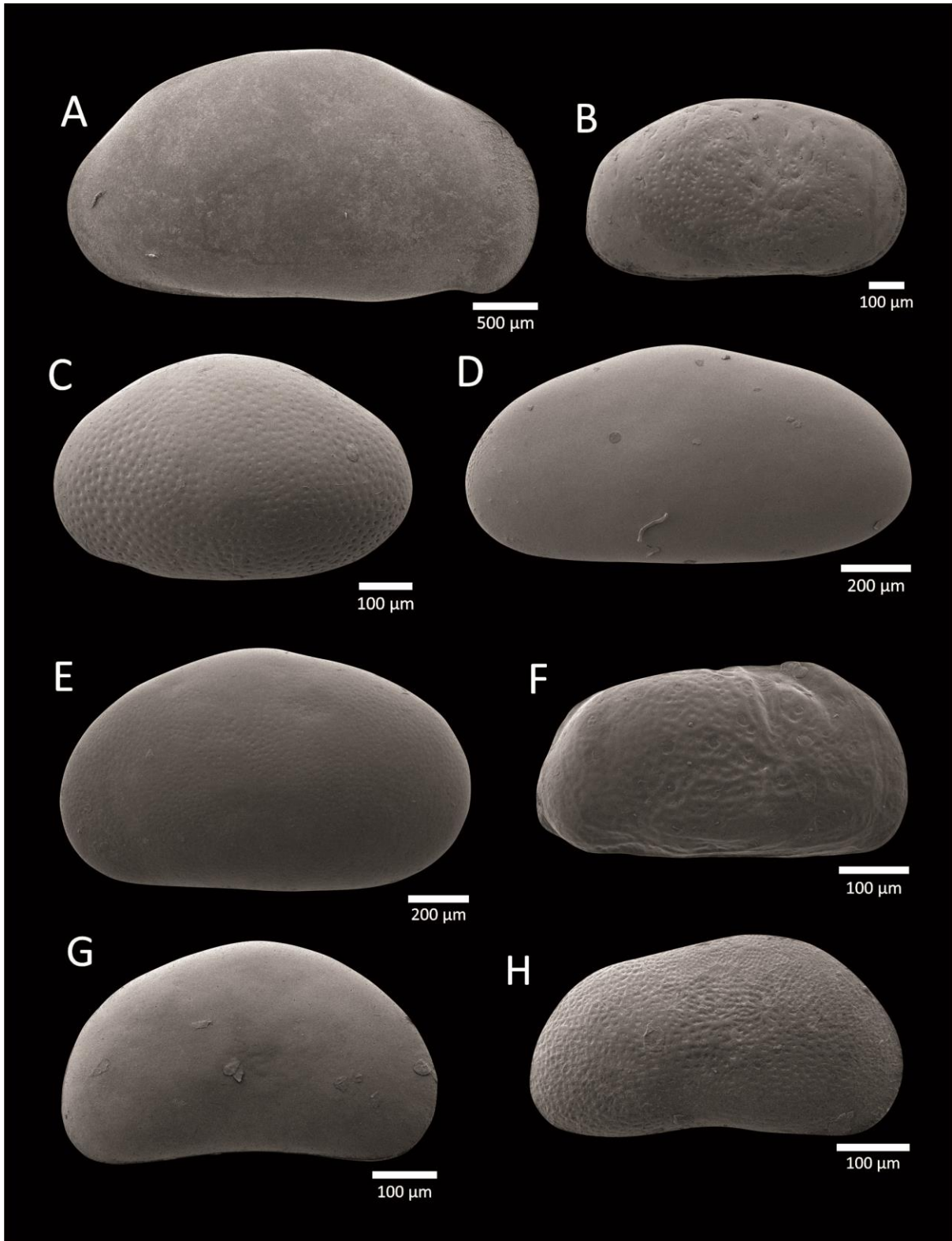


Figure 7: SEM photographs of the eight (8) ostracod species identified in the FWP sediment core. (A) *Chlamydotheca* sp., LV-EV, (B) *Cyprideis edentata*, LV-EV, (C) *Cypridopsis viduella*, LV-EV, (D) *Heterocypris antillaris*, LV-EV, (E) *Heterocypris punctata*, LV-EV, (F) *Perissocytheridea cribosea*, LV-EV, (G) *Potamocypris* sp.1, (H) *Potamocypris* sp. 2

Cyprididae (Family)
Cypridopsis (Genus)
Cypridopsis vidua (Species)

Cypridopsis vidua is a freshwater ostracod known to have a wide ecological tolerance and geographical distribution such that it is considered a cosmopolitan species (Külköylüođlu, 2005). It has been recorded in oligohaline to slightly hypersaline waters in a broad range of aquatic environments ranging from ephemeral to permanent systems. It is often found in waters with dense aquatic vegetation and is frequently associated with weeds of *Chara* sp (Roca et al., 1993). Given its eurythermic nature, it can exist in temperatures ranging from 2-32°C but prefers warmer environments (>13°C). In addition, this species can withstand large variations in dissolved oxygen, pH, and other physio-chemical variables.

