



Water for a Healthy Country

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

Sasi Nayar and Maylene G K Loo

April 2009



SARDI



SOUTH AUSTRALIAN
RESEARCH AND
DEVELOPMENT
INSTITUTE



Government
of South Australia



FLINDERS
UNIVERSITY
ADELAIDE
AUSTRALIA



Water for a Healthy Country

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

Sasi Nayar* and Maylene G K Loo

SARDI Aquatic Sciences, PO Box 120, Henley Beach, SA 5022 Australia

*Corresponding author: nayar.sasi@saugov.sa.gov.au

April 2009

Water for a Healthy Country Flagship Report series ISSN: 1835-095X
ISBN : 978 0 643 09735 3

The Water for a Healthy Country National Research Flagship is a research partnership between CSIRO, state and Australian governments, private and public industry and other research providers. The Flagship aims to achieve a tenfold increase in the economic, social and environmental benefits from water by 2025.

The Australian Government, through the Collaboration Fund, provides \$97M over seven years to the National Research Flagships to further enhance collaboration between CSIRO, Australian universities and other publicly funded research agencies, enabling the skills of the wider research community to be applied to the major national challenges targeted by the Flagships initiative.

© Commonwealth of Australia 2009 All rights reserved.

This work is copyright. Apart from any use as permitted under the Copyright Act 1968, no part may be reproduced by any process without prior written permission from the Commonwealth.

Citation: Nayar, S and Loo, M. G. K. 2009. Phytoplankton and phytobenthic productivity along a salinity gradient in the Coorong and Murray Mouth. CSIRO: Water for a Healthy Country National Research Flagship and South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 19pp.

DISCLAIMER

CSIRO advises that the information contained in this publication comprises general statements based on scientific research. The reader is advised and needs to be aware that such information may be incomplete or unable to be used in any specific situation. No reliance or actions must therefore be made on that information without seeking prior expert professional, scientific and technical advice. To the extent permitted by law, CSIRO (including its employees and consultants) excludes all liability to any person for any consequences, including but not limited to all losses, damages, costs, expenses and any other compensation, arising directly or indirectly from using this publication (in part or in whole) and any information or material contained in it.

For more information about Water for a Healthy Country Flagship or the National Research Flagship Initiative visit www.csiro.au.

Printed in Adelaide

SARDI Publication Number F2009/000263-1
SARDI Research Report Series Number 352

Author(s): Sasi Nayar and Maylene Loo
Reviewers: Rod Oliver and Peter Fairweather
Approved by: Jason Tanner
Signed:

Date: 30 April 2009
Distribution:
Circulation: Public Domain

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>

Table of Contents

Acknowledgements	ii
Executive Summary	iii
1. Introduction	1
2. Methods	2
2.1. Sampling sites and times.....	2
2.2. Physico-chemical parameters.....	2
2.3. Phytoplankton Productivity	4
2.3.1. Dissolved oxygen technique.....	4
2.3.2. ¹⁴ C technique.....	4
2.4. Phytobenthic net productivity and community respiration rates	4
2.5. Data Analyses.....	5
3. Results	6
3.1. Physico-chemical parameters.....	6
3.2. Phytoplankton productivity.....	6
3.3. Phytobenthic productivity.....	8
4. Discussion	10
5. Summary, Conclusions & Management Implications	11
6. References	12
Appendix A Photographic description of the study	16

Acknowledgements

This research was supported by the CSIRO Flagship Collaboration Fund and represents collaboration between CSIRO, the University of Adelaide, Flinders University and SARDI Aquatic Sciences.

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 ^{14}C technique and dissolved oxygen technique were used to measure phytoplankton productivity. Comparison of phytoplankton productivity indicated that measurements made using the ^{14}C 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 ^{14}C 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 ^{14}C technique.

Phytoplankton productivity in April 2008 ranged from 0.7 (Mundoo Channel) to 7.4 $\text{mgC m}^{-2} \text{h}^{-1}$ (Jack Point). On the other hand, net phytobenthic productivity ranged from $7.67 \pm 0.70 \text{ mgC m}^{-2} \text{h}^{-1}$ (mean \pm SE; Mundoo Channel; September 2007) to $24.86 \pm 1.06 \text{ mgC m}^{-2} \text{h}^{-1}$ (Noonameena; April 2008). Phytobenthic community respiration ranged from $12.76 \pm 1.43 \text{ mgC m}^{-2} \text{h}^{-1}$ (Jack Point; September 2007) to $33.48 \pm 11.70 \text{ mgC m}^{-2} \text{h}^{-1}$ (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 Youngusband 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 trophic 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.

