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N and C Isotope Variations Along an Extreme Eutrophication and Salinity Gradient in the Coorong Lagoon, South Australia

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The Coorong Lagoon is a unique hydrological and depositional system at the terminus of the Murray–Darling Basin, the largest river system in Australia. It exhibits large salinity, nutrient, and organic matter gradients, providing a modern analogue to study and validate the use of δ^{15}N and δ^{13}C as tracers of past and contemporary geochemical cycles in estuarine environments. To this end, water and surface sediment samples were analyzed for particulate organic nitrogen (PON) and carbon (POC) concentrations, and the respective δ^{15}N and δ^{13}C signatures of particulate nitrogen and carbon. PON and POC exhibited positive relationships to chlorophyll-a, indicating the dominance of phytoplankton production upon suspended organic matter. There was also a general trend of increasing δ^{15}N of PON ($\delta^{15}N_{PON}$) values and decreasing δ^{13}C of particulate carbon ($\delta^{13}C_{PC}$) values with increasing salinity and eutrophication in the restricted South Lagoon. In a multiple linear regression for $\delta^{15}N_{PON}$, the best two predictors in combination are PON and C:N molar ratio, highlighting the importance of productivity and the type or source of organic matter. For $\delta^{13}C_{PC}$, the best two predictors are total dissolved phosphorus and latitude, suggesting influences from productivity and proximity to the ocean. Sediment δ^{15}N values across the Coorong Lagoon overlap with the $\delta^{15}N_{PON}$ in the water column, suggesting that PON derived from algal material represents the main source of nitrogen to lagoon sediments. We hypothesize that limited N loss via denitrification leads to PON being recycled almost exclusively to ammonium, due to low rates of nitrification and dominance of dissimilatory nitrate reduction to ammonium (DNRA). We propose that preferential volatilization of ^{14}N in ammonia increases the δ^{15}N of ammonium assimilated by phytoplankton, thereby increasing the δ^{15}N within suspended organic matter and surface sediment in the South Lagoon. By contrast, the gradient exhibited in $\delta^{13}C_{PC}$ data was countered by a relatively constant sedimentary organic carbon δ^{13}C. Data from the Coorong, therefore, suggest that δ^{15}N values in sediments can be used to infer palaeoproductivity in this hypereutrophic and hypersaline depositional environment, however, the measured $\delta^{13}C_{PC}$ may be influenced by $\delta^{13}C_{DIC}$ or preferential loss of ^{13}C during sedimentation that alter the sedimentary $\delta^{13}C$ record of organic carbon.

Keywords: $\delta^{15}N$, $\delta^{13}C$, particulate organic matter, palaeoenvironment, hypersaline, hypereutrophic, Coorong Lagoon, Australia

INTRODUCTION

Nitrogen and carbon are bioessential elements and key constituents of living organisms and accumulated organic matter in both marine and terrestrial environments. The isotopic compositions of these elements can provide source and process-related information for both modern and past depositional environments (Casciotti 2016; DeNiro and Epstein 1978; Mettam and Zerkle 2021; Miyake and Wada 1967; Ohkouchi, et al., 2015; Sigman and Casciotti 2001). Nitrogen stable isotope ($\delta^{15}N$) composition in sedimentary archives are used to infer changes in the biogeochemical nitrogen cycle, water column redox, anoxia/euxinia, and nutrient conditions in past marine and coastal environments (e.g., Sigman and Casciotti, 2001; Wang et al., 2018; Cox et al., 2019; Davis et al., 2019; Isaji et al., 2019; Obrist-Farner et al., 2019; Tuite et al., 2019; Zhu et al., 2020). The stable isotope composition of carbon ($\delta^{13}C$) in marine sedimentary archives, including both carbonates and organic sediments, is also interpreted to reflect aquatic productivity and carbon cycling from local to global scales, as well as to assess the relative contributions of terrestrial and marine organic matter, and marine vs. freshwater mixing in past aquatic environments (e.g., Popp et al., 1997; Meyers and Lallier-Verges 1999; Wilson et al., 2005; Lamb et al., 2006). Sediment $\delta^{13}C$ records have also been used to determine relative sea level fluctuations in marine, coastal, and estuarine environments (e.g., Chmura and Aharon et al., 1995; Lamb et al., 2006; Goslin et al., 2017). Carbon and nitrogen isotope analyses are often complimented by the molar ratio of C:N within sediments, which represents an index for primary producers in the system, where higher C:N ratios (>20) are usually found in organic matter with a higher lignin or cellulose content, namely, derived from higher plant matter (Elser et al., 2000). By contrast, C:N ratios <10 are more commonly found in algal, bacterial, and cyanobacterial biomass due to the absence of reinforced cell walls and, thus, the greater relative contribution of amino acids and pigments to the total molecular composition (Meyers and Lallier-Verges 1999; Cadd et al., 2018).

Interpretation of $\delta^{15}N$ and $\delta^{13}C$ from sedimentary archives, however, requires a detailed understanding of the above processes and their impacts on the isotopic fractionation and cycling of nutrient and carbon species in modern marine and coastal systems (Casciotti 2016; Mettam and Zerkle 2021). This is particularly important in hypersaline and eutrophic environments, which are common in coastal and lacustrine settings, where the state and composition of the biological community is strongly affected by changes in the physiochemical parameters (Brookes, et al., 2009; Isaji, et al., 2019; Tweedley, et al., 2019). Nevertheless, to date, only a limited number of studies have examined variability in the $\delta^{15}N$ and $\delta^{13}C$ of organic matter within modern depositional systems characterized by extreme hypersaline and hypereutrophic conditions (e.g., Chen et al., 2017; Isaji, et al., 2019; Šajnović, et al., 2020). Rather, studies in hypersaline environments have predominantly focused on using $\delta^{13}C$ in diatoms, ostracods, microbial mat deposits, and carbonates, or sedimentary facies and evaporate deposits as proxies of palaeoclimate and palaeosalinity (e.g., Sylvestre et al., 2005; Frantz et al., 2014; Schröder et al., 2018; Buongiorno et al., 2019; Cuna-Rodriguez et al., 2020).

The Coorong Lagoon and Murray Mouth Estuary in South Australia, the terminus of the largest river system in Australia (the Murray–Darling Basin), is a Ramsar-listed wetland of international importance. It comprises a unique coastal aquatic and depositional system that exhibits a strong salinity gradient, ranging from fresh in the northern end, which receives riverine inflows to hypersaline in the south (e.g., 3–160 PSU). There is also a progressive increase in total nutrient and organic matter stocks in the more restricted and hypersaline South Lagoon, which reaches hypereutrophic conditions due to reduced freshwater flushing and nutrient retention (Mosley, et al., 2020). The transition to hypereutrophic conditions has caused deposition of organic rich sulfidic black muds in the modern system (Herczeg et al., 2001; Fitzpatrick et al., 2019; Haynes et al., 2019). The natural salinity and eutrophication gradient, existence of both terrestrial and marine water and nutrient sources, and current depositional environment makes the Coorong Lagoon an interesting analogue to aid interpretations of sedimentary $\delta^{15}N$ and $\delta^{13}C$ proxy records from ancient coastal lagoon systems and euxinic ocean conditions.

The aim of this study is to investigate the variability in the $\delta^{15}N$ and $\delta^{13}C$ of organic matter in the waters and surface sediments of the Coorong Lagoon in the context of a broad salinity and nutrient gradient. These findings are intended to support the interpretation of $\delta^{15}N$ and $\delta^{13}C$ data from sedimentary archives rich in organic matter (e.g., organic-rich shales), with implications for ancient hypersaline and hypereutrophic environments in euxinic ocean and semi-restricted coastal settings.