Cyprididae (Family)
Chlamydotheca (Genus)

This species has not yet been formally documented, therefore, its ecological preferences cannot be described in detail. However, ostracods from the genus *Chlamydotheca* are known to have a largely Neotropical distribution with several species having previously been identified in the Caribbean region. Based on the evidence from previous studies, species in the genus *Chlamydotheca* are typically classified as nektobenthic and have a preference for shallow freshwater environments (Burn et al., 2016). The distribution of species in this genus has also been observed to be dependent on their ecological relations with other ostracod species and the presence of dense aquatic vegetation.

Cyprididae (Family)
Heterocypris (Genus)
Heterocypris antillensis (Species)

H. antillensis is a freshwater ostracod that has previously been identified in several aquatic environments in the Caribbean (Broodbakker, 1982; Broodbakker, 1983). This species is adapted to many fast-changing environmental factors and is known to be a rapid colonizer of temporary water bodies that are less than 1.5m in depth. These aquatic systems are generally coloured, somewhat polluted, of low chlorinity and have a muddy substrate. Given that it preferentially inhabits temporary water bodies with restricted space, competitive exclusion is most probably the most important factor that controls its distribution and abundance.

Cyprididae (Family)
Potamocypris (Genus)

There are species belonging to the genus *Potamocypris* present on all the continents apart from Antarctica and Australia. The majority of these species have been found in freshwater habitats, however, there are a few species of the genus that colonize brackish coastal aquatic environments. Given their wide geographical distribution, a practical description of their ecological preferences cannot be provided.

Analysis.

