Phytoplankton and Phytobenthic Productivity along a Salinity Gradient in the Coorong and Murray Mouth

Sasi Nayar and Maylene G K Loo

April 2009
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Foreword

The environmental assets of the Coorong, Lower Lakes and Murray Mouth (CLLAMM) region in South Australia are currently under threat as a result of ongoing changes in the hydrological regime of the River Murray, at the end of the Murray-Darling Basin. While a number of initiatives are underway to halt or reverse this environmental decline, rehabilitation efforts are hampered by the lack of knowledge about the links between flows and ecological responses in the system.

The CLLAMM program is a collaborative research effort that aims to produce a decision-support framework for environmental flow management for the CLLAMM region. This involves research to understand the links between the key ecosystem drivers for the region (such as water level and salinity) and key ecological processes (generation of bird habitat, fish recruitment, etc). A second step involves the development of tools to predict how ecological communities will respond to manipulations of the “management levers” for environmental flows in the region. These levers include flow releases from upstream reservoirs, the Lower Lakes barrages, and the Upper South-East Drainage scheme, and dredging of the Murray Mouth. The framework aims to evaluate the environmental trade-offs for different scenarios of manipulation of management levers, as well as different future climate scenarios for the Murray-Darling Basin.

One of the most challenging tasks in the development of the framework is predicting the response of ecological communities to future changes in environmental conditions in the CLLAMM region. The CLLAMMecology Research Cluster is a partnership between CSIRO, the University of Adelaide, Flinders University and SARDI Aquatic Sciences that is supported through CSIRO’s Flagship Collaboration Fund. CLLAMMecology brings together a range in skills in theoretical and applied ecology with the aim to produce a new generation of ecological response models for the CLLAMM region.

This report is part of a series summarising the output from the CLLAMMecology Research Cluster. Previous reports and additional information about the program can be found at http://www.csiro.au/partnerships/CLLAMMecologyCluster.html
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Acknowledgements

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We also acknowledge the contribution of several other funding agencies to the CLLAMM program and the CLLAMMecology Research Cluster, including Land & Water Australia, the Fisheries Research and Development Corporation, SA Water, the Murray Darling Basin Commission’s (now the Murray-Darling Basin Authority) Living Murray program and the SA Murray-Darling Basin Natural Resources Management Board. Other research partners include Geoscience Australia, the WA Centre for Water Research and the Flinders Research Centre for Coastal and Catchment Environments. The objectives of this program have been endorsed by the SA Department of Environment and Heritage, SA Department of Water, Land and Biodiversity Conservation, SA Murray-Darling Basin NRM Board and Murray-Darling Basin Commission.

We thank the editor (Jason Tanner) and the reviewers (Rod Oliver and Peter Fairweather) for their critical but constructive feedback. We also wish to acknowledge Jason Nichols and Bruce Miller Smith for their significant assistance with field-work. Leonardo Mantilla and Sharon Drabsch are thanked for their assistance in the laboratory. We acknowledge Sunil Sharma who kindly provided the map for the study region used in this report. Brian Deegan, Kane Aldridge and Justin Brookes, University of Adelaide are thanked for inputs on field sites and accommodating our request to loan their benthic chambers for phytobenthic productivity measurements. The National Collaborative Research Infrastructure Strategy - National Photobioreactor Facility is thanked for granting us access to the microfiltration apparatus, liquid scintillation counter and the discrete nutrient analyser.
Executive Summary

The Coorong, Lower Lakes (Lake Alexandrina and Lake Albert) and Murray Mouth, is one of Australia's largest estuaries, at the terminal end of Australia's two longest rivers. This unique area of the Murray basin also has significant value in terms of indigenous heritage, commercial and recreational fishing, water sports and tourism. There is a paucity of data on primary productivity and nutrient cycles in the Coorong and Murray Mouth. This study was undertaken to map seasonal variations in primary production along a salinity gradient in the Coorong and the Murray Mouth. Very low values were obtained for phytoplankton productivity using the dissolved oxygen technique during the first two sampling times (September and November 2007). An underestimation of gross productivity is suspected resulting from sensitivity issues with the oxygen-based technique in low productivity conditions, coupled with significant community respiration occurring. Consequently, in April 2007, both the 14C technique and dissolved oxygen technique were used to measure phytoplankton productivity. Comparison of phytoplankton productivity indicated that measurements made using the 14C technique were approximately ten times higher than gross productivity using the dissolved oxygen technique at the three study sites. In April 2008, comparisons of phytoplankton productivity measurements using the 14C technique with net phytobenthic productivity indicated that phytoplankton productivity could be significant at Jack Point. However, this needs to be verified further with more sites and sampling times using the 14C technique.

