

Uptake of inorganic phosphorus by temperate seagrass beds of Posidonia and Amphibolis in Southern Australia

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Abstract Seagrasses occupy a narrow band of sandy seabed close to the coast and are therefore vulnerable to anthropogenic influences, particularly meadows near large population centres. Over 5000 ha of seagrasses have been lost from Adelaide coastal waters (South Australia) over the past 70 years and much of this loss has been attributed to nutrient inputs from wastewater, industrial and stormwater discharges. This led to the Adelaide Coastal Waters Study to understand processes along the Adelaide metropolitan coast that led to seagrass loss. This study, a subset of the larger ACWS study, used in situ nutrient spike approach to obtain ecologically relevant estimates of seasonal variability in phosphorus uptake in two species of temperate seagrass common to this coast (Amphibolis antarctica and Posidonia angustifolia). Total uptake of phosphorus by biological components in the seagrass beds, viz., seagrass, epiphytes and phytoplankton, was negligible, never exceeding 0.5 % of the total resource. Phosphorus uptake rate