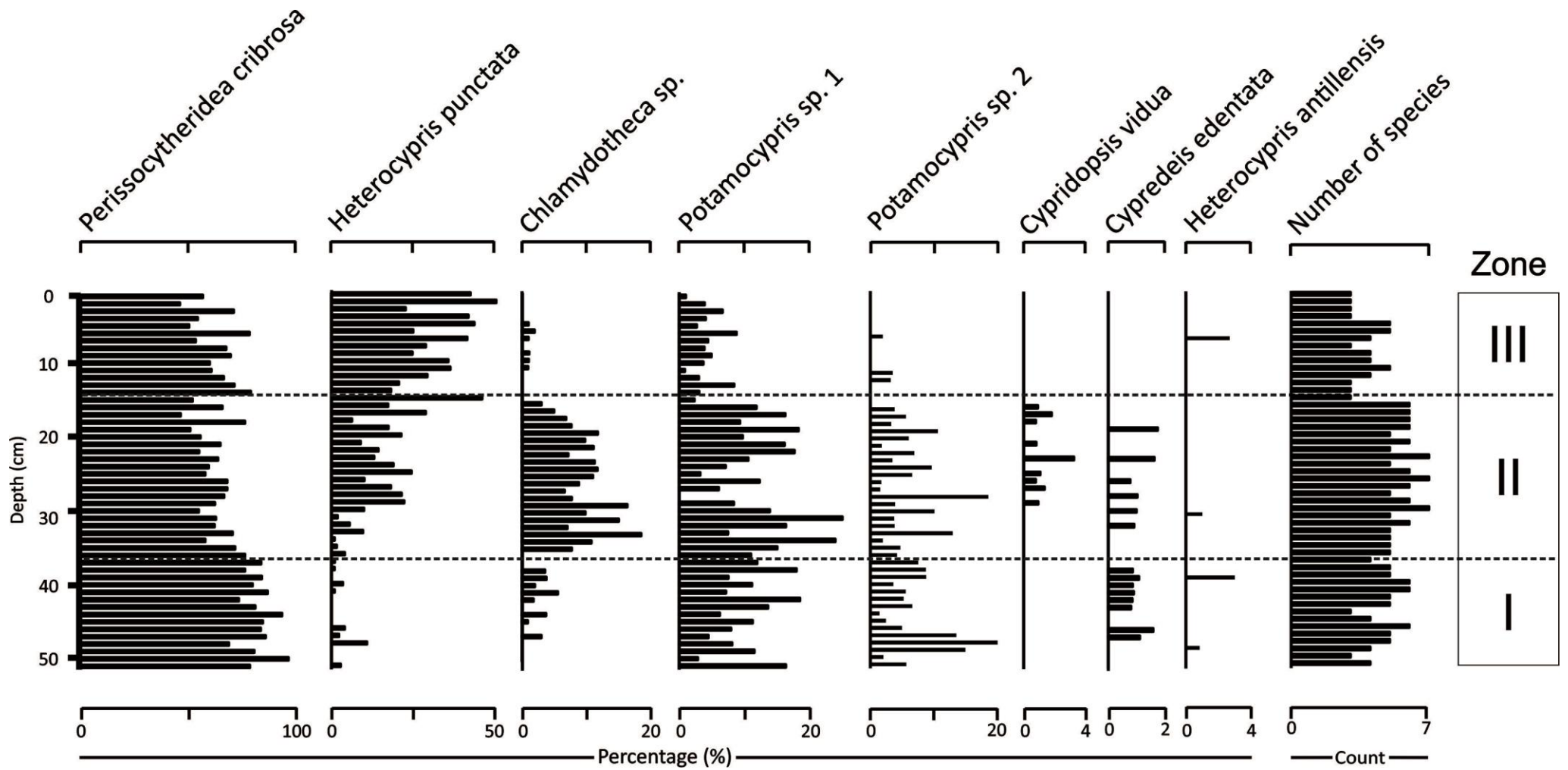


Figure 8: Ostracod fauna of Freshwater Pond sediment core FWP. The biostratigraphic units labelled Zone 1 – Zone 3 are delimited by boundaries defined by a Hierarchical Cluster Analysis.

3.5.2. Ostracod faunal assemblage

The composition of the ostracod faunal assemblage from FWP varies significantly throughout the core but is generally dominated by *P. cribrosa* which accounts for 68% of the total valves counted (Figure 8). Despite this dominance, species richness is relatively high throughout the core with an average of 4.8 species per sample (maximum = 8, minimum = 3). The presence of a more diverse range of species within a sediment sequence generally indicates that environmental conditions were favourable to ostracod growth. Therefore, although the other species identified in this assemblage are present in much smaller proportions, understanding their variance over time is of critical importance. As such, based on the presence and relative abundance of each ostracod species three distinctly different faunal zones (FWP1- FWP 3) have been identified and will be described in detail below.

FWP-1

The lowermost section of the core (51–38 cm) is mainly dominated by *P. cribrosa* (81%) but displays high biodiversity with seven of the eight identified species being present. Both unidentified species from the genus *Potamocypris* are also most abundant in this zone comprising 14% of the FWP-1 fauna. All other species except *C. vidua* are present but in extremely small quantities (<5%). Most notably, FWP-1 has the lowest abundance of *H. punctata* which is the second most dominant species in the core. Therefore, it appears that environmental conditions during this period were only suitable for ostracods that were able to survive in specific conditions.

FWP-2

Of the three faunal units, this zone (34–15 cm) has the highest diversity with all eight species being identified at least once. Although there is a notable decrease in its abundance, *P. cribrosa* (66%) is still the most dominant species. When compared to the lower assemblage, the most significant difference is the drastic increase in *Chlamydotheca sp.* which is by far most abundant in this zone. In addition, there is a gradual increase in *H. punctata* which only had a minor presence in FWP-1. Although it is not particularly abundant, there is also a very small number of *C. vidua* in this zone which is quite significant because it represents the only appearance of this species. Therefore, the observed changes suggest a shift to environmental conditions that were more tolerable for a wider range of species.

FWP-3

This is the least diverse zone (14 cm to the top of the core) and is marked by a gradual decrease in the dominant species *P. cribrosa* (61%) which continues towards to the top of the core. Conversely, there is an increase in *H. punctata* (32%) which is significantly more abundant relative to the underlying zones. The other species identified in this zone are present in negligible quantities and do not display any considerable trends. However, due to the exceptionally higher sedimentation rate (0.78 cm/yr) in this zone, it is possible that some post-mortem transportation has occurred. However, when compared to the other zones valve preservation is generally much better which would suggest that the assemblage is in situ and represents the living population.