Phytoplankton productivity in April 2008 ranged from 0.7 (Mundoo Channel) to 7.4 mgC m⁻² h⁻¹ (Jack Point). On the other hand, net phytobenthic productivity ranged from 7.67 ± 0.70 mgC m⁻² h⁻¹ (mean ± SE; Mundoo Channel; September 2007) to 24.86 ± 1.06 mgC m⁻² h⁻¹ (Noonameena; April 2008). Phytobenthic community respiration ranged from 12.76 ± 1.43 mgC m⁻² h⁻¹ (Jack Point; September 2007) to 33.48 ± 11.70 mgC m⁻² h⁻¹ (Mundoo Channel; September 2007). There was significant interaction between sampling times and sites for phytobenthic productivity and for phytobenthic respiration, significant differences were found for sites. While it is evident from the present study that the phytobenthic component is dominant, it is also hypothesized that there is heterotrophic productivity in the water column and sediments, which could also be a significant driver of the ecosystem processes in the Coorong and the Murray Mouth.
1. Introduction

It is recognised that phytoplankton are the major contributors to global marine primary production in estuaries, coastal lagoons and other intertidal habitats. Phytobenthos has also been reported to be of great significance in these shallow marine and intertidal habitats (Charpy-Roubaud and Sourina 1990), and may account for as much as one-third, to two-thirds of the total primary production in such systems (Asmus 1982, Sullivan and Moncreiff 1988). In certain instances phytobenthic production has been reported to exceed phytoplankton productivity by up to ten-fold in shallow habitats (Cadee and Hegeman 1974, Varela and Penas 1985).

These ecosystems are highly dynamic with regard to their physical and chemical properties that regulate biological productivity. Characterised by high levels of productivity (Borges et al. 2006) and a great diversity of ecological processes (Hopkinson and Smith 2005), these ecosystems are also arguably the most anthropogenically impacted ecosystems on this planet (Edgar et al. 2000). The iconic Coorong, Lower Lakes and the Murray Mouth system in South Australia is a good example of such an ecosystem that is ecologically threatened due to anthropogenic impacts (Phillips and Muller 2006).

The Coorong, Lower Lakes (Lake Alexandrina and Lake Albert) and Murray Mouth, is one of Australia’s largest estuaries, at the terminal end of Australia’s two longest rivers. The Coorong is a coastal lagoon that lies parallel to the coast, and is several kilometres wide and more than 100 km long from the Murray Mouth. This is divided into the North and the South lagoons. The Coorong lagoon occupies most of the inter-dune area and is connected to the sea via the mouth of the River Murray (Deckker and Geddes 1980). Access to the open sea is restricted by the sand barriers of the dunes on the Younghusband Peninsula, which separates the lagoons of the Coorong from the high energy environment of the Southern Ocean on its western flank (Palinska et al. 1999). The Coorong and the Lower Lakes form a unique wetland system that is Ramsar-listed and classified as one of the six Living Murray “significant Environmental Assets”. This unique area of the Murray basin is also significant in terms of indigenous heritage, commercial and recreational fishing, water sports and tourism (Lamontagne et al. 2004). The functioning of this highly diverse and dynamic ecosystem is coupled to changes in salinity and water levels driven by the interaction between changing sea levels (Webster 2005), rainfall, evaporation, wind, and the now infrequent freshwater riverine inflow and land runoff, resulting in permanently inundated, intermittently wetted and dried areas that are subjected to varying salinities, fluctuating according to seasonal water influxes (Palinska et al. 1999, Ford 2007). A series of barrages constructed inside the mouth separate the lower lakes from the saline waters of the Coorong, which exchange with the sea through the Murray Mouth. The barrages thus prevent the ingress of seawater into the lakes and the Lower Murray. In the past, during times of high discharge in the Murray, significant volumes of freshwater were released across the barrages with flows deemed essential to keep the mouth of the Murray open. However, in the past few decades, the flow in the River Murray has been substantially lower, attributed mainly to irrigation abstraction upstream (Webster 2005). Significantly lower inflow of freshwater has resulted in increased frequency of the closure of the Murray Mouth accompanied by increasing salinity levels in the Coorong causing biophysical changes, with a decline in ecosystem integrity (Lamontagne 2004). The resulting salinity gradient runs from the mouth of the River Murray with a salinity close to seawater in recent years, becoming progressively more saline southeast away from the mouth, terminating in salt flats (Bisson and Kirst 1983, Lamontagne 2004). These changes in salinity gradient in the Coorong have been implicated in large-scale impacts on the distribution of primary producers (such as the keystone species Ruppia), fish and bird communities, a defining feature of the ecology of the Coorong (Geddes and Butler 1984, Geddes 1987, Lamontagne et al. 2004).

While Brookes (2002) hypothesized that the system supports high productivity through efficient recycling of nutrients fostered by the shallow depth of the lagoons, it is recognised that there is a paucity of data on primary productivity and nutrient cycles in the Coorong and...
Murray Mouth (Ford 2007). Key groups of primary producers in this system respond to a wide range of salinities and other physico-chemical parameters, and include phytoplankton, benthic micro- and macroalgal mats, *Ruppia* beds and other seagrasses (Geddes 2005, Ford 2007). This study was undertaken to map seasonal variation in primary production along a salinity gradient in the Coorong and the Murray Mouth. It is expected that the results from this study will assist in developing system models for managers to evaluate benefits through assessment of potential scenarios and ecosystem responses involving primary and secondary producers and consumers, and tertiary consumers. The CLLAMMecology project is significant given the complex management challenges associated with this environment, with significant ecological risks at higher tropic levels (secondary and tertiary), as reflected in the rate of degradation of this fragile ecosystem.