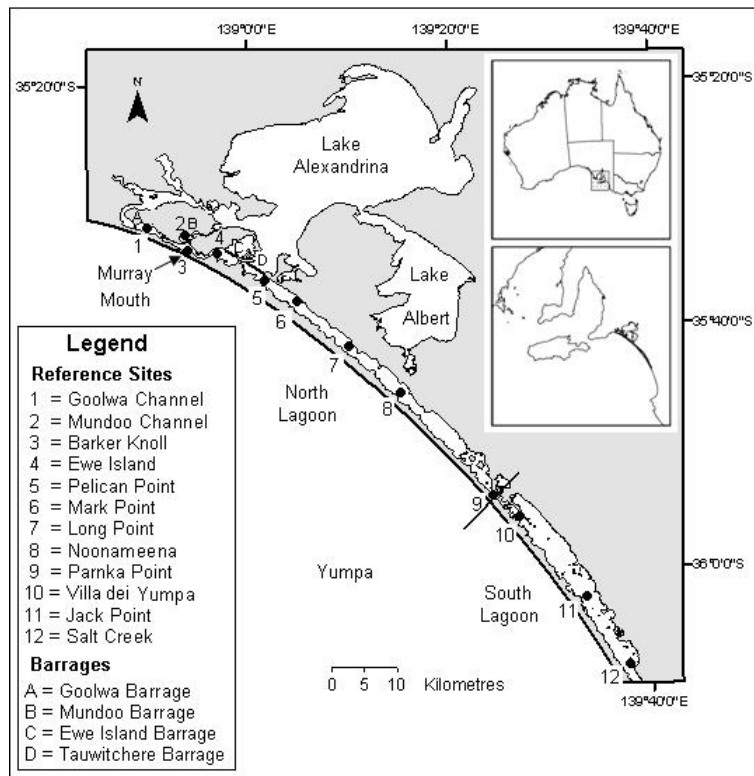
Table 1. Coordinates of the three study sites within the Coorong and Murray Mouth in degrees, minutes and seconds (WGS84).

Sites	Latitude	Longitude
Mundoo Channel	35° 32' 16" S	138° 53' 07" E
Noonameena	35° 44' 59" S	139° 15' 15" E
Jack Point	36° 01' 54" S	139° 34' 04" E

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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. 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 NO_x (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} , $1 \mu\text{g L}^{-1}$ and 0.013 mg L^{-1} respectively.



Mundoo Channel



Nooameena



Jack Point

Coorong, Lower Lakes and the Murray Mouth

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.

Phytoplankton productivity (net productivity) and phytoplankton 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 used 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 ¹⁴C technique in April 2008. While, gross phytoplankton productivity ranged between 0.03 to 0.10 mgC m⁻² h⁻¹, the ¹⁴C 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.