4. Discussion

4.1. Lake Hydrology

In lacustrine systems, such as Freshwater Pond, relative changes in past lake hydrology have often been inferred through the use of a number of well-documented proxies. Although the absolute value of the lake level changes cannot be discerned from these proxies, it is theoretically possible to obtain sufficient data about its variations over time. This data provides information which is particularly useful given that hydrological changes are known to have a significant influence on the structure and function of both aquatic and terrestrial ecosystems (cite). In this way, the results of the analyses conducted as part of this study indicate that the lake level of Freshwater Pond varied significantly in the Late Holocene. This inference is made based on the known relationship between climate-induced relative lake level change and the oxygen-isotopic composition of lake waters. In particular, changes in the $\delta^{18}\text{O}$ of the lake water in hydrologically closed coastal basins in the tropics are predominantly controlled by the balance between the amount of lake-water input (precipitation) versus output (evaporation) (Li & Ku, 1997). Due to the difference in atomic mass of the two main oxygen isotopes, an increase in the P/E (Precipitation/Evaporation) ratio will produce a rise in $\delta^{18}\text{O}$ ratios due to the fact that the lighter ^{16}O isotope is preferentially evaporated which leaves the waterbody enriched in ^{18}O (Gat, 1995; Leng, 2005). This suggests that relatively wet periods are generally characterized by lower $\delta^{18}\text{O}$ values because there is less evaporation of water from the lake basin when compared to the influx of precipitation. Granted that precipitation patterns are the main natural factor affecting water levels at FWP, observed changes in the $\delta^{18}\text{O}$ ratio can therefore be interpreted as variations in lake level. In addition, it is assumed that greater precipitation would also increase the amount of weathering and erosion in the lake's drainage basin. Therefore, observed changes in the grain size distribution and sediment lithology may also record water level shifts.

Based on the combined results of these proxies, this study has provided a detailed water level history for FWP which spans the late Holocene. Evidenced primarily by changes in $\delta^{18}\text{O}$ values, there have been numerous abrupt fluctuations in the lake's water level since its formation. According to the core chronology, major fluctuations occur on decadal to multi-decadal timescales and are likely to be controlled by the ENSO and the AMO which are the principal drivers of contemporary rainfall patterns in the Caribbean (Burn et al., 2016). On shorter timescales, variations can be attributed to the annual bimodal precipitation structure that defines the northeastern Caribbean (Angeles et al., 2010). In response to these drivers, the lake system has regularly transitioned between high and low-level lake stands. The observed fluctuations in $\delta^{18}\text{O}$ suggest that the contemporary lake levels are as high as they have ever been. Interestingly, the most notable low stand occurred around ~1500 CE and was marked by a major increase in productivity in the lake. Additionally, this period also coincided with the most diverse ostracod fauna in the core. This indicates that there is some correlation between ostracod populations and lake hydrology at FWP. This is further supported by the fact that the three faunal zones (FWP 1- FWP 3) appear to correspond with major changes in the hydrodynamics of the lake system

Specifically, FWP 1 is broadly characterized by high $\delta^{18}\text{O}$ values indicative of a low lake level which is typical of a newly formed lake system. Based on the observed changes in $\delta^{18}\text{O}$ values, the water level gradually increases over time and experienced an abrupt period of aridity near the boundary of the faunal zone. Given that the lake is in its early stages of development the ostracod fauna in FWP 1 is not found to be very diverse. In spite of this, there is an abundance of *P.cribroso* along with a substantial population of both species from the genus *Potamocypris*. These populations appear to respond to changes in lake level but the exact relationship is not fully understood. The transition to FWP 2 is marked by a sustained period of relatively high lake levels which abruptly transitions to the most significant and prolonged arid period within the sequence. Interestingly, the ostracod assemblage is much more diverse with all eight (8) species being identified in this period suggesting that environmental conditions were more favourable for ostracod production. Notably, the species *Chlamydotheca sp.* and *C.vidua* are most abundant in this zone which is quite significant because they are both known to have a preference for shallow freshwater lake systems. Within this fauna, there is also a significant increase in the abundance of *H.punctata* which also has a known preference for freshwater environments which is mirrored by a decrease in *P.cribroso*. Therefore, it appears as though changes in the lake water salinity at FWP are also a dominant factor regulating the ostracod assemblage. However, based on the known correlation between lake level fluctuations and salinity changes in hydrologically closed basins the observed relationship is not clear. Typically, freshening of a lake water system would be indicated by a decrease in the P/E ratio resulting in a decrease in $\delta^{18}\text{O}$ values (Horton et al., 2016). Granted that the opposite response is observed it is assumed that the assemblage change could have been driven by the prolonged physiological effect of salinity-related stress during the previous wet period which led to the restructuring of the ecosystem. Additionally, the relationship explored here also suggests that changes in lake hydrology may not be the only control on the ostracod faunal assemblages in FWP 2. Both species of *Chlamydotheca sp.* and *C.vidua* are also known to have a preference for shallow waters and dense vegetation. Therefore, it may be possible that the observed fluctuation in water level allowed the growth of denser vegetation in the pond leading to their proliferation. This suggests that hydrological changes still had a secondary effect on the ostracod assemblage within this zone.