2. Methods

2.1. Sampling sites and times

Three study sites were chosen in the Coorong and Murray Mouth to be representative of the salinity gradient and to give the best spatial coverage (Figure 1). Mundoo Channel in the Murray Mouth represented the estuarine region, Noonameena in the North Lagoon had intermediate salinity and Jack Point represented a hypersaline site in the South Lagoon. Using a GPS, coordinates of all sites were taken on the first sampling trip (Table 1). All field sampling and deployments were carried out during spring (5-7 September 2007), summer (23-25 November 2007) and autumn (8-10 April 2008), with depths kept consistent at 0.6 m for all sites.

Table 1. Coordinates of the three study sites within the Coorong and Murray Mouth in degrees, minutes and seconds (WGS84).

<table>
<thead>
<tr>
<th>Sites</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mundoo Channel</td>
<td>35° 32' 16&quot; S</td>
<td>138° 53' 07&quot; E</td>
</tr>
<tr>
<td>Noonameena</td>
<td>35° 44' 59&quot; S</td>
<td>139° 15' 15&quot; E</td>
</tr>
<tr>
<td>Jack Point</td>
<td>36° 01' 54&quot; S</td>
<td>139° 34' 04&quot; E</td>
</tr>
</tbody>
</table>

2.2. Physico-chemical parameters

Specific conductivity, pH and water temperature were measured at the start of each field sampling using a Hach Senslon 156 multi-parameter probe. Specific conductivity measurements in mS cm\(^{-1}\) were converted to salinity reported as dissolved solid concentrations (g L\(^{-1}\)) using the equation cited in Williams (1986). Photosynthetically Active Radiation (PAR) was measured using a Licor LI 1400 data logger with an underwater quantum sensor. The sensor was secured to a stake at least 5 cm above the sediment surface at a distance of ~2 m from the deployments of chambers and bottles. PAR was logged at 5 minute intervals and measured in µmol photons m\(^{-2}\) s\(^{-1}\). Ambient dissolved oxygen (DO) measurements were made using a TPS DO logger (WP-82) compensated for salinity and temperature. At each of the three sites, the calibrated sensor was fastened to ensure it was at least 10 cm above the sediment surface (Appendix A). The ambient DO logger was set to log every 10 minutes over a 24 hour period. Spot DO measurements were made using a Hach Portable LDO Dissolved Oxygen meter (Model HQ10 with Luminescent Technology LDO Probe). Water samples for dissolved nutrients were filtered through a 0.2 µm pore size syringe filter. About 60 ml of water was filtered into acid washed, double rinsed...
screw capped polyethylene bottle and frozen at -5°C within 5 hours of collection. The frozen samples were brought back to the laboratory and stored at -20°C pending analysis. The nutrient samples were analysed using an Aquakem 250 Discrete nutrient analyser adopting standard protocols for oxidised nitrogen NO₃ (US EPA Protocol 353.1), soluble reactive phosphorus (US EPA Protocol 365.1) and reactive silica (US EPA Protocol 370.1) outlined in APHA (2005). Detection limits for oxidised nitrogen, soluble reactive phosphorus and reactive silica were 0.003 mg L⁻¹, 1 µg L⁻¹ and 0.013 mg L⁻¹ respectively.

Figure 1. Location of the three sampling sites (red arrows) in the Murray Mouth and the Coorong.
2.3. Phytoplankton Productivity

2.3.1. Dissolved oxygen technique

Phytoplankton productivity and community respiration were measured using the dissolved oxygen technique with light and dark bottles as described by Williams et al. (1979). The technique involves parallel incubations in clear (light) and opaque (dark) bottles of water samples from the environment and measuring the rate of oxygen evolution (net production) or uptake (community respiration) in the bottles. The bottles used for incubation were flat rectangular tissue culture flasks with a total surface area of 0.0225 m² and a total volume of 1 L. All bottles were rinsed with filtered sea-water (500 µm mesh) from the site prior to use. All four light and dark bottles were filled with filtered water samples (500 µm mesh) from the site and incubations were carried out in situ at 5 cm below the water surface. Mixing within the bottles was achieved through agitation by the surrounding waters. Two incubations of 150 minutes each were carried out per day in parallel with the chamber incubations for phytobenthic productivity at every site. DO measurements in the bottles were made using the Hach Portable LDO Dissolved Oxygen meter. Net productivity is calculated as the increment in dissolved concentrations in the light bottles over the course of the incubation for each replicate. Community respiration is equated to the rate of deficit in dissolved oxygen concentrations in the dark bottle between the beginning and the end of the incubations. Mean net primary productivity and community respiration were then calculated for each season at each site. Gross phytoplankton productivity was calculated as the sum of net productivity and community respiration.