Parameters	Stations	September 2007	November 2007	April 2008
Water Temperature ¹ (°C)	Mundoo Channel	13.3	17.2	17.8
	Noonameena	11.6	17.5	17.0
	Jack Point	10.9	19.0	18.2
Salinity (g L ⁻¹) ¹	Mundoo Channel	28.5	31.8	36.7
	Noonameena	55.2	87.0	53.3
	Jack Point	66.1	99.9	114.6
pH ¹	Mundoo Channel	7.7	8.3	8.3
	Noonameena	8.1	8.1	8.3
	Jack Point	8.0	7.8	7.9
Photosynthetically Active Radiation ² (µmol cm ⁻¹ s ⁻¹)	Mundoo Channel	892.7 ± 37.8	616.1 ± 16.3	800.9 ± 39.2
	Noonameena	ND	881.4 ± 11.6	818.8 ± 30.3
	Jack Point	576.8 ± 40.8	501.5 ± 26.7	408.7 ± 26.5
Ambient Dissolved Oxygen ³ (mg L ⁻¹)	Mundoo Channel	7.29 ± 0.05	7.75 ± 0.07	8.69 ± 0.08
	Noonameena	7.95 ± 0.12	3.53 ± 0.07	6.24 ± 0.14
	Jack Point	8.04 ± 0.10	4.54 ± 0.05	3.53 ± 0.06
Oxidised Nitrogen ⁴ (Nitrates + Nitrites) (mg L ⁻¹)	Mundoo Channel	0.07 ± 0.03	NDL	0.17 ± 0.02
	Noonameena	NDL	0.11 ± 0.01	0.19 ± 0.01
	Jack Point	0.33 ± 0.01	0.15 ± 0.00	0.25 ± 0.03
Soluble Reactive ⁴ Phosphorus ³ (mg L ⁻¹)	Mundoo Channel	0.01 ± 0.00	0.06 ± 0.00	0.03 ± 0.00
	Noonameena	0.05 ± 0.01	0.03 ± 0.01	0.02 ± 0.00
	Jack Point	0.05 ± 0.00	0.01 ± 0.00	0.03 ± 0.00
Reactive Silica ⁴ (mg L ⁻¹)	Mundoo Channel	0.95 ± 0.04	0.23 ± 0.01	0.52 ± 0.01
	Noonameena	0.18 ± 0.01	1.08 ± 0.08	0.30 ± 0.02
	Jack Point	1.72 ± 0.02	2.59 ± 0.01	2.75 ± 0.24

¹Single point measurement at the start of incubation

²Values in mean ± SE with n = 49; ND - no data available (data from 1130 – 1530h)

³Concentrations in mean ± SE with n = 40 (data from 0900 – 1500h)

⁴Concentrations in mean ± SE with n = 3; NDL - non-detectable levels

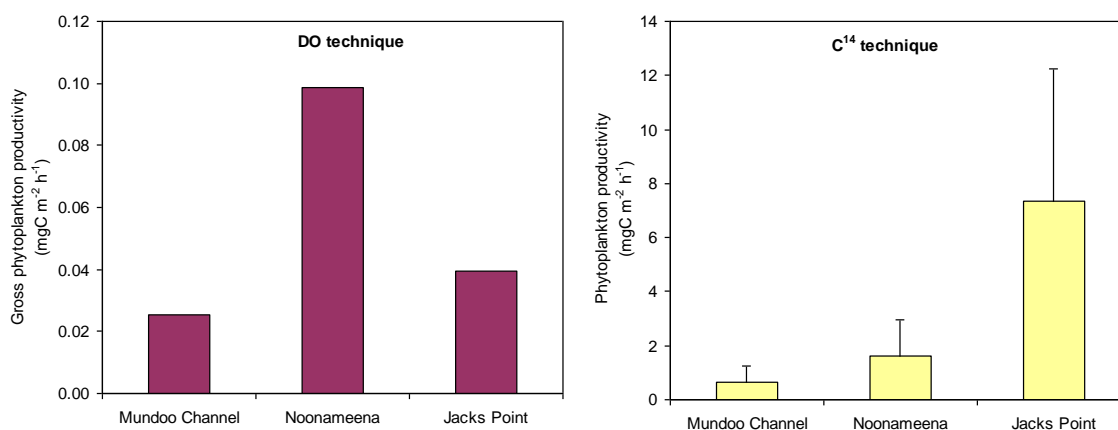


Figure 2. Gross phytoplankton productivity ($\text{mgC m}^{-2} \text{h}^{-1}$) measured by the dissolved oxygen (DO) technique compared with productivity measurements by the ^{14}C technique ($\text{mgC m}^{-2} \text{h}^{-1}$) at the three sampling sites, Mundoo Channel, Noonameena and Jack Point in April 2008. Error bars are standard error (SE). Gross productivity was calculated as the sum of the means of net productivity and community respiration and therefore has no error bars.