Nevertheless, the FWP 3 fauna displays a more direct relationship between lake-level fluctuations and ostracod populations. This zone represents the least diverse ostracod assemblage in the core, with *P.cribroso* and *H.punctata* comprising over 90% of the overall population. Similar to FWP 2, both species are observed to have a very distinct inverse relationship. At the beginning of FWP 3, there is a notable resurgence of *P.cribroso* which did not particularly favour the conditions present in FWP 2. However, this increase was short-lived and was soon followed by a gradual decrease which persisted towards the top of the sequence. In contrast, the FWP2 - FWP 3 transition saw a slight decrease in *H.punctata* populations right after they appeared to have reached their maximal abundance. Based on the known ecological preference of both species and the observed variations in $\delta^{18}\text{O}$, it is assumed that there was a minor reduction in lake level which led to more saline conditions. During this period, other species such as *Chlamydotheca sp.* and *C.vidua* disappeared and then struggled to reintegrate themselves into the ecosystem when conditions became more favourable. This allowed *H.punctata* to thrive as water levels rose and the lake system became more stable

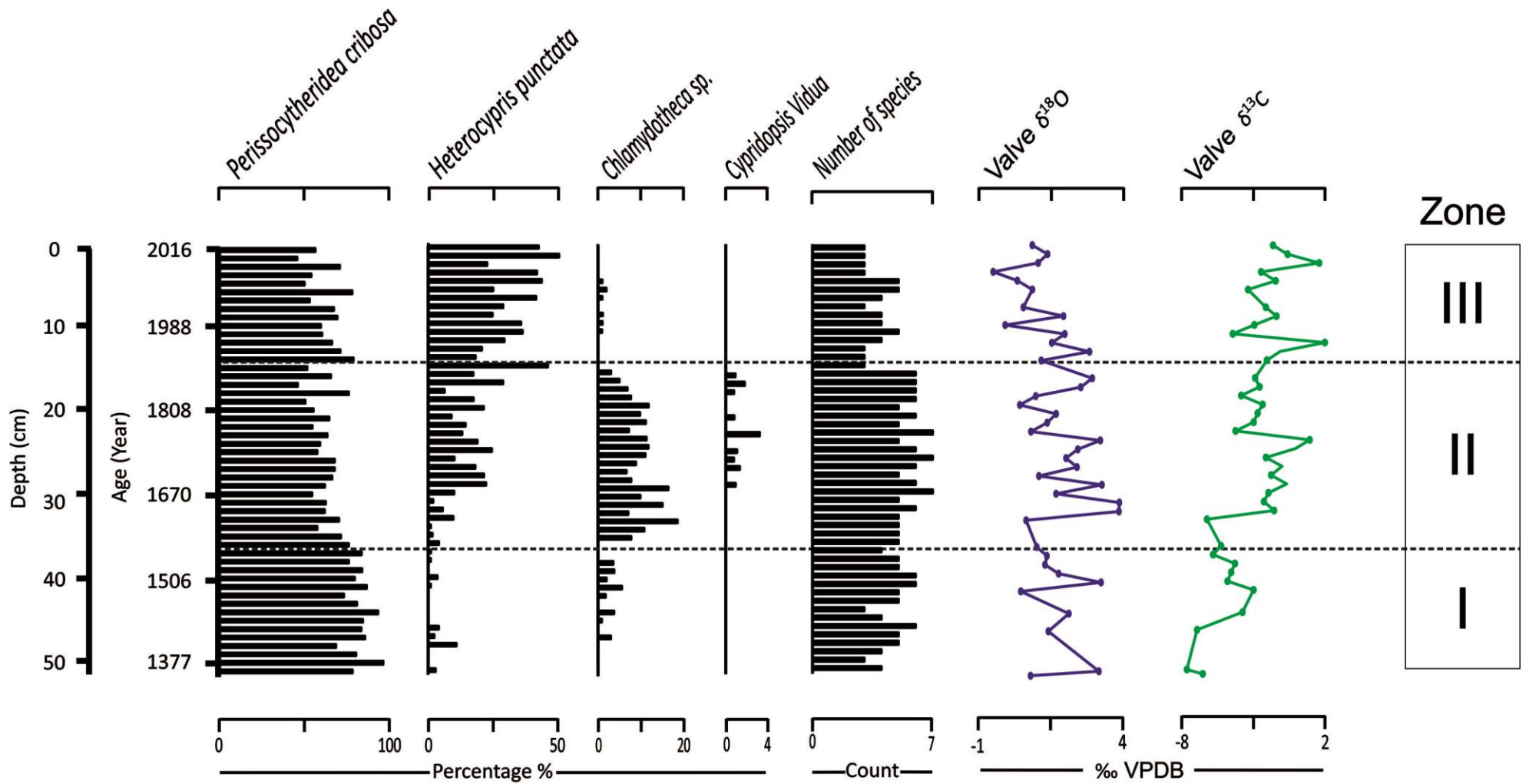


Figure 9: Combination plot highlights changes in key ostracod taxa in relation to variations in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$

4.2. Paleoproductivity

Numerous studies suggest that ecosystem dynamics within lacustrine systems are often strongly correlated with changes in primary productivity (Carpenter et al., 1987; Goldman & Jassby, 2001; Jia et al., 2020). In this study, it is also observed that changes in primary production play an integral role in shaping both species richness and diversity of the ostracod assemblage in FWP. This relationship was identified through the use of the stable carbon isotope composition ($\delta^{13}\text{C}$) derived from the individual ostracod valves of *H.punctata*. $\delta^{13}\text{C}$ is utilized as an indicator of (paleo)productivity due to the fact that the lighter isotope ^{12}C is preferentially absorbed up by plants during photosynthesis, which leaves the lake water TDIC enriched in the heavier ^{13}C isotope (Aravena