2.3.2. ¹⁴C technique

The ¹⁴C productivity technique was used to verify the results from the DO technique. These measurements were only carried out in April 2008. Incubation bottles used in this study were 100 ml screw cap clear glass bottles from Schott. Equal numbers of clear bottles were wrapped around by several layers of black Gaffer tape to make up the dark bottles. All bottles were rinsed with deionised water followed by filtered sea-water (500 µm mesh) from the site prior to use. About 100 ml of filtered water (500 µm mesh) from the site was measured accurately and dispensed into each of four light and four dark bottles. The bottles were spiked with 1 ml of 5 µCi of NaH¹⁴CO₃ from a stock solution prepared from an ampule of 5 mCi NaH¹⁴CO₃ (GE Healthcare UK with a specific activity of 2.22 GBq/mmol) made up to 1000ml with filtered nutrient free artificial seawater. The tightly capped bottles were incubated in situ 5 cm below the water surface for 150 minutes. At the end of the incubations, the samples were filtered under vacuum on site through a 0.22 µm pore size, 47 mm diameter membrane filter (Whatman). The filter paper was folded into a 20 ml PE scintillation vial and frozen at −5°C and transported to the laboratory. In the laboratory, the scintillation vials were opened under a fume cupboard. Approximately 500 µml of 0.5N HCl was added to the vial to remove any unfixed tracer on the filter paper and left overnight. The following day, 10 ml of Perkin Elmer Ultima Gold liquid scintillation cocktail was added to the vial. The caps were then screwed on to the vial, the contents agitated and the vials left in the dark overnight. The vials were then read in a Perkin Elmer Tricarb 2900TR liquid scintillation counter, corrected for blank and quenching, and phytoplankton productivity calculated as per Parsons et al. (1989). Mean phytoplankton productivity was then calculated for each site.

2.4. Phytobenthic net productivity and community respiration rates

Benthic chambers used in this study were transparent Perspex domes with a total volume of 9.5 L (Appendix A). A skirt extended outwards from the open end and limited the depth to which the chamber could be pushed into the sediments. The open end of the chamber had a
sharpened edge, which was fully pushed (~100 mm) into the sediments, it enclosed a volume of 4.8 L and covered a surface area of 0.063794 m². All chambers were incubated at a water depth of ~0.6 m.

Seven chambers were deployed at each site for a morning run (~0900h) and an afternoon run (~1200h). Three 'dark chambers' were covered by high-density double-layered black plastic bags with a sinker chain to hold them in place over the chambers underwater (Appendix A). The other three 'light chambers' were left exposed to light. The last chamber with a water-tight lid at the bottom (the open end), enclosing the column water, was a ‘water blank’ to account for water column productivity. Each of the chambers was deployed by pushing into the sediment. Care was taken to ensure minimal disturbance to the sediment and entrapment of air bubbles in the dome. In-line 6 V DC pumps were connected to the chamber by water-tight tygon fittings (Appendix A). These pumps recirculated water through the chamber and over the sensor of the DO probe during incubation. A regulator in line with the power source and the submersible pump (Whale inline 991) was adjusted to regulate and maintain a flow rate of 2L/min. Prior to data logging, the pumps were run for about 5 minutes with the outlet of the pump disconnected from the chamber to ensure mixing of the water within the chamber with that outside. After this, the pumps were re-connected to recirculate the water within the chambers during incubation. The power source was a bank of 6V sealed lead acid batteries with a total capacity of 120 Ah held on an inflatable dinghy (Appendix A). The DO probe of the TPS DO logger was seated firmly in a port on top of the chamber with the water tight seal maintained using teflon tape wrapped around the body of the probe. The loggers used in the seven chambers were TPS WP-82 dissolved oxygen-temperature meters (TPS Pty Ltd, Australia). These were placed in a splash proof box on the dinghy (Appendix A). After the DO probes were left to equilibrate for about 5 minutes, the logger was turned on, with a recording every minute for a run lasting 150 minutes. At the end of the first deployment, the plastic bags for the dark chambers and the probes were removed; and the pumps were left to run for approximately an hour to ensure mixing of the water in the chamber with the ambient water before the next deployment.

Phytobenthic productivity (net productivity) and phytobenthic community respiration were calculated by performing a linear regression of oxygen concentration versus time (using the software package SPSS ver 17). The function obtained was then used to calculate the start and end dissolved oxygen concentrations in the chambers (in mg L⁻¹). This gave the change in oxygen over the incubation time, which was further adjusted for the sediment area and volume of overlying water to determine the rates of oxygen production and consumption. Net productivity and community respiration rates were estimated from these oxygen values for each chamber. Photosynthetic and respiratory quotients of 1.0 were use to convert oxygen data to carbon units.

2.5. Data Analyses

A mixed design repeated measures Analysis of Variance (ANOVA) was used to analyse the net primary productivity and respiration with sampling time treated as a within-subject effect and site as a between-subject effect. Mauchly’s test of sphericity was employed to test for significant differences between the variances of the differences between sampling times. If Mauchly’s test was significant (p < 0.05), F tests were evaluated using adjusted degrees of freedom based on Greenhouse-Geisser epsilon; otherwise, no adjustments were made. Levene’s test was also used to test for homogeneity of variances for each site over time. Where data were found to be heterogeneous, an appropriate transformation was applied and the data re-tested. However, since ANOVA is a robust test where the reliability of the results is only affected by severe deviations (Zar 1996), if the data did not meet the assumption of homogeneity, analyses were carried out on untransformed data. If the results of the ANOVA were significant (p < 0.05), the Tukey test was used to locate the source of the differences, i.e. to determine which sites were significantly different from one another (Zar 1996). The ANOVA analyses were carried out using the software package SPSS (Ver 17).
3. Results