STUDY AREA

The Coorong Lagoon is a shallow (~1.3 m deep) and narrow (~2 km wide) lagoon system that runs northwest to southeast along the South Australian coast for approximately 110 km, separated from the ocean by a sand barrier (**Figure 1**). A narrow constriction (~100 m wide) in the middle of the Coorong Lagoon, at Parnka Point, separates the lagoon into

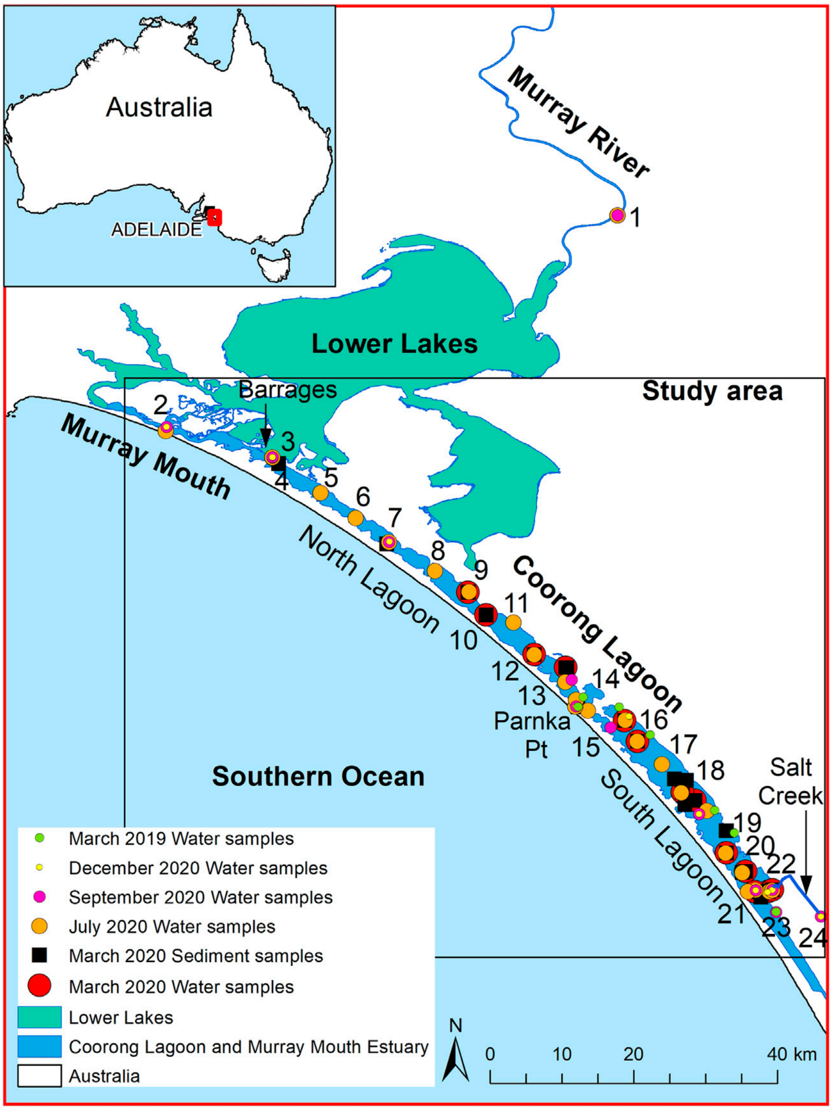

FIGURE 1 | Map of the Coorong Lagoon including location of water and sediment sampling sites. Parnka Point is located at site number 14 and Policeman's point is located at site number 19.

two: the North Lagoon and South Lagoon (**Figure 1**; Mosley, 2016; Stone et al., 2016; Gibbs et al., 2019).

The Murray Mouth, a constricted outlet to the Southern Ocean at the northwestern end of the Coorong Lagoon, allows exchange of seawater into the North Lagoon, influencing water levels in the Coorong Lagoon (Kingsford, et al., 2011). To the east of the Murray Mouth, Murray River waters enter the Coorong Lagoon via the Lower Lakes from regulated barrage structures along the Lower Lakes–Murray Mouth connection, with the Tauwitchere barrage (site 3; **Figure 1**) being the largest and closest to the Coorong Lagoon (Mosley, 2016). Rising tides and high freshwater flows from the Murray River refill the lagoon and lower salinities throughout the Coorong Lagoon in winter (Brookes et al., 2009; Brookes et al., 2020; Ryan, 2019). Fresh to brackish continental waters also enter the southern end of the endorheic South Lagoon from Salt Creek, however, flows are not sufficient to counter evaporation and to lower salinity in this "terminal" lagoon with no major outflows (**Figure 1**). Thus, the Coorong operates as a reverse estuary with salinity increasing from the Murray Mouth toward the South Lagoon (Geddes and Butler, 1984; Geddes et al., 2016: **Figure 2**). While there is a latitudinal gradient, the water column is well mixed vertically with no salinity or other gradients present due to strong wind mixing in the shallow lagoon (Mosley et al., 2019).

Prior to European settlement, there is evidence that the Coorong was less saline, less turbid, and had lower nutrient concentrations compared with the system today (Dick, et al., 2011; Krull, et al., 2009; McKirdy, et al., 2010). Annual sedimentation rates during the Holocene ranged from 1.6 mm in the North Lagoon to <1 mm in the South Lagoon (Haynes

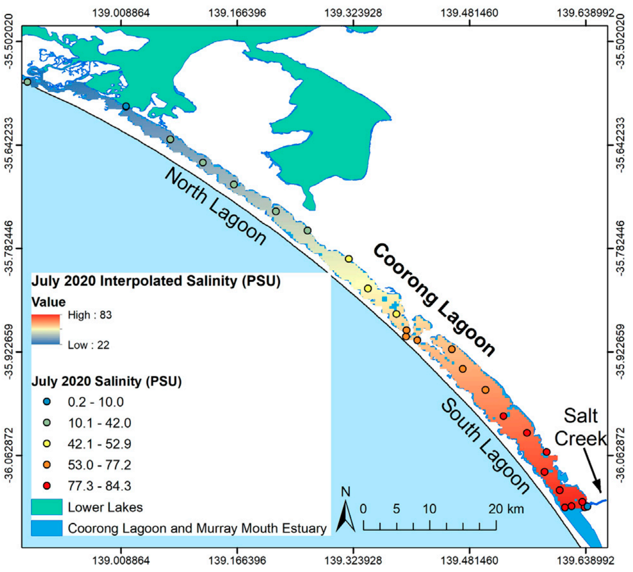

FIGURE 2 | Winter July 2020 salinity measurements and interpolated surface (linear trend in ArcGIS).

et al., 2019). Since European settlement, waters from the Murray–Darling Basin have been diverted, and the rivers within the basin have become highly regulated with streamflow reduced by 60% (Aldridge, et al., 2019; Ryan, 2019).