et al., 1992; Griffiths, 1993). Thus, positive (negative) excursions in $\delta^{13}\text{C}$ are typically indicative of enhanced (decreased) periods of ecosystem productivity. However, it is important to note that changes in the $\delta^{13}\text{C}$ of ostracod valves are also influenced by a number of other factors. The exchange of CO_2 between the atmosphere and the lake water as well as the rate of plant respiration and decay are two examples of these factors. In the previous study conducted at FWP, Burn et al., 2016 indicated that TDIC may not have been in complete isotopic equilibrium with the atmosphere and that there were several factors possibly influencing the isotopic signature. Nevertheless, variations in $\delta^{13}\text{C}$ are still interpreted as an indicator of changes in ecosystem (paleo)productivity.

Based on the observed fluctuations in $\delta^{13}\text{C}$, primary productivity in FWP varied significantly since the lake was formed. A comparison of the carbon isotopy with the ostracod assemblage indicates that there is generally a unimodal relationship between primary production and the number of species present. This suggests that following the establishment of the lake, the species richness-productivity relationship has consisted of an increasing phase which was soon followed by a decrease towards the present. Based on the intermediate disturbance hypothesis (IDH), it is proposed that at the lower end of the increasing phase, primary productivity could not sustain the rarest species, resulting in low species richness and diversity (Dial & Roughgarden, 1998). As primary productivity gradually increased, the conditions were more favourable not only for the existing ostracods but also for a larger number of species, resulting in a much richer and more diverse assemblage (Figure). However, there came a point at which the number of species began to decrease. This was a consequence of competition between existing species which resulted in a few highly competitive species monopolising all of the available resources. In this view, the ostracod assemblage at FWP is driven by competition for both scarce resources at the low end and for abundant resources at the high end. However, the availability of these resources is driven primarily by primary production within the lake system.