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 ($24.86 \pm 1.06 \text{ mgC m}^{-2} \text{h}^{-1}$; all values are mean \pm SE,) and decreased at Jack Point ($7.67 \pm 0.70 \text{ mgC m}^{-2} \text{h}^{-1}$) 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 $33.48 \pm 11.70 \text{ mgC m}^{-2} \text{h}^{-1}$ in September 2007 decreasing to $\sim 20 \text{ mgC m}^{-2} \text{h}^{-1}$ in November 2007 and April 2008. Noonameena had a mean of $20.95 \pm 3.10 \text{ mgC m}^{-2} \text{h}^{-1}$ in September 2007 and was not much different in the later two sampling months. Jack Point had a mean phytobenthic community respiration of $12.76 \pm 1.43 \text{ mgC m}^{-2} \text{h}^{-1}$ 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 ($\epsilon = 0.694$). 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 ($p = 0.013$).

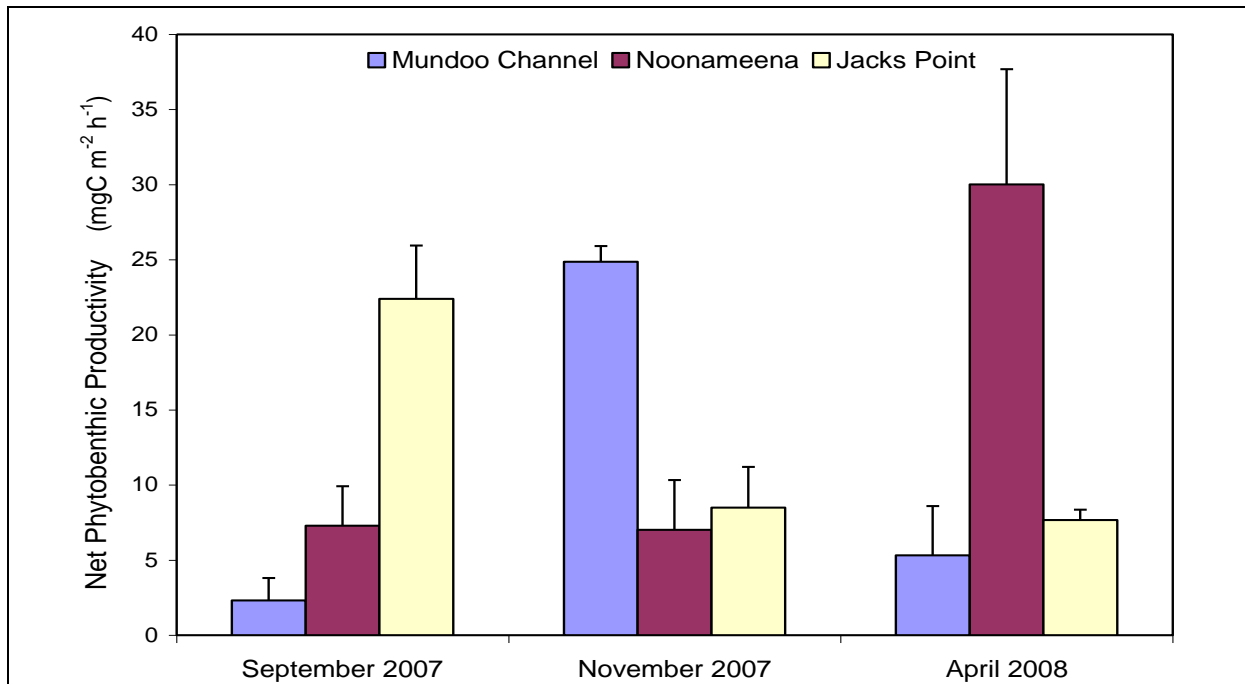


Figure 3. Net phytothetic productivity (mgC m⁻² h⁻¹) at the three sampling sites, Mundoo Channel, Noonameena and Jack Point measured in September 2007, November 2007 and April 2008. Error bars are SE.