3.1. Physico-chemical parameters

Water temperatures did not vary spatially, but there were seasonal variations (Table 2). Water temperatures did not differ markedly between November 2007 (summer) and April 2008 (autumn) with values ranging from 17°C at Noonameena to 19°C at Jack Point. Temperatures in September 2007 were cooler ranging from 10.9°C at Jack Point to 13.3°C in Mundoo Channel. Salinity on the other hand registered marked differences spatially and seasonally at Noonameena (North Lagoon) and Jack Point (South Lagoon). At Noonameena, salinity increased from 55.2 g L\(^{-1}\) in September 2007 to 87 g L\(^{-1}\) in November 2007, but decreased to 53.3 g L\(^{-1}\) in April 2008 (Table 2). At Jack Point, salinity increased from 66.1 g L\(^{-1}\) in September 2007 to 99.9 g L\(^{-1}\) in November 2007 with a further increase to 114.6 g L\(^{-1}\) in April 2008. Increases in salinity at Mundoo Channel were not as high, from 28.5 g L\(^{-1}\) in September 2007 to 36.7 g L\(^{-1}\) in April 2008 (Table 2). Changes in pH were small with values ranging from 7.7 to 8.3 across sites and between sampling times (Table 2).

Photosynthetically Active Radiation (PAR) did not show a seasonal pattern. However, PAR values at Jack Point were comparatively lower than those at Mundoo Channel and Noonameena (Table 2). PAR during the study period ranged from 408.7 ± 26.5 µmol cm\(^{-1}\) s\(^{-1}\) (mean ± SE, Jack Point in April 2008) to 892.7 ± 37.8 µmol cm\(^{-1}\) s\(^{-1}\) (Mundoo Channel in September 2007). Ambient dissolved oxygen measurements revealed relatively oxygenated waters in Mundoo Channel with values ranging from 7.29 ± 0.05 to 8.69 ± 0.08 mg L\(^{-1}\) (mean ± SE) and negligible temporal variations. However, Noonameena and Jack Point recorded relatively lower DO concentrations in November 2007 and April 2008 when compared to September 2007 (Table 2).

Oxidised nitrogen (NO\(_x\)) concentrations were higher in April 2008 at all sites, ranging from 0.17 ± 0.02 mg L\(^{-1}\) (mean ± SE) at Mundoo Channel to 0.25 ± 0.03 mg L\(^{-1}\) at Jack Point. Among the study sites, Jack Point registered relatively higher concentrations of NO\(_x\) during all seasons (Table 2). Soluble reactive phosphorus recorded lower concentrations at all sites during the study period with no discernable temporal or spatial trends. Concentrations ranged between 0.01 to 0.06 mg L\(^{-1}\) during the study (Table 2). Reactive silica on the other hand, showed distinct spatial variations with comparatively higher concentrations recorded at Jack Point (Table 2). Silicate concentrations ranged from 0.18 ± 0.01 mg L\(^{-1}\) (mean ± SE, September 2007 at Noonameena) to 2.75 ± 0.24 mg L\(^{-1}\) (April 2008 at Jack Point).