Interestingly, each of the ostracod faunal zones (FWP 1- FWP 3) represent one of the IDH phases that have previously been described, highlighting the strong ostracod-productivity relationship (Figure 10). In this way, primary productivity in FWP 1 was relatively low and gradually increased over time which was mirrored by an increase in the species richness and diversity in the zone. The assemblage is dominated by *P.cribrosa* which accounts for 81% of the fauna with both species from the genus *Potamocypris* also accounting for 14% of the fauna in this zone. This implies that the other four species that were identified existed in negligible quantities. Therefore, the dominance of these species points to the relatively low diversity in

the zone which was probably driven by low levels of primary productivity which led to increased competition for limited resources. In this way, as productivity gradually increased so did the number of species that would coexist within the lake. However, the transition from FWP 1 to FWP 2 was marked by a decrease in productivity which affected the ostracod assemblage. Specifically, small populations of *Chlamydotheca sp.* that began to develop in the later part of FWP 1 disappeared for a brief period. In spite of this species richness within the lake remained fairly constant. After this brief decline, primary productivity then abruptly increased around ~1650 CE which led to a synchronous increase in ostracod species richness and diversity. Within this zone, all eight (8) species coexist because the competitively dominant species *P. cribrosa* was unable to control all of the available resources. As such, species that were rare/non-existent in FWP 1 such as *Chlamydotheca sp.*, *H. punctata* and *C. vidua* were by far most abundant in this zone. This increase in productivity was also marked by a progressive increase in the abundance of freshwater gastropods and charophyte oospores. The correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in FWP 2 is strong ($r^2=0.6$) which suggests that changes in the lake's hydrological regime may be driving variations in primary productivity and ultimately the ostracod population. This is not surprising given that in a small coastal lake like FWP, increased periods of precipitation would lead to both more surface runoff and usually greater input of nutrients, supporting higher levels of productivity (Prairie & Cole, 2022). However, given that $\delta^{18}\text{O}$ values have increased, it suggests that this period is marked by a significant decrease in both precipitation and lake levels. This is quite surprising given that freshwater species and vegetation appear to be thriving. Nevertheless, it is suggested that the higher temperatures and high evaporation that led to the reduced lake level played an essential role in promoting primary productivity. As time progressed, the lake level did not fluctuate very much which allowed attached algal and rooted macrophyte communities to gradually establish themselves in the lake. Their presence can be mapped by the appearance of *C. vidua* which is well known for its association with weeds of *Chara sp* (Roca et al., 1993). Therefore, it is clear that both species diversity and richness are at their peak when there are sufficient resources for all species to coexist and ecosystem disturbance is neither too rare nor too frequent.

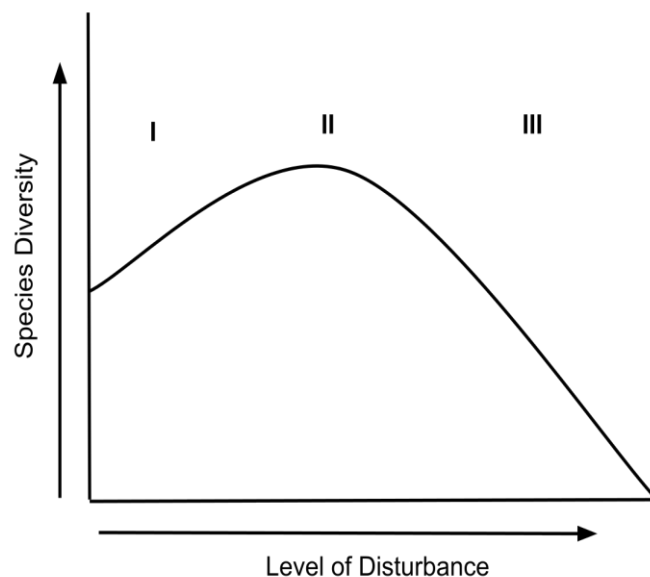


Figure 10: Graph highlighting the principles of the intermediate disturbance hypothesis.