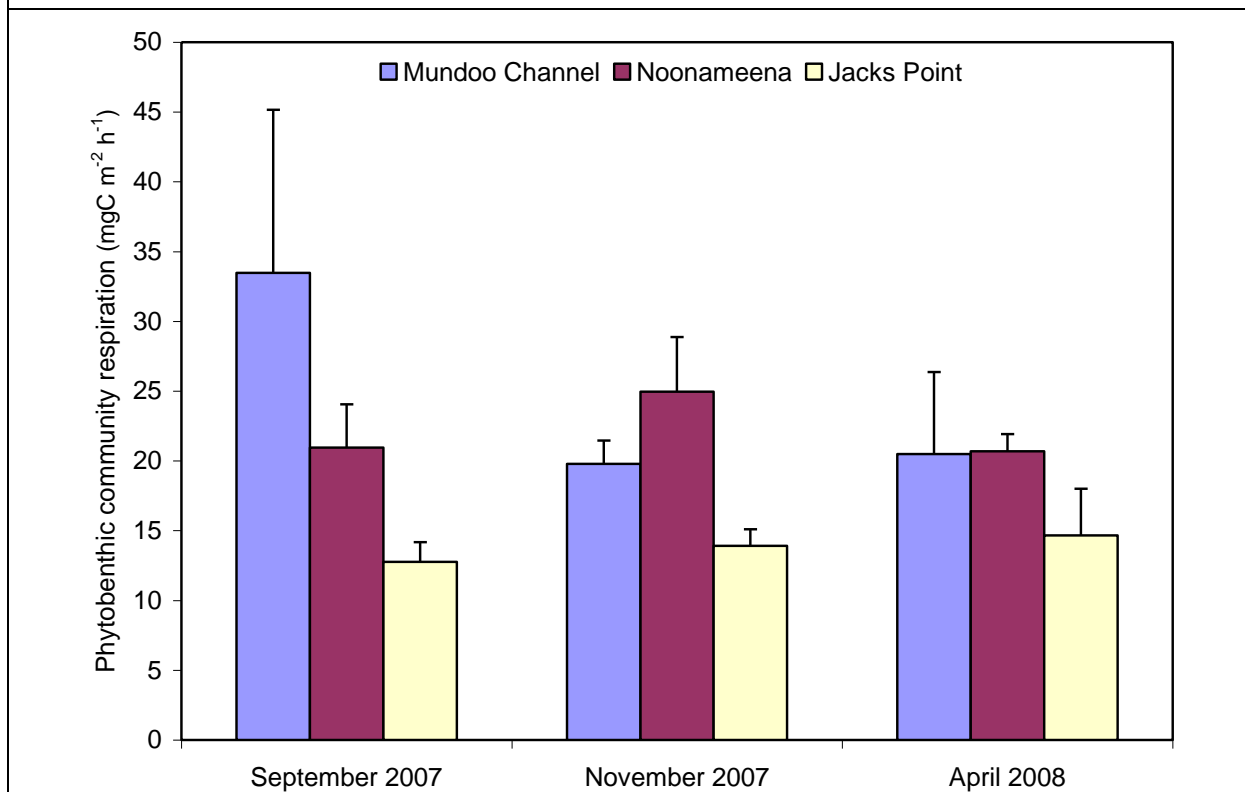


Figure 4. Phytobenthic community respiration rates (mgC m⁻² h⁻¹) at the three sampling sites, Mundoo Channel, Noonameena and Jack Point measured in September 2007, November 2007 and April 2008. Error bars are SE.

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 $\mu\text{mol cm}^{-1} \text{s}^{-1}$ to 892.7 $\mu\text{mol cm}^{-1} \text{s}^{-1}$ during this study. Literature values for minimum light intensity at which phytobenthic photosynthesis saturates usually range from 300 to 500 $\mu\text{mol cm}^{-1} \text{s}^{-1}$ (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 $\text{gC m}^{-2} \text{y}^{-1}$ (~ 0.6 to 103 $\text{mgC m}^{-2} \text{h}^{-1}$) by Beardall and Light (1994). A review by Underwood and Kromkamp (1999) reported values ranging from 29 to 314 $\text{gC m}^{-2} \text{y}^{-1}$ (3.3 – 36 $\text{mgC m}^{-2} \text{h}^{-1}$). Therefore the phytobenthic productivity reported in this study (~ 2 to 25 $\text{mgC m}^{-2} \text{h}^{-1}$) 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 ($<10 \text{ mgC m}^{-2} \text{h}^{-1}$) in an environment with high community respiration. This was verified in this study on the last survey with comparisons made between the more sensitive ^{14}C 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 ^{14}C measurements, CO_2 / 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