Currently, the lack of fresh water flushing and evaporation of the lagoon water concentrates salts, nutrients, and other solutes in the water column, especially in the South Lagoon, and has accelerated sedimentation rates. The impact of these reduced flows, land-use changes, and evaporation of the lagoon water has caused increasing trends in salinity, total nutrients, and chlorophyll-a, and a shift to a system dominated by phytoplankton rather than submerged aquatic plants (Herczeg, et al., 2001; Mosley, et al., 2020; Reeves, et al., 2015; Stone, et al., 2016). Consequently, a large proportion of the nutrient inputs from the Murray River and Salt Creek are retained within the lagoon, especially the South Lagoon, and not exported to the ocean (Cook, et al., 2010; Stone, et al., 2016). Thus, the Coorong Lagoon is hypereutrophic with high total nutrient loads and very high algal loads all increasing southward, although dissolved nutrients are low due to rapid uptake by algae (Aldridge, et al., 2019; Ford 2007; Geddes and Butler 1984; Stone, et al., 2016). These impacts have led to a shift in the phytoplankton community from microalgae to cyanobacteria dominated throughout the lagoon, with filamentous green algae blooms becoming an ongoing problem in the South Lagoon (Leterme et al., 2015; Collier et al., 2017; Aldridge et al., 2019). Additionally, sedimentation rates have exponentially increased throughout the Coorong Lagoon due to anoxic preservation of the increased organic matter, and these changes are reflected in the deposition of organic-rich sulfidic black muds since the 1950s (Herczeg et al., 2001; Fitzpatrick et al., 2019; Haynes et al., 2019).

METHODS

Sample collection and preservation

Coorong Lagoon water samples were collected in March 2019; and March, July, September, and December 2020, and sediment samples were collected in March 2020. As the water column throughout the Coorong Lagoon is shallow and well mixed, representative water samples were collected from ~50 cm below the water surface. Onsite measurements of physical and chemical water properties were recorded using a calibrated YSI™ Pro DSS Sonde and handheld meter, including the temperature, dissolved oxygen concentration, salinity, turbidity, and pH. Most samples were collected by boat; however, due to inclement weather and/or boat access issues, some samples were collected by wading from the northern shore. The location of all samples collected in these field trips are shown in **Figure 1**, and the sampling methods used are specified in **Supplementary Table S1**.

For isotope analysis of particulate N and C, aliquots of unfiltered water samples were passed separately through PALL type A/E glass fiber filters with a 1-μm pore size. For total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), and NH_4^+ concentrations, water samples were filtered using 0.2-μm PES syringe filters into acid-cleaned HDPE bottles. All samples including filters containing particulate matter were stored frozen until analysis.

Sediment samples, with a water column of approximately 1 m above, were collected using a "Russian D" auger to a depth of approximately 50 cm. Some shallow shoreline samples were collected with a polycarbonate core tube pushed into the sediment. To investigate the recent transition to hypersaline and eutrophic conditions in the Coorong Lagoon subsamples of the surface (0–2 or 0–5 cm layer), "modern" sediment identified by the organic rich layer, due to rapid mixing in the top up to 5 cm (Krull et al., 2009), were homogenized at the time of sampling for analysis. Samples were immediately placed in sealed vials with no air gap and cooled on ice. Upon return to the laboratory (within 48 h), samples were frozen at −20°C until analysis.

Additionally, *Ruppia tuberosa* (hereafter Ruppia) and cyanobacteria mat biomass samples were collected from Noonamenna, and Ruppia and filamentous algae samples were collected from Salt Creek sampling sites in March 2020.

Analytical procedure for nutrient concentrations and isotopes in water samples

Analyses for total particulate nitrogen and carbon concentration, $^{15}N/^{14}N$ ratio and $^{13}C/^{12}C$ ratio were analyzed from the PALL type A/E glass fibe filters at Monash University analytical and stable isotope facility using a continuous flow isotope ratio mass spectrometer (CF-IRMS; Sercon Ltd., UK; Russell et al., 2018).

The C/N molar ratio was estimated based on beam area using internal standards with known amount of carbon and nitrogen along with the samples for each analysis. Previous comparisons between the concentrations of organic carbon and total carbon suspended in Coorong waters indicated that inorganic carbon accounted for a minor (undetectable) fraction of the suspended load. As a consequence, due to the small sample sizes available, and due to the primary focus of this study being the nitrogen isotope system, particulate carbon samples were not acidified prior to isotope analysis. As a consequence, the suspended carbon isotope data reported here are strictly "total particulate carbon;" however, we interpret this signal to primarily reflect the $^{13}C/^{12}C$ of particulate organic carbon. The isotopic and elemental composition of these samples, as described below, supports this interpretation. Concentrations of NH_4^+, TDN, and TDP were analyzed at Monash University analytical and stable isotope facility. Nutrient concentrations were quantified spectrophotometrically following the procedures in Standard Methods for Water and Wastewater (APHA 2005), using a Lachat QuikChem 8000 Flow Injection Analyzer (FIA). Samples for TDN and TDP were digested with alkaline persulfate prior to analysis via FIA. Dissolved phosphorus was measured as orthophosphate using method 4500-P G as described in APHA (2005). The accuracy of these analyses was within ±2%. Chlorophyll-a were measured at the Australian Water Quality Centre (AWQC), South Australia, a National Association of Testing Authorities (NATA) accredited laboratory.

Analytical procedure for nutrient concentrations and isotopes in sediment and aquatic plant samples

Total carbon and nitrogen concentrations were measured via high-temperature combustion and infrared detection using a LECO CNS TruMAC Analyzer in the Environmental Analysis Laboratory, Lismore, Australia. Total organic carbon ($\%C_{org}$) was measured using the same analytical method following pretreatment of the sample with dilute HCl to remove inorganic carbon. The $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios of sedimentary organic matter were analyzed by EA-IRMS in the Environmental Analysis Laboratory, Lismore, Australia, with HCl pretreatment prior to carbon isotope analysis as above. All carbon and nitrogen isotope data are reported using the standard delta notation, relative to the standards of air for nitrogen and PDB for carbon.

Ruppia, cyanobacteria, and filamentous algae samples were dried at 60°C, pulverized, and weighed into tin cups before being analyzed at Monash University on an ANCA GSL2 elemental analyzer interfaced to a Hydra 20–22 continuous-flow isotope ratio mass spectrometer (Sercon Ltd. UK). Quality control was carried out using four internal standards (ammonium sulfate, sucrose, gelatine, and bream), which were calibrated against internationally recognized reference materials including USGS 40, USGS 41, IAEA N1, USGS 25, USGS 26, and IAEAC-6. The internal standards were used to correct for any variations as a result of peak size linearity and instrumental drift with typical reproducibility of ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. Based on these internal standards, the accuracy of our data was calculated to fall within ±0.3‰ for $\delta^{15}N$ and ±0.2‰ for $\delta^{13}C$.

Statistical analysis

Processes controlling water column nutrient and POM concentrations were explored through principal component analysis (PCA; Jackson 1992) of the variable latitude, salinity, pH, DO, temperature, turbidity, alkalinity, chlorophyll-a, PON, POC, TOC, DOC, TN, TDN, DON, TKN, TP, TDP, FRP, and C:N molar ratio (**Supplemental Analysis and Results; Supplementary Table S1**) using the *vegan* package (Oksanen, et al., 2020) in R. Best subset regression was performed using the *regsubsets* function in the package *leaps3.1* for R (Lumley, 2020) to guide exploratory data analysis to identify the best single and combination of variables that explain variability in $\delta^{15}N_{PON}$ and $\delta^{13}C_{PC}$. These proposed relationships were then explored using classical multiple linear regression, with model significance tests conducted using analysis of variance (ANOVA; Chambers and Hastie, 1992), and only models that were significant with variance inflation factors (VIF) close to 1 are kept and presented (Fox and Monette 1992; Fox and Weisberg 2018).

RESULTS

Water column results

There is a general pattern of increasing salinity (**Figure 3A**), and PON (**Figure 3B**) and POC concentrations (**Figure 3C**) from the North Lagoon to the South Lagoon. PON and POC concentrations increase from the North Lagoon (~0.2 mg L^{-1} N and ~1.4 mg L^{-1} C, respectively) to the South Lagoon (up to 0.9 mg L^{-1} N and 6.7 mg L^{-1} C; **Figures 3B, C**). In the warmer seasons, salinity in the South Lagoon can become concentrated by evaporation to >100 PSU (**Figure 3A**), however, PON and POC do not appear to increase in concentration to a similar extent (**Figure 3D**).