3.2. Phytoplankton productivity

Mean net phytoplankton productivity measured by the dissolved oxygen (DO) technique ranged between 0 (Noonameena, November 2007 and April 2008) to 0.15 mgC m\(^{-2}\) h\(^{-1}\). To verify that such low values were measured, calculated gross productivity using the DO technique was compared against productivity measurements made using the \(^{14}\)C technique in April 2008. While, gross phytoplankton productivity ranged between 0.03 to 0.10 mgC m\(^{-2}\) h\(^{-1}\), the \(^{14}\)C technique gave productivity values ranging from 0.67 ± 0.58 to 7.35 ± 4.89 mgC m\(^{-2}\) h\(^{-1}\) (Figure 2).
Table 2. Summary of the physico-chemical parameters measured at the three sampling sites, Mundoo Channel, Noonameena and Jack Point, measured in September 2007, November 2007 and April 2008.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Stations</th>
<th>September 2007</th>
<th>November 2007</th>
<th>April 2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water Temperature¹ (°C)</td>
<td>Munnoo Channel</td>
<td>13.3</td>
<td>17.2</td>
<td>17.8</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>11.6</td>
<td>17.5</td>
<td>17.0</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>10.9</td>
<td>19.0</td>
<td>18.2</td>
</tr>
<tr>
<td>Salinity (g L⁻¹)¹</td>
<td>Munnoo Channel</td>
<td>28.5</td>
<td>31.8</td>
<td>36.7</td>
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<td></td>
<td>Noonameena</td>
<td>55.2</td>
<td>87.0</td>
<td>53.3</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>66.1</td>
<td>99.9</td>
<td>114.6</td>
</tr>
<tr>
<td>pH¹</td>
<td>Munnoo Channel</td>
<td>7.7</td>
<td>8.3</td>
<td>8.3</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>8.1</td>
<td>8.1</td>
<td>8.3</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>8.0</td>
<td>7.8</td>
<td>7.9</td>
</tr>
<tr>
<td>Photosynthetically Active Radiation² (μmol cm⁻¹ s⁻¹)</td>
<td>Munnoo Channel</td>
<td>892.7 ± 37.8</td>
<td>616.1 ± 16.3</td>
<td>800.9 ± 39.2</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>ND</td>
<td>881.4 ± 11.6</td>
<td>818.8 ± 30.3</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>576.8 ± 40.8</td>
<td>501.5 ± 26.7</td>
<td>408.7 ± 26.5</td>
</tr>
<tr>
<td>Ambient Dissolved Oxygen³ (mg L⁻¹)</td>
<td>Munnoo Channel</td>
<td>7.29 ± 0.05</td>
<td>7.75 ± 0.07</td>
<td>8.69 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>7.95 ± 0.12</td>
<td>3.53 ± 0.07</td>
<td>6.24 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>8.04 ± 0.10</td>
<td>4.54 ± 0.05</td>
<td>3.53 ± 0.06</td>
</tr>
<tr>
<td>Oxidised Nitrogen⁴ (Nitrates + Nitrites) (mg L⁻¹)</td>
<td>Munnoo Channel</td>
<td>0.07 ± 0.03</td>
<td>NDL</td>
<td>0.17 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>NDL</td>
<td>0.11 ± 0.01</td>
<td>0.19 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>0.33 ± 0.01</td>
<td>0.15 ± 0.00</td>
<td>0.25 ± 0.03</td>
</tr>
<tr>
<td>Soluble Reactive Phosphorus³ (mg L⁻¹)</td>
<td>Munnoo Channel</td>
<td>0.01 ± 0.00</td>
<td>0.06 ± 0.00</td>
<td>0.03 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>0.05 ± 0.01</td>
<td>0.03 ± 0.01</td>
<td>0.02 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>0.05 ± 0.00</td>
<td>0.01 ± 0.00</td>
<td>0.03 ± 0.00</td>
</tr>
<tr>
<td>Reactive Silica⁴ (mg L⁻¹)</td>
<td>Munnoo Channel</td>
<td>0.95 ± 0.04</td>
<td>0.23 ± 0.01</td>
<td>0.52 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Noonameena</td>
<td>0.18 ± 0.01</td>
<td>1.08 ± 0.08</td>
<td>0.30 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>Jack Point</td>
<td>1.72 ± 0.02</td>
<td>2.59 ± 0.01</td>
<td>2.75 ± 0.24</td>
</tr>
</tbody>
</table>

¹ Single point measurement at the start of incubation
² Values in mean ± SE with n = 49; ND - no data available (data from 1130 – 1530h)
³ Concentrations in mean ± SE with n = 40 (data from 0900 – 1500h)
⁴ Concentrations in mean ± SE with n = 3; NDL - non-detectable levels
3.3. Phytobenthic productivity

In September 2007, the mean net phytobenthic productivity was highest at Jack Point and lowest at Mundoo Channel (Figure 3). In November 2007, net benthic primary productivity increased at Mundoo Channel (24.86 ± 1.06 mgC m⁻² h⁻¹; all values are mean ± SE,) and decreased at Jack Point (7.67 ± 0.70 mgC m⁻² h⁻¹) while Noonameena remained unchanged (Figure 3). In April 2008, net benthic primary productivity at Noonameena increased while Mundoo Channel recorded a decrease and Jack Point was similar to the sampling in November 2007 (Figure 3). These variable trends resulted in ANOVA indicating significant interaction between sampling times and sites $F_{(4,30)} = 12.722, p < 0.001)$. Mauchly’s test showed that the assumption of sphericity was not violated for the effect of sampling time ($\chi^2(2) = 5.847, p = 0.054$), therefore the degrees of freedom need not be corrected. Levene’s test for homogeneity was significant for two of the three sampling times ($p = 0.032$ for September, $p = 0.004$ for November). Homogeneity of variances was not attained even after transformation, therefore the results from the untransformed analyses were used.

Phytobenthic community respiration decreased from Mundoo Channel to Jack Point in September 2007 (Figure 4). Mundoo Channel had the highest mean phytobenthic community respiration of 33.48 ± 11.70 mgC m⁻² h⁻¹ in September 2007 decreasing to ~20 mgC m⁻² h⁻¹ in November 2007 and April 2008. Noonameena had a mean of 20.95 ± 3.10 mgC m⁻² h⁻¹ in September 2007 and was not much different in the later two sampling months. Jack Point had a mean phytobenthic community respiration of 12.76 ± 1.43 mgC m⁻² h⁻¹ in September 2007 and similar results were obtained in the two later sampling times.

The results of ANOVA indicated significant differences in phytobenthic community respiration between sites ($F_{(1,15)} = 5.909, p = 0.013$) but not between sampling times ($F_{(1,39,20.82)} = 0.421, p = 0.589$). There was also no interaction effect between sampling times and sites ($F_{(2,78,20.82)} = 0.983, p = 0.116$). Mauchly’s test indicated that the assumption of sphericity was violated for the effect of sampling time ($\chi^2(2) = 8.149, p = 0.017$), therefore the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\eta = 0.694$). Levene’s test for homogeneity was significant for two of the three sampling times ($p = 0.047$ for September, $p = 0.019$ for April). Homogeneity of variances was not attained even after transformation, therefore the results from the untransformed analyses were used. Power analysis showed that to detect differences between sampling times, the number of samples required would need to be doubled to attain a power of 0.8. However, this was not feasible, being limited by the number of chambers available for each incubation run. Post-hoc Tukey comparisons of
sites indicated significant differences only between Mundoo Channel and Jack Point ($p = 0.013$).