- APHA. (2005). Standard Methods for the Examination of Water and Wastewater, 21st Edition., (Eds.) Eaton, A.D., Clesceri, L.S., Rice, E.W. and Greenberg, A.E. Published by American Public Health Association, Water Environment Federation, and American Water Works Association. 1368 p.
- Asmus, R. (1982). Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the northern Wadden Sea. *Netherlands Journal of Sea Research* **16**:389-402.
- Barranguet, C., Plante-Cuny, M.R. and Aviron, E. (1996). Microphytobenthic production in the Gulf of Fos, French Mediterranean coast. *Hydrobiologia* **333**:181-193.
- Beardall, J. and Light, B. (1994). Biomass, productivity and nutrient requirements of microphytobenthos, Technical Report 16. Port Phillip Bay Environmental Study, Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia. 20 p.
- Bisson, M.A. and Kirst, G.O. (1983). Osmotic adaptations of charophyte algae in the Coorong, South Australia and other Australian lakes. *Hydrobiologia* **105**:45-51.
- Blanchard, C.F. and Montana, P.A. (1992). Photosynthetic response of natural assemblages of marine benthic microalgae to short- and long-term variations of incident irradiance in Baffin Bay, Texas. *Journal of Phycology* **28**:7-14.
- Blanchard, G.F. and Gall, V.C. (1994). Photosynthetic characteristics of microphytobenthos on Marennes-Oleron Bay, France : Preliminary results. *Journal of Experimental Marine Biology and Ecology* **182**:1-14.
- Borges, A.V., Schiettecatte, L.S., Abril, G., Delille, B. and Gazeau, F. (2006). Carbon dioxide in European coastal waters. *Estuarine, Coastal and Shelf Science* **70**:375-387.
- Brookes, J.D. (2002). Implications of Murray Mouth closure and/or restriction on water quality. In : The Murray Mouth: exploring the implications of closure or restrictions. A Report to the Murray Darling Basin Commission. Invited paper. pp. 33- 53.
- Cadee, G.C. and Hegeman, J. (1974). Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* **8**:260-291.
- Cahoon, L.B. (1999). The role of benthic microalgae in neritic ecosystems. *Oceanography and Marine Biology* **37**:47-86.
- Charpy-Roubaud, C. and Sourina, A. (1990). The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary productions in the oceans. *Marine Microbial Food Webs* **4**: 31-57.
- Daehnick, A.E., Sullivan, M.J. and Moncreiff, C.A. (1992). Primary production of the sand microflora in seagrass beds of Mississippi Sound. *Botanica Marina* **35**:131-139.
- Dalsgaard, T. (2003). Benthic primary production and nutrient cycling in sediments with benthic microalgae and transient accumulation of macroalgae. *Limnology and Oceanography* **48**:2138-2150.
- De Deckker, P. and Geddes, M.C. (1980). Seasonal fauna of ephemeral saline lakes near the Coorong Lagoon, South Australia. *Australian Journal of Marine and Freshwater Research* **31**:677-699.
- Decho, A.W. and Moriarty, D.J.W. (1990). Bacterial exopolymer utilization by a harpacticoid copepod : A methodology and results. *Limnology and Oceanography* **35**:1039-1049.