In general, salinity, PON and POC concentrations in the Murray River are low (<1 PSU, <0.2 mg L^{-1} N, and <0.5 mg L^{-1} C, respectively), although relatively high PON and POC concentrations occur in the Lower Lakes (upstream of Tauwitchere barrage; up to 1.1 mg L^{-1} N and 11 mg L^{-1} C, respectively; **Figures 3B, C**) and salinities in the Murray Mouth can reach that of seawater (~35 PSU). Finally, salinity, PON and POC concentrations in Salt Creek are generally low compared with the South Lagoon (<15 PSU, <0.2 mg L^{-1} N, and <2.8 mg L^{-1} C, respectively). However, during the March sampling period, PON and POC concentrations were similar to that of the South Lagoon (0.8 mg L^{-1} N and 6 mg L^{-1} C, respectively).

C:N molar ratios of POM average 9 ± 4 in the North Lagoon, 9 ± 1 in the South Lagoon, 9 ± 4 in Salt Creek, 8 ± 4 in the Murray River, with larger C:N ratios in the Lower Lakes (14 ± 2) and Murray Mouth (14 ± 8; **Supplementary Table S2**). These are all higher than the Redfield C:N ratio of 6.6 and represent phytoplankton.

The $\delta^{15}N_{PON}$ values average 4.3 ± 2.9‰ (**Figure 4A**; **Supplementary Table S2**), and the $\delta^{13}C_{PC}$ values average −26.5 ± 1.9‰ in the Coorong (**Figure 4B**; **Supplementary Table S2**). The $\delta^{15}N_{PON}$ and $\delta^{13}C_{PC}$ values in the Coorong show opposite trends with $\delta^{15}N_{PON}$ increasing from the North

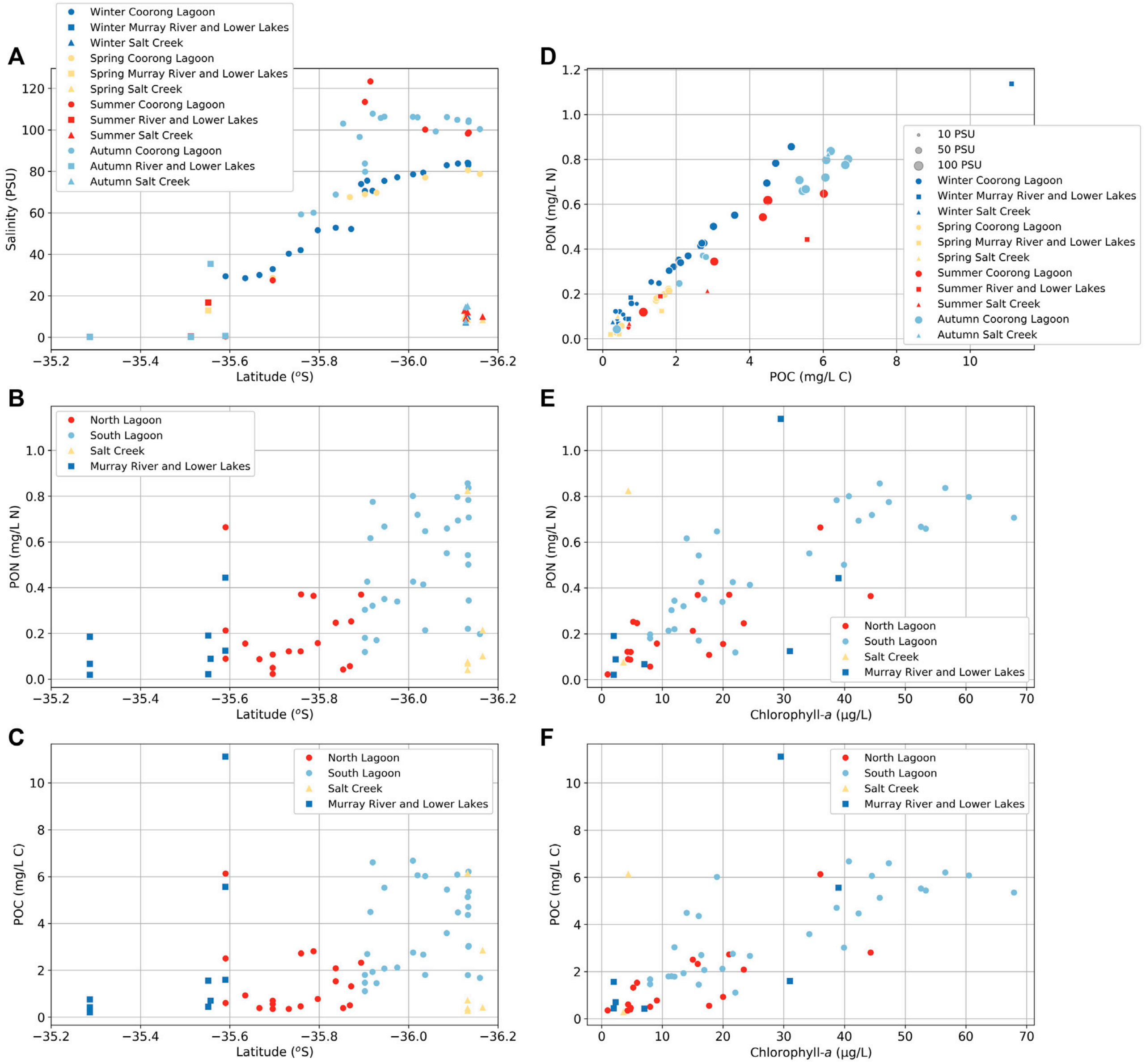

FIGURE 3 | (A) Salinity plotted along sample latitude showing sampling season. **(B)** Particulate organic nitrogen (PON) concentrations and **(C)** particulate organic carbon (POC) concentrations plotted against sample latitude. **(D)** PON against POC showing sampling season. **(E)** PON concentrations and **(F)** POC concentrations plotted against chlorophyll-a concentrations.

Lagoon to South Lagoon, and $\delta^{13}C_{PC}$ values decreasing across the same latitudinal gradient. The average $\delta^{15}N_{PON}$ in the South Lagoon (+4.5 ± 1‰) is ~1‰ higher compared with the North Lagoon (+3.8 ± 2‰; **Supplementary Table S2**). There is also a 2‰ increase in $\delta^{13}C_{PC}$ values from the South Lagoon (−27.4 ± 1.5‰) to the North Lagoon (−25.2 ± 1.8‰; **Supplementary Table S2**). Lower Lakes $\delta^{13}C_{PC}$ values also average −25.1 ± 0.7‰, whereas the Murray River $\delta^{13}C_{PC}$ values average −29.3 ± 0.9‰, and the Salt Creek $\delta^{13}C_{PC}$ values average −25.3 ± 2‰. The $\delta^{15}N_{PON}$ values in Salt Creek and Murray River are (+3.43 ± 1.5‰ and +3.9 ± 3.5‰, respectively). Ruppia from the North Lagoon and Salt Creek regulator had $\delta^{13}C$ values of −13.8‰ and −15.3‰, whereas filamentous algae from the Salt Creek regulator had $\delta^{13}C$ values of −12.5‰ and a cyanobacterial mat from Noonamenna in the North Lagoon had $\delta^{13}C$ values of −18.1‰ (**Supplementary Table S2**).