Based on this relationship, the notable decrease in both precipitation and primary productivity in the latter period of FWP 2 caused too much disturbance within the ecosystem which led to the observed decrease in ostracod species richness. Specifically, populations of *Chlamydotheca*, *C.vidua*, *C.Edentata* and *Potamocypris sp.2* steadily declined following this period and were all unable to recover when conditions became more favourable in FWP 3. This suggests that the conditions that existed in FWP 2 represented the intermediated level of productivity which was most ideal for species to coexist and the FWP 2-FWP 3 boundary marks the transition to a high productivity environment where only a few highly competitive species dominate. Therefore, within FWP 3 the most notable variations are found in the two most common species, *P.cribrosa* and *H.punctata* which for much of the sequence were observed to be mutually exclusive. Given their ecological preferences, it is unlikely that both *P.cribrosa* and *H.punctata* were in direct competition for the same resources which is why they were able to coexist. In FWP 3, both of these species make up more than 90% of the assemblage, thus, supporting the theory of competitive exclusion which states that it is impossible for species that compete for the same limited resources to coexist in populations that are constant (Kneitel, 2008). However, it is assumed that *H.punctata* was in direct competition with several species but was able to gain a slight advantage over other weaker species such as *Chlamydotheca* and *C.vidua* during the brief period of aridity which led to their domination in the long term. This theory was also proposed by Burn et al., 2016 and was further supported by the prolonged relative abundance of the freshwater gastropod populations found within the lake. Had the decline in *Chlamydotheca* and *c.vidua* populations been driven by hydrological changes alone, a corresponding decline in the population of *P. parvulus* would have occurred. It is also important to note that during this time there was a substantial increase in the sedimentological characteristics such as mean grain size and the sediment accumulation rate. Based on the evidence there is a possibility that this shift in sedimentological properties and by extension productivity was driven by an increased human presence on the landscape. FWP 3 spanned from 1963-2013 which is well known as a period of increased population growth and the expansion of the tourism industry on the island (Bain et al., 2017). As such, it is possible that human activities led to increased input of sediment and eutrophication which increased primary production and ultimately drove the observed change in the ostracod fauna.

The results presented here highlight the relationship between primary production and the ostracod faunal assemblage at FWP. This relationship was defined as unimodal and provides an excellent case study for the IDH. The faunal zones clearly correspond to each distinct phase of the IDH, with FWP 2 representing the intermediate levels of disturbance within the lake system where ostracod species richness and diversity peaked. Therefore, it can be concluded that during the late Holocene the dominant control on the ostracod faunal assemblage in FWP was interspecies competition which was driven by changes in the lakes' primary production with secondary contributions from changes in precipitation, lake level, sediment accumulation and human activity.

5. Conclusion

The primary aim of this research project was to identify the environmental factors controlling observed changes within the ostracod assemblage at Freshwater Pond. The data presented here suggest that the sediment sequence at FWP could be divided into three (3) distinct biostratigraphic units on the basis of its ostracod fossil content. These units serve as significant indicators of the lake water environment with their boundaries marking the outermost ecological limits for the specific species that are present in that zone. With this in mind, the occurrence of these zones was correlated with changes in lake hydrology and primary productivity which are environmental factors that are known to influence the composition of ostracod assemblages in tropical freshwater lakes. Lake levels were inferred from variations in the oxygen-stable isotopic ($\delta^{18}\text{O}$) composition of ostracod valves from the species *H.punctata*, which were coupled with changes in the sedimentological characteristics of the core. The combined results indicate that large fluctuations in lake hydrology have occurred over the past few hundred years. Based on the observed correlation between these fluctuations and changes in the ostracod assemblage, there are several instances within the sequence that suggest lake-level changes may have indirectly influenced changes in ostracod populations but it was never the dominant control. These findings contradict the position that was taken by Burn et al who suggested that changes in lake level may have been a leading control on the ostracod population at FWP. On the other hand, there is a strong unimodal relationship observed between changes in the ostracod assemblage and primary productivity. From this relationship, it has been concluded that variations in primary productivity represent the availability of resources within the lake system. Therefore, in periods of low productivity (FWP 1), the ostracod assemblage was less diverse due to increased competition for limited resources. In contrast, once there was an increase in productivity and an abundance of resources (FWP 2), ostracod populations were able to thrive. However, an overabundance of resources (FWP 3) represented by an additional increase in primary productivity led to the decline in species diversity due to the fact that the two most competitive species of *P.Cribrosa* and *H.Punctata* were able to take control of all the available resources. Therefore, it can be concluded that during the late Holocene the dominant control on the ostracod faunal assemblage in FWP was competition which was driven by changes in the lakes' primary production with secondary contributions from changes in precipitation, lake level, sediment accumulation and human activity.

6. Auto Critique

The results obtained from this study were difficult to interpret so I decided to stick with what I assumed to be the simplest explanation, although another author may have interpreted them differently. However, I do believe that this study would have benefited from additional analysis of the ostracod assemblage. Specifically, I would have liked to pay closer attention to both the carapace-to-valve ratio and the age structure of the ostracod populations to gain a better understanding of the depositional environment. I also would have liked to quantify downcore variations in the gastropod and *Chara* sp. populations that we observed in the sediments. This would have clarified some of the uncertainties regarding changes in the lake's salinity. Similarly, it may have been useful to identify changes in the diatom population with the lake as well. Thus, there is certainly scope for additional work to be done on this core. Nonetheless, I still strongly believe the current conclusions are accurate.

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