- Dring, M.J. and Jewson, D.H. (1982). What does ^{14}C uptake by phytoplankton really measure? A theoretical modelling approach. *Proceedings of the Royal Society of London* **214**:351-368.
- Edgar, G.J., Barrett, N.S., Graddon, D.J. and Last, P.R. (2000). The conservation significance of estuaries: a classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation* **92**:383-397.
- Falkowski, P.G. and Raven, J.A. (1997). Aquatic photosynthesis. Blackwell science, Massachusetts. USA. 375 p.
- Ford, P.W. (2007). Biogeochemistry of the Coorong : Review and identification of future research requirements. CSIRO Water for a Healthy Country National Research Flagship, Canberra. 22 p.
- Geddes, M. (1987). Changes in salinity and in the distribution of macrophytes, macrobenthos and fish in the Coorong Lagoons, South Australia following a period of River Murray flow. *Transactions of the Royal Society of South Australia* **111**:173-181.
- Geddes, M.C. (1984b). Seasonal studies on the zooplankton community of Lake Alexandrina, River Murray, South Australia, and the effects of nutrients and light on the phytoplankton community structure. *Australian Journal of Freshwater Research* **35**:399-415.
- Geddes, M.C. (2005). Ecological outcomes for the Murray Mouth and Coorong from the managed barrage release of September – October 2003. Report prepared for the Department of Water, Land and Biodiversity Conservation. South Australian Research and Development Institute Aquatic Sciences Publication No. RD03/0199-2. 77 p.
- Geddes, M.C. and Butler, A.J. (1984). Physicochemical and biological studies on the Coorong lagoons, South Australia, and the effect of salinity on the distribution of the macrobenthos. *Transactions of the Royal Society of South Australia* **108**:51-62.
- Goto, N., Mitamura, O. and Terai, H. (2001). Biodegradation of photosynthetically produced extracellular organic carbon from intertidal benthic algae. *Journal of Experimental Marine Biology and Ecology* **257**:73-86.
- Holloway, P.E. (1980). A criterion for thermal stratification in a wind-mixed system. *Journal of Physical Oceanography* **10**:861-869.
- Hopkinson, C.S.J., and Smith, E.M. (2005). Estuarine respiration: an overview of benthic, pelagic and whole system respiration. p.123-147. In : del Giorgio, P.A. and Williams, P.J.L. (Eds.), *Respiration in Aquatic Ecosystems*. Oxford University Press, Oxford.
- Krause-Jensen, D., Christensen, P.B. and Rysgaard, S. (1999). Oxygen and nutrient dynamics within mats of the filamentous macroalga *Chaetomorpha linum*. *Estuaries* **22**: 31-38.
- Lamontagne, S., McEwan, K., Webster, I., Ford, P., Leaney, F. and Walker, G. (2004). Coorong, Lower Lakes and Murray Mouth. Knowledge gaps and knowledge needs for delivering better ecological outcomes. CSIRO Water for a Healthy Country National Research Flagship, Canberra. 28 p.
- McGlathery, K.J., Krause-Jensen, S., Rysgaard, S. and Christensen, P.B. (1997). Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum*. *Aquatic Botany* **59**:99-115.
- Middleburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T. and Heip, C.H.R. (2000). The fate of intertidal microphytobenthos carbon : An in situ C-labelling study. *Limnology and Oceanography* **45**:1224-1234.
- Moncreiff, C.A., Sullivan, M.J., Daehnick, A.E. (1992). Primary production dynamics in seagrass beds of Mississippi Sound: The contributions of seagrass, epiphytic algae, sand microflora and phytoplankton. *Marine Ecology Progress Series* **87**:161-171.