N and C isotope results for sediments

Total organic carbon and total nitrogen in the South Lagoon sediments (6.6 ± 2.6% and 0.4 ± 0.3%, respectively) are double

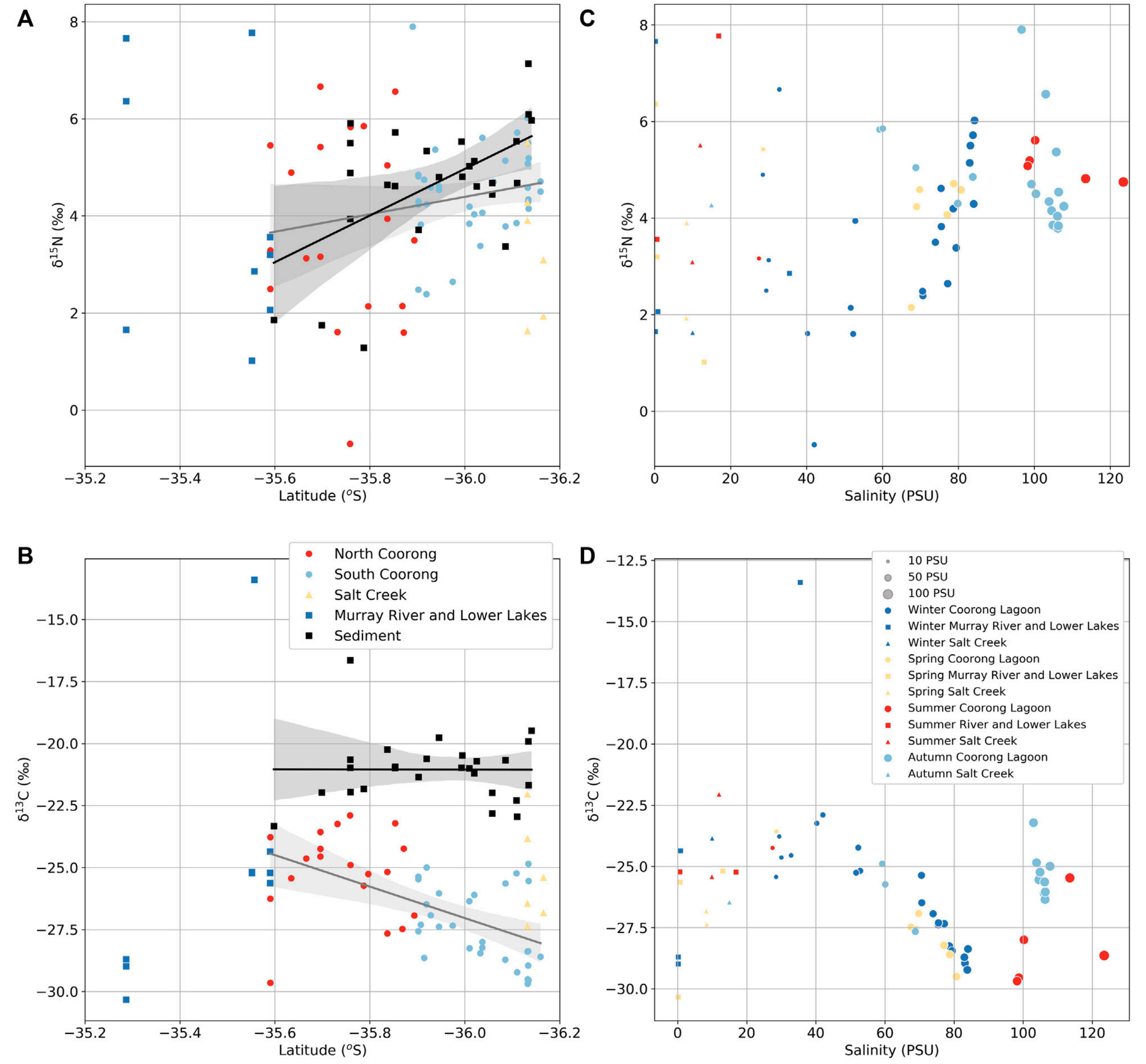

FIGURE 4 | (A) PON and bulk sediment δ^{15}N results and **(B)** particulate carbon (PC) and bulk sediment δ^{13}C results against sample latitude. Legend in **(B)** applies to **(A)** as well. **(C)** $\delta^{15}N_{PON}$ results and **(D)** $\delta^{13}C_{PC}$ results against salinity. In both, the gray regression line represents all Coorong Lagoon POM isotope values and black regression line represents the bulk sediment isotope values. Legend in **(D)** applies to **(C)** as well.

that of the North Lagoon sediments (1.8 ± 1.8% and 0.2 ± 0.2%, respectively; **Supplementary Table S3**). The C:N molar ratios of both the North Lagoon and South Lagoon are 9 ± 2 (**Supplementary Table S3**).

Sedimentary organic matter δ^{15}N values range from +1.3‰ up to +7.1‰ and increase from the North Lagoon (+4.0 ± 1.7‰) to South Lagoon (+5.1 ± 0.9‰; **Figure 4A**; **Supplementary Table S3**). By contrast, there is no significant difference between the North Lagoon (−21 ± 1.8‰) and South Lagoon (−21 ± 1.0‰) bulk sediment δ^{13}C values, with the full range from −16.6‰ to −23.3‰ (**Figure 4B**).

DISCUSSION

Processes controlling water column nutrient and POM concentrations

Salinity increases from north to south along the Coorong Lagoon (**Figure 2**) with higher concentrations of dissolved ions in summer compared with winter, especially in the South Lagoon (**Figure 3A**), due to evaporation and the lack of seasonal flushing owing to the Coorong Lagoon being a reverse estuary (Webster 2010). Similar trends to those seen for salinity are also shown for PON, POC (**Figures 3B, C**), and other nutrient concentrations,

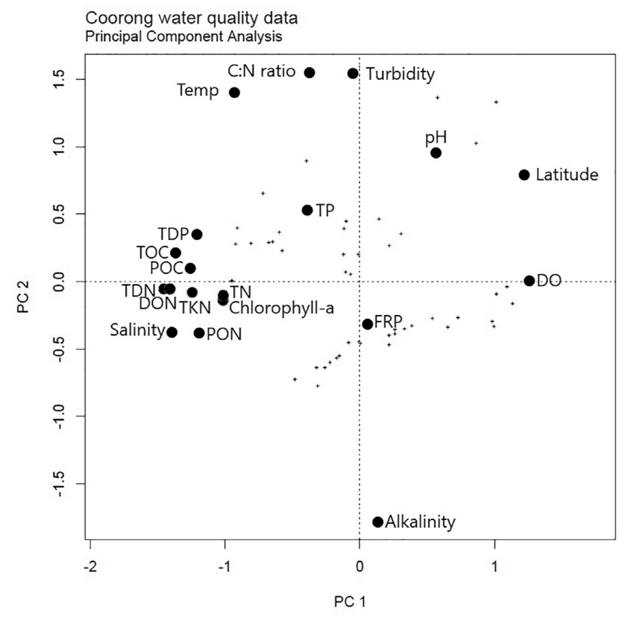

FIGURE 5 | Principal component analysis (PCA) results for the Coorong Lagoon water dataset (**Supplementary Table S1**).

such as TN, TOC, and DOC, which also exhibit increasing concentrations from north to south, as previously reported (e.g., Aldridge et al., 2019). Interestingly, the range of variability in PON and POC across the latitudinal gradient is greater than that of salinity, and they do not increase in concentration to a similar extent in summer compared with winter (**Figure 3D**). Instead, the variability in PON and POC across the lagoon primarily reflects phytoplankton biomass, as reflected by the correlation with chlorophyll-a concentration (**Figures 3E, F**), whereby biomass is higher in the South Lagoon (Mosley et al., 2019; Mosley et al., 2020). Carbon: chlorophyll-a ratios of ~50:1 support this interpretation, and that of Ford (2007), who found that most of the POC in the Coorong can be accounted for by phytoplankton production (Reynolds 1997). Additionally, the C:N molar ratios (9 ± 3; **Supplementary Table S2**) of POM throughout the North and South Lagoons are consistent with predominantly phytoplankton-derived suspended organic matter (cellulose, lipid, and protein, etc.; Cadd et al., 2018; Huang et al., 2020; Meyers and Lallier-Vergès 1999; Tyson 1995).