**Figure 3.** Net phytobenthic productivity (mgC m$^{-2}$ h$^{-1}$) at the three sampling sites, Mundoo Channel, Noonameena and Jack Point measured in September 2007, November 2007 and April 2008. Error bars are SE.

**Figure 4.** Phytobenthic community respiration rates (mgC m$^{-2}$ h$^{-1}$) at the three sampling sites, Mundoo Channel, Noonameena and Jack Point measured in September 2007, November 2007 and April 2008. Error bars are SE.
4. Discussion

The oxygen-based technique for the measurement of phytoplankton productivity is known to be less sensitive than the $^{14}$C technique, especially in oligotrophic systems (Williams 1993). However, it is important to consider that photosynthetic rates measured by the $^{14}$C technique are usually in excess of net photosynthesis (Steemann-Nielsen 1955, Ryther 1956), but usually between net and gross photosynthesis as measured by the oxygen-based technique (Falkowski and Raven 1997). In particular, for incubations of less than or equal to one hour, $^{14}$C productivity exceeds net photosynthesis (Dring and Jewson 1982). In this study, with incubations lasting more than one hour (~2.5 hours), phytoplankton productivity as measured by the $^{14}$C technique was greater than gross productivity (oxygen-based technique) by a factor of approximately ten in April 2008. It is therefore suspected that this underestimation of gross productivity might be due to sensitivity issues with the oxygen-based technique in low productivity conditions, coupled with significant community respiration occurring.

Based on these results, it seems that phytoplankton productivity only makes a small contribution to the overall productivity at the three study sites in the Coorong and Murray Mouth. However, comparing phytoplankton productivity measurements using the $^{14}$C technique with net phytobenthic productivity, it appears that phytoplankton could make a significant contribution at Jack Point (Figure 2 and 3). Given that no data were available for the other sampling times, this is left to be further tested.

The assumption that phytoplankton productivity is relatively low at the study sites could be due to temporary stratification limiting light for phytoplankton photosynthesis (Geddes et al. 1984b). Temperature and salinity stratification in the Coorong have also been reported by Holloway (1980) based on a 1-year study using continuously recording moored instruments. Besides stratification-induced light limitation, turbidity and nutrients can also limit phytoplankton productivity. While riverine inputs are the main source of nutrients in this system, these have been minimal in recent times due to insignificant river flow into the Coorong. However, Bisson and Kirst (1983) reported seepage of freshwater from soaks in the sand dunes on the Younghusband Peninsula. That said, nutrient recycling within the system has been reported to be significant, a process that is sensitive to changes in salinity. Key processes such as nitrification can cease at salinities above twice seawater (Lamontagne et al. 2004). The low nutrient concentrations measured in this study, especially for nitrogen, may be limiting productivity in this system (See Table 2), as was hypothesised by Lamontagne et al. (2004). As for the effects of salinity, Lamontagne et al. (2004) stated that although long-channel mixing tends to homogenise salinities, the exchange of water between the South and North Lagoons and mixing of water past Parnka Point is restricted, allowing evaporation to concentrate salinities in the South Lagoon to levels over that of seawater. The salinities in the two lagoons are both seasonally and geographically variable, being regulated by the changing patterns of freshwater influx against more significant high evaporation rates. Webster (2005) reported that the water in the South Lagoon has salinities from ~80 g L$^{-1}$ in October 2001, increasing to ~125 g L$^{-1}$ in April 2002. This historic trend in the South Lagoon is comparable to the results from this study, where evaporation caused salinities to be the highest in autumn.

Besides phytoplankton, primary producers in the Coorong also include $Ruppia$, benthic mat forming macroalgae and seagrass (Lamontagne et al. 2004). $Ruppia$, a keystone species in the Coorong, was observed to be very seasonal and limited in biomass (Lamontagne et al. 2004). This could be attributed to the hypersaline conditions, resulting in mat forming benthic macroalgae dominating the phytobenthos (Lamontagne et al. 2004). Palinska et al. (1999) reported four major genera of cyanobacteria, $Pleurocapsa$, $Myxosarcina$, $Leptolyngbia$ and $Microcoleus$, to dominate the phytobenthic mats in the Coorong, in addition to a large number of cyanobacterial genera such as $Phormidium$, $Synechococcus$, $Synechocystis$, $Spirulina$, $Oscillatoria$ and $Gloeocapsa$. Green algae $Dunaliella$ sp. and benthic diatoms such as $Nitzschia$ and $Mastogloia$ have also been reported to occur in the mats. In coastal systems with sufficient light reaching the sediments, mats of floating macroalgae can develop (Morand and Briand 1996, Valiela et al. 1997). These macroalgae have a high capacity for...
growth and nutrient uptake (Viaroli et al. 1996, Dalsgaard 2003). Consequently, they grow on the sediment surface, like microphytobenthos, controlling the exchange of nutrients between the sediments and the water column, giving the macroalgae a competitive advantage over phytoplankton (McGlathery et al. 1997, Krause-Jensen et al. 1999). In addition to nutrients, there was sufficient light available to support the phytobenthic community, with PAR ranging from 408.7 μmol cm⁻¹ s⁻¹ to 892.7 μmol cm⁻¹ s⁻¹ during this study. Literature values for minimum light intensity at which phytobenthic photosynthesis saturates usually range from 300 to 500 μmol cm⁻¹ s⁻¹ (e.g. Pinckney and Zingmark 1993, Blanchard and Montana 1992, Blanchard and Gall 1994, Wolfstein and Hartig 1998) indicating that light was sufficient during all seasons in this study.