- Morand, P. and Briand, X. (1996). Excessive growth of macroalgae : A symptom of environmental disturbance. *Botanica Marina* **39**:491-516.
- Palinska, K.A., Scholz, J., Sterflinger, K., Gerdes, G. and Bone, Y. (1999). Microbial mats associated with bryozoans (Coorong Lagoon, South Australia). *Facies* **41**:1-14.
- Parsons, T.R., Maita, Y. and Lalli, C.M. (1989). A manual of chemical and biological methods of seawater analysis. Pergamon Press, Oxford. 173 p.
- Phillips, B., and Muller, K. (2006). Ecological Character of the Coorong, Lakes Alexandrina and Albert Wetland of International Importance. South Australian Department for Environment and Heritage, Adelaide.
- Pinckney, J.L. and Zingmark, R.G. (1993). Photophysical responses of intertidal benthic microalgal communities to in situ light environments : Methodological considerations. *Limnology and Oceanography* **38**:1373-1383.
- Ryther, J.H. (1956). Interrelation between photosynthesis and respiration in marine flagellate, *Dunaliella euchlora*. *Nature* **178**:861-862.
- Schreiber, R.A. and Pennock, J.R. (1995). The relative contribution of benthic microalgae to total microalgal production in a shallow sub-tidal estuarine environment. *Ophelia* **42** : 335-352.
- Steemann-Nielsen, E. (1955). The interaction of photosynthesis and respiration and its importance for the determination of ^{14}C discrimination in photosynthesis. *Physiologia Plantarum* **8**:945-953.
- Sullivan, M. and Moncreiff, C. (1988). Primary production of edaphic algal communities in a Mississippi salt marsh. *Journal of Phycology* **24**:49-58.
- Underwood, G.J.C. and Kromkamp, J. (1999). Primary production by phytoplankton and microphytobenthos in estuaries. *Advances in Ecological Research* **23**:153-171.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D. and Foreman, K. (1997). Macroalgal blooms in shallow estuaries – controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* **42**:1105-1118.
- Varela, M. and Penas, E. (1985). Primary production of benthic microalgae in an intertidal sand flat of the Ria Arosa, NW Spain. *Marine Ecology Progress Series* **25**:111-119.
- Viaroli, P., Naldi, M., Bondavalli, C. and Bencivelli, S. (1996). Growth of the seaweed *Ulva rigida* C. Agardh in relation to biomass densities, internal nutrient pools and external nutrient supply in the Sacca de Goro lagoon (northern Italy). *Hydrobiologia* **329**:93-103.
- Webster, I.T. (2005). An overview of the hydrodynamics of the Coorong and Murray Mouth : Water levels and salinity – key ecological drivers. CSIRO Water for a Healthy Country National Research Flagship, Canberra. 23 p.
- Webster, I.T., Ford, P.W. and Hodgson, B. (2002). Microphytobenthos contribution to nutrient-phytoplankton dynamics in a shallow coastal lagoon. *Estuaries* **25**:540-551.
- Williams, P.J. leB. (1993). Chemical and tracer methods for measuring plankton production. *ICES Marine Science Symposium* **197**:20-36.
- Williams, P.J. leB., Raine, R.C.T. and Bryan, J.R. (1979). Agreement between the ^{14}C and oxygen methods of measuring phytoplankton production : reassessment of the photosynthetic quotient. *Oceanologia Acta* **2**:411-416.
- Williams, W. D. (1986). Conductivity and salinity of Australian salt lakes. *Australian Journal of Marine and Freshwater Research* **37**:177-182.
- Wolfstein, K. and Hartig, P. (1998). The photosynthetic light dispensation system : Application to microphytobenthic primary production measurements. *Marine Ecology Progress Series* **166**:63-71.

Wolfstein, K. and Stal, L.J. (2002). Production of extracellular polymeric substances (EPS) by benthic diatoms : effect of irradiance and temperature. *Marine Ecology Progress Series* **236**:13-22.

Zar, JH (1996). Biostatistical analysis. 3rd edn. Prentice-Hall, New Jersey. 662 p.

Appendix A Photographic description of the study



Sampling site at Mundoo Channel



Sampling site at Noonameena



Sampling site at Jack Point



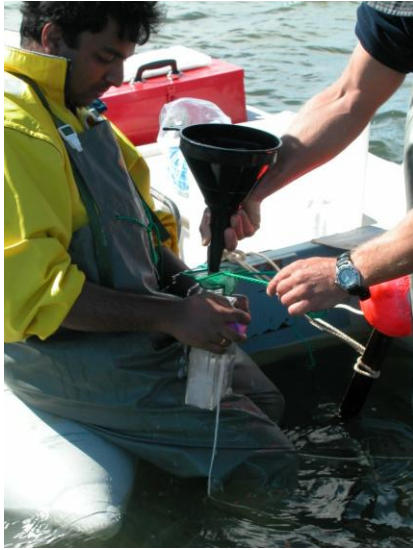
Ambient DO logging for 24 hours



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



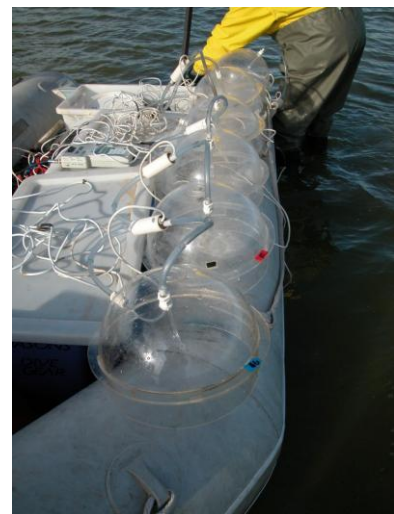
Dark and light bottles being incubated in situ for phytoplankton productivity measurements



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



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 pump 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*