Principal components analysis (PCA) of the water chemistry data shows that chlorophyll-a, PON, POC, DON, TDN, TKN, TN, TOC, and salinity all covary with the first principal component (**Figure 5**). This confirms that nutrient concentrations are the primary driver for productivity and, hence, PON and POC concentrations in Coorong waters. Additionally, covariation of salinity with nutrient, chlorophyll-a, and POM concentrations highlights that all are primarily controlled by the lack of flushing. Thus, the overall increase in productivity and nutrient concentrations from north to south in the Coorong appears to primarily be controlled by the lack of flushing due to hydrological restriction of the South Lagoon that acts as an endorheic system, or a "closed basin" with no major outflows.

A lack of flushing ensures that the nutrients, suspended load, and sediments are inefficiently removed from the lagoon system into the ocean, further exacerbating their progressive accumulation in the South Lagoon. The reduced amount of flushing over recent years is linked to the shallowing of the South Lagoon due to enhanced evaporation, and physical restrictions caused by the buildup of sediments in the narrower channels of the Coorong (Haynes et al., 2019). The high salinity also inhibits macroinvertebrate survival and bioturbation (Dittmann et al., 2015; Remaili et al., 2018), thus promoting anoxia and sulfate reduction in the surface sediments, especially in the South Lagoon. Thus, we hypothesize that this lack of flushing and restriction of the South Lagoon are one of the fundamental causes of its salinization, the accumulation of nutrients, enhanced productivity, and hence, the buildup of particulate organic matter, all of which contribute to local sediment anoxia, especially in the South Lagoon (Mosley et al., 2020).

Processes controlling POM isotope values

The combined effects of flushing, salinization, and eutrophication also appear to affect the $\delta^{15}N_{PON}$ and $\delta^{13}C_{PC}$ isotope values throughout the entire Coorong Lagoon (**Figure 4**). There is a general decrease in $\delta^{13}C_{PC}$ from north to south with increasing salinity (**Figures 4B, D**). However, the $\delta^{13}C_{PC}$ values of samples near Salt Creek are higher (~26‰) compared with the rest of the South Lagoon samples (**Figures 4B, D**). Likewise, there is a subtle increase in average $\delta^{15}N_{PON}$ from north to south with increasing salinity (**Figures 4A, C**).

Redundancy analysis (RDA) and best subsets regression were used to preliminarily explore which of the environmental variables in the Coorong best predict variability in $\delta^{15}N_{PON}$ and $\delta^{13}C_{PC}$. These observations were then formally tested using multiple linear regression, with models validated using model-to-model ANOVA tests and by rejecting models with variance inflation factors >1.5. The best single predictor of $\delta^{15}N_{PON}$ was POC (R^2 = 0.15, p = 0.004; **Table 1**), followed closely by PON (R^2 = 0.13, p = 0.006; **Table 1**). The best two predictors for $\delta^{15}N_{PON}$ in a multiple linear regression are PON and C:N molar ratio (R^2 = 0.26, ANOVA p-value < 0.001; **Table 1**), beyond which more complex models failed to meet significance test criteria. This suggests that of the measured variables, phytoplankton biomass or productivity, in addition to the composition of the suspended organic matter—either

TABLE 1 | Redundancy analysis and best subsets regression analysis results.

Variable	Predictors	R^2	p-Value
$\delta^{15}N_{PON}$	Particulate organic carbon (POC)	0.15	0.004
$\delta^{15}N_{PON}$	Particulate organic nitrogen (PON)	0.13	0.006
$\delta^{15}N_{PON}$	PON and C:N atomic ratio	0.26	<0.001
$\delta^{13}C_{PC}$	Total Kjeldahl nitrogen (TKN)	0.35	<0.001
$\delta^{13}C_{PC}$	Total dissolved phosphorus (TDP) and latitude	0.44	0.006

taxonomic make up or input from other sources—are the principal controls over $\delta^{15}N_{PON}$, although with a large amount of variance unexplained. The correlation between $\delta^{15}N_{PON}$ and biomass can be potentially explained by the higher productivity and recycling of nitrogen between the sediment and water column in the South Lagoon. Additionally, changes in nitrification/denitrification, as well as the Rayleigh fractionation of nitrogen during assimilation, may also promote an increase in $\delta^{15}N_{PON}$ by preferentially removing ^{14}N from the lagoonal water (e.g., Wada 1980; Zanden and Rasmussen 1999; Ohkouchi et al., 2015). Overall, our data from the Coorong Lagoon suggest that variability in suspended PON concentration and $\delta^{15}N_{PON}$ are best interpreted as tracers of productivity and associated nitrogen cycling.

The best single predictor of $\delta^{13}C_{PC}$ is total Kjeldahl nitrogen (TKN), a measure of the total concentration of organic nitrogen and ammonia ($R^2 = 0.35$, p-value < 0.001; **Table 1**). In a multiple linear regression, the best two predictors in combination are TDP and latitude ($R^2 = 0.44$, ANOVA p-value $= 0.006$; **Table 1**). Broadly speaking, this relationship between $\delta^{13}C_{PC}$, TDP, and latitude is best explained by proximity to marine carbon sources, in combination with a complex array of factors linked to nutrient driven productivity (Krull, et al., 2009; McKirdy, et al., 2010). The influence of marine–freshwater mixing on $\delta^{13}C_{PC}$ values is manifested by the higher, marine-like $\delta^{13}C$ values near the Murray Mouth (Middelburg and Nieuwenhuize 1998), which decline with both increasing or decreasing salinity (**Figure 4D**). This marine effect is likely countered by possible kinetic isotopic fractionation during CO_2 hydration and hydroxylation during periods of intense productivity in hypersaline waters, which could contribute to observed ^{13}C-depleted DIC values and the trend of the decreasing $\delta^{13}C_{PC}$ at salinities between 40 and 100 PSU (**Figure 4D**) (Clark, et al., 1992; Lazar and Erez 1992). The higher $\delta^{13}C_{PC}$ values of the hypersaline (>100 PSU) South Lagoon in summer and autumn sampling periods are more readily interpreted in the context of eutrophication and changes in phytoplankton composition as progression to filamentous algae ($\delta^{13}C_{PC} = -12.5‰$) dominance during high evaporation periods in the South Lagoon (Leterme et al., 2015; Collier et al., 2017) could lead to increased $\delta^{13}C_{PC}$. Additionally, higher $\delta^{13}C_{PC}$ values could be due to decreased photosynthetic carbon isotope fractionation at higher phytoplankton growth rates (e.g., Laws et al., 1995; Zanden and Rasmussen 1999; Ohkouchi et al., 2015). Nevertheless, several other potential mechanisms and processes may contribute to the relationship between $\delta^{13}C_{PC}$ and nutrient concentration, which require further investigation. For example, in organic rich sediments, higher $\delta^{13}C_{PC}$ can be linked to microbial mineralization of detrital organic matter, leading to the release of ^{13}C enriched carbon into the water column. In addition, it is known that the South Lagoon receives a considerable amount of dissolved Sr from Salt Creek and/or via groundwater inputs (Shao, et al., 2018; Shao, et al., 2021), and thus it is also plausible that such alkaline continental water inputs also contain ^{13}C-enriched DIC, which may thus contribute to the higher $\delta^{13}C_{PC}$ observed in the southernmost part of the Coorong Lagoon (**Figure 4D**). Future research into $\delta^{13}C$ of DIC is required to verify this hypothesis.