Annual net phytobenthic productivity has been measured to range from 5 to 900 gC m⁻² y⁻¹ (~0.6 to 103 mgC m⁻² h⁻¹) by Beardall and Light (1994). A review by Underwood and Kromkamp (1999) reported values ranging from 29 to 314 gC m⁻² y⁻¹ (3.3 – 36 mgC m⁻² h⁻¹). Therefore the phytobenthic productivity reported in this study (~2 to 25 mgC m⁻² h⁻¹) is within the range of what has been reported from similar ecosystems elsewhere in the world. As in this study, where phytoplankton productivity was insignificant in relation to phytobenthic productivity, there is an emerging consensus in the literature that in shallow habitats, benthic algal biomass and productivity often equal or exceed biomass and production of phytoplankton in the water column (e.g. Daehnick et al. 1992, Moncreiff et al. 1992, Schreiber and Pennock 1995, Cahoon 1999). It has also been reported that phytobenthos have better access to nutrients than pelagic phytoplankton (Barranguet et al. 1996, Webster et al. 2002), which is the most likely explanation for the significant contribution by the phytobenthos to the total primary production in the system. Webster et al. (2002) also reported a similar phenomenon in Lake Illawarra, a shallow coastal lagoon in South-eastern Australia. The authors further state that phytobenthos not only act as a sink for nutrients but also as a source of oxygen that diffuses from the sediments to the water column in shallow, well-illuminated estuaries (like the Coorong and Murray Mouth), thereby making them more significant than pelagic phytoplankton in determining the overall nutrient status and productivity.

5. Summary, Conclusions & Management Implications

This study on phytoplankton and phytobenthic productivity at three sites in the Murray Mouth and Coorong provides baseline estimates of primary productivity in this system over a salinity gradient. However, phytoplankton productivity as measured by the DO technique may not be sensitive enough to measure the low rates of water column productivity (<10 mgC m⁻² h⁻¹) in an environment with high community respiration. This was verified in this study on the last survey with comparisons made between the more sensitive ¹⁴C technique and the DO technique.

To obtain more reliable estimates of the whole ecosystem primary productivity for the Coorong and Murray Mouth, it is recommended that future studies should include more sites and more frequent sampling using sensitive techniques such as ¹⁴C measurements, CO₂ / Dissolved Inorganic Carbon fluxes and stable isotope spike trials. It is hypothesized from this study that heterotrophic productivity is significant in the water column and sediments, although no measurements were made to support this claim. However, it has been reported by Palinska et al. (1999) that the benthic algal mats in the Coorong produce significant amounts of extracellular polymeric substances (EPS), which act as an important organic carbon source for heterotrophs and promote trapping of sand-size or even coarser sediments (Decho and Moriarty 1990, Middleburg et al. 2000, Goto et al. 2001, Wolfstein and Stal 2002). Given this background, Tritiated thymidine (³H-thymidine) uptake studies could be planned for future surveys in addition to primary productivity studies, both for the sediments and the water column to quantify heterotrophic bacterial production, which may be significant.
6. References


Appendix A  Photographic description of the study

Sampling site at Mundoo Channel

Sampling site at Noonameena

Sampling site at Jack Point

Ambient DO logging for 24 hours

Licor PAR sensor

Daily calibration of DO meters and membrane changes were performed on probes that failed the calibration tests
Filtering samples to remove zooplankton prior to phytoplankton productivity incubations

Measuring changes in dissolved oxygen prior to and after incubation to assess phytoplankton productivity

Dark and light bottles being incubated in situ for phytoplankton productivity measurements

Fixing biological samples on shore

Filtration for $^{14}C$ productivity measurements to counter verify results with DO productivity technique

Benthic chambers being prepared for in situ measurements of phytobenthic productivity

Phytoplankton and phytobenthic productivity
Deployment of chambers on the sediments for phytobenthic productivity measurements

Placing weighted dark plastic bags to simulate dark conditions

Dark, light and blank chambers ready for incubation with the data loggers on a floating dinghy

Close up of the chambers

Close up of a light chamber showing the DO sensor and the inline submersible water to circulate water within the chamber

Close up of a dark chamber showing a thick gauge weighted plastic sheet covering the chamber to measure benthic respiration
Close up of the loggers on the floating dinghy

Close up of the pump regulators and bank of 6V, 120Ah sealed lead acid batteries as the power source

Core sampling

Sampling phytobenthic biomass from sediment cores

A core sample revealing *Ruppia*

Resuspended benthic algal mats comprising filamentous macroalgae and *Ruppia*