Processes controlling sediment N and C isotope values

Before delving into the sediment $\delta^{15}N$ and $\delta^{13}C$ results, it is important to note that the South Lagoon sediments have a greater proportion of total organic carbon and total nitrogen than those in the North Lagoon (**Supplementary Table S3**), reflecting higher net deposition of organic matter in the South Lagoon (Haynes et al., 2019). In fact, the total organic carbon contents in the South Lagoon sediments are approaching those of black shales.

It has been determined above that water column $\delta^{15}N_{PON}$ and $\delta^{13}C_{PC}$ values, and the total organic carbon and total nitrogen in the sediment, throughout the Coorong Lagoon are affected by nutrient concentrations and associated productivity, as well as proximity to the ocean. However, for sediment-derived $\delta^{15}N$ and $\delta^{13}C$ proxy signals to be useful tracers of the above processes in palaeolagoon or coastal systems, it is essential to understand the preservation and "transfer" of $\delta^{15}N_{PON}$ and $\delta^{13}C_{PC}$ signals into a local sediment.

Comparison of $\delta^{15}N_{PON}$ and sediment $\delta^{15}N$ values (**Figure 4A**) shows that generally sediment $\delta^{15}N$ overlaps with the "long-term" average $\delta^{15}N_{PON}$ suggesting autochthonous phytoplankton-derived nitrogen represents the primary source of N to the lagoon sediment. This is consistent with algal deposition from a highly eutrophic water column (Pérez-Ruzafa, et al., 2019) and previous research using nitrogen and carbon isotopic biomarkers (Krull et al., 2009; McKirdy et al., 2010). In fact, McKirdy et al. (2010) found South Lagoon sediments to be continuously richer in total nitrogen reflecting higher productivity and hence net deposition of organic matter and nutrients compared with the North Lagoon during the mid-to-late Holocene. They also found a decrease in $\delta^{15}N$ in the upper ~50 cm due to a greater contribution by halotolerant cyanobacteria, and this is also preserved in our data with an increase in sediment $\delta^{15}N$ from 3.9‰ to 5.5‰ from 0–2 to 5–10 cm from a site in the North Lagoon (**Supplementary Table S3**).

Currently, it is likely that the sediment $\delta^{15}N$ values are not significantly altered from the $\delta^{15}N_{PON}$ values due to the shallow water column (Tesdal, et al., 2013). Nitrification of ammonium is also likely severely limited in the oxygen-poor, organic matter and sulfide-rich sediments, as nitrifying bacteria have a lower affinity for oxygen than aerobic heterotrophs and other chemoautotrophs and are outcompeted by these under oxygen-limited conditions (Kemp, et al., 1990). This effect would be reinforced by the extremely low macroinvertebrate diversity and abundance in the South Lagoon sediments (Dittmann, et al., 2015; Tweedley, et al., 2019), as the presence of macrofauna typically enhances benthic nitrification by increasing sediment oxygenation and the provision of aerobic niches for nitrifying bacteria in their burrow wall sediments (Welsh, 2003; Stief, 2013). Limited nitrification rates would also intrinsically limit N-losses from the lagoon as gaseous products via denitrification and competition with the alternative nitrate reduction process dissimilatory nitrate reduction to ammonium (DNRA) would further decrease N-loss (An and Gardner 2002; Ford 2007; Valiente et al., 2022). DNRA competes with denitrification and, therefore, limits N-loss as N_2 by recycling the nitrate produced from ammonium by nitrification back to ammonium leading to enhanced retention of nitrogen in the system (e.g., Burgin and Hamilton 2007; Giblin et al., 2013; Hardison, et al., 2015; Magri, et al., 2020). The organic matter-rich, highly reduced sediments that are present in the South lagoon would favor DNRA over denitrification as a nitrate reduction process (An and Gardner, 2002; Nizzoli et al., 2006; Molnar et al., 2013). Thus, overall benthic N-cycling is dominated by processes that favor the retention, accumulation, and recycling of N, rather than N-loss processes and thereby supporting ongoing eutrophication of the South Lagoon. This hypothesis is supported by the higher nitrogen content in sediments in the South Lagoon (**Supplementary Table S3**), as well as high NH_4^+ concentrations (up to 10 mg L^{-1}: **Supplementary Table S1**) measured in sediment pore waters in the South Lagoon, which would support high diffusive fluxes of ammonium to the overlying water to fuel phytoplankton production and further PON loads to the sediment. Additionally, in the absence of other quantitatively significant N-loss processes (flushing and denitrification) volatilization of ammonia (NH_3) to the atmosphere may be a quantitatively important N-loss process, which would be facilitated by the Coorong water with pH values >8 (**Supplementary Table S1**). This would also result in isotopic fractionation due to preferential volatilization of light $^{14}NH_3$ compared with $^{15}NH_3$ (Li et al., 2012). This would result in the residual dissolved ammonium available for phytoplankton being ^{15}N-enriched and the ammonium regenerated during remineralization of this phytoplankton biomass also being ^{15}N-enriched. Thus, progressively over time repeated cycles of ammonium assimilation and remineralization, isotopic fractionation during ammonia volatilization may have contributed to the heavy $\delta^{15}N$ values (5.6‰–6.8‰) in sediment and PON in the South Lagoon, and the overlap in the sediment and PON $\delta^{15}N$ values (**Figure 4A**).

The transfer of $\delta^{13}C_{PC}$ variability into the sediment $\delta^{13}C$ record appears more complex. The sediment $\delta^{13}C$ signatures are consistently higher (5‰–7‰) and less geographically variable compared with $\delta^{13}C_{PC}$ (**Figure 4B**), with the $\delta^{13}C$ of sedimentary TOC varying around −21 ± 1‰ (**Figure 4B**). It is possible that the sediment $\delta^{13}C$ values represent a mixture between aquatic plant and algae deposition, since the Ruppia, cyanobacterial mat, and filamentous algae $\delta^{13}C$ values range between −12.5‰ and −18.1‰. However, this observation contrasts with the general absence of aquatic plants in the majority of the South Lagoon presently due to hypersalinity and light limitations due to turbidity and phytoplankton blooms (Dick, et al., 2011, Kim, et al., 2013; Aldridge et al., 2019). An alternative interpretation is that terrestrial detritus from areas bordering the lagoons also contributes to the sedimentary pool (Middelburg and Nieuwenhuize 1998). However, isotope signatures for local terrestrial plants ($\delta^{13}C$ values between −25‰ and −30‰; Krull et al., 2009) indicate that this mixture cannot entirely explain the observed sediment $\delta^{13}C$ values. Also, a previous study at nearby Lake Alexandrina showed that <10% of organic matter preserved in sediments was from terrestrial plants (Herczeg, et al., 2001). Instead, it is also possible that isotopically light carbon could have been lost from the sediment due to methanogenesis or preferential microbial mineralization of ^{12}C. Conversely, if isotopically heavy carbon is delivered to the lagoon sediment as carbonate, whereupon it dissolves in the low pH environment of the sediment, the isotopically heavy CO_2 produced could be assimilated by phytoplankton and bacteria. Alternatively, it is possible that the $\delta^{13}C$ of sedimentary carbon reflects a contribution by a large mass of recalcitrant carbon (i.e., resistant to decomposition) preserved from the now absent macrophyte communities. However, Krull et al. (2009) found that *Ruppia megacarpa* ($\delta^{13}C$ of −13‰) was the predominant source of organic carbon in the North Lagoon prior to the 1950s. They determined that the upper modern 0–5 cm of sediment organic matter $\delta^{13}C$, which fluctuates around −22 ± 1.2‰ and is identical within error to our analyses of −21 ± 1.3‰ (**Supplementary Table S3**), is predominantly degraded phytoplankton. In addition, the sediment C:N ratios of 9 ± 2 are consistent with a phytoplankton source (Krull et al., 2009; McKirdy et al., 2010). Thus, it is possible that the $\delta^{13}C_{PC}$ measured in this study is influenced by DIC and the sediment organic $\delta^{13}C$ carbon is a result of algal deposition similar to the sediment $\delta^{15}N$ values. The above interpretations to explain the observed $\delta^{13}C$ variability in sedimentary carbon archives across the Coorong Lagoon thus need further process-based investigations to corroborate the validity of these different hypotheses and scenarios.

Implications for palaeo-environmental reconstructions based on $\delta^{15}N$-$\delta^{13}C$ proxies

The acquired data from the restricted, hypersaline, and hypereutrophic Coorong Lagoon represent a useful case study to test the sensitivity and fidelity of $\delta^{15}N$ and $\delta^{13}C$ proxies as tracers of past environmental conditions and their temporal changes in lagoonal and coastal systems. Here we show that the $\delta^{15}N$ in both suspended and sedimentary organic matter is sensitive to spatial variability in phytoplankton biomass, which, in turn, is primarily controlled by local nitrogen mineralization or recycling with eutrophication primarily being driven by internal processes not external nutrient inputs. In part, this is linked to the hypersalinity and eutrophic conditions related to lagoon restriction and the associated decrease in flushing of nutrient-rich lagoonal waters, which yielded progressively higher $\delta^{15}N$ signatures (up to +8‰) in the South Lagoon. Furthermore, surficial lagoon sediment $\delta^{15}N$ values follow the same general pattern as the overlying water column $\delta^{15}N_{PON}$ suggesting that processes that determine $\delta^{15}N$ in the water column are also reflected in the sediments. This is due to a high degree of dominance of internal processes, as N assimilation into PON is being regenerated by breakdown of PON in the sediment. Whereas, if the $\delta^{15}N_{PON}$ was driven by external nutrient inputs, then $\delta^{15}N_{PON}$ would be intermediate between that of these inputs and the ammonium coming from the sediment. Thus, the correlation between $\delta^{15}N_{PON}$ and sediment $\delta^{15}N$ values representing modern sediment (Krull et al., 2009) is mostly a function of the unique restricted, hypersaline, and hypereutrophic conditions characteristics of the Coorong

Lagoon, and especially for its southern parts. However, there is greater variance in the $\delta^{15}N_{PON}$ values compared with the sediment $\delta^{15}N$ values suggesting that the sediment is an integration of the relatively long-term signals derived from the water column. Therefore, based on this case study, it would appear that $\delta^{15}N_{PON}$ is largely recorded and preserved in the sediment $\delta^{15}N$ archives in these types of lagoonal and coastal systems, and that nitrogen isotope analysis of ancient estuarine/lagoon or coastal marine sediments has the potential to be used as a proxy for palaeo-productivity in hypersaline and hypereutrophic depositional systems. These results also have relevance for understanding deep time sedimentary systems, particularly the ancient anoxic (Archean) sediments where organic matter and N may be preserved from the water column sources.

In contrast, the $\delta^{13}C$ of the surficial sediments in the Coorong does not directly reflect that of $\delta^{13}C_{PC}$, suggesting the $\delta^{13}C_{PC}$ is influenced by variable $\delta^{13}C_{DIC}$. An additional hypothesis is that preferential mineralization of nitrogen over carbon is occurring, where carbon spends relatively more time tied up as sediment organic matter. Additionally, the $\delta^{13}C$ of the surficial sediments could be the result of diagenetic alteration on $\delta^{13}C$ at sediment–water interface upon the deposition of local organic matter. If the former is the case, it is conceivable that $\delta^{13}C$ of sediment organic matter is autochthonous phytoplankton derived carbon. In order to verify these effects more research is needed into the influence of various inputs, sources, and local biogeochemical cycling of both inorganic and organic carbon in the Coorong Lagoon.

Overall, the Coorong Lagoon with its extreme gradient in environmental conditions and processes, and deposition of organic rich sulfidic sediments, can provide potential insights into ancient ocean conditions in relation to nitrogen and carbon isotope patterns under highly sulfidic conditions with no significant bioturbation. Similar conditions are considered to have occurred during ocean anoxic events and the deposition of ancient black shale environments in deep time (Meyer and Kump 2008; Rickard, 2012). Thus, the Coorong Lagoon represents a useful analogue to better understand C and N isotope records and redox conditions during deposition of organic-rich sediments in ancient and redox-stratified basins.

CONCLUSION

Investigations into contemporary carbon and nitrogen cycles and associated isotope variability are essential for interpreting sedimentary $\delta^{15}N$ and $\delta^{13}C$ records in the context of past salinity and nutrient conditions in restricted estuarine/lagoonal and coastal systems. To this end, the $\delta^{15}N$ and $\delta^{13}C$ of suspended particulate matter and underlying sediments were investigated in the Coorong Lagoon, South Australia, to test the effect of eutrophication and increased salinity across a wide natural environmental gradient.

In the highly restricted Coorong Lagoon, the lack of freshwater flushing and high evaporation rates causes hypersalinity and eutrophication of local lagoonal waters, particularly in the South Lagoon. This lack of flushing causes a north–south trend of increasing nutrient load, which is also reflected by increasing POM and chlorophyll-a concentrations due to increased phytoplankton productivity in more restricted and nutrient-rich parts of the lagoon. This nutrient-productivity gradient, in addition to changes in marine–freshwater mixing and differences in organic matter composition, is reflected by both the $\delta^{15}N$ and $\delta^{13}C$ of suspended particulate matter in the water column.

Importantly, this water column $\delta^{15}N$ signal or an isotope gradient of particulate organic matter ($\delta^{15}N_{PON}$) is also effectively transferred and recorded in local sediment archives deposited in the Coorong Lagoon. By contrast, $\delta^{13}C$ differs markedly between suspended particulate matter and surficial lagoon sediments, suggesting the influence of either recalcitrant legacy organic matter derived from now absent aquatic macrophytes, or the effects of diagenetic processes and carbon remineralization at the sediment–water interface. Overall, our results suggest that variability in the $\delta^{15}N$ of sediment organic matter could provide a robust proxy for palaeo-productivity in the Coorong and/or similar coastal lagoon/estuarine systems elsewhere. It is possible that, similar to the sediment $\delta^{15}N$ values, sediment organic $\delta^{13}C$ carbon is a result of algal deposition and $\delta^{13}C_{PC}$ measured in this study is influenced by variable $\delta^{13}C_{DIC}$. However, if $\delta^{13}C_{PC}$ is not influenced by DIC sedimentary organic $\delta^{13}C$ signal and archives in this system offers a more complex record of past environmental change, which may be still representative of previous conditions, or instead considerably modified and altered by diagenetic processes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

SP, JT, LM, and JF contributed to the conception and design of the study. WW performed the sample analysis. SL, YS, and ZW contributed to the data collection. SP wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2021.727971/full#supplementary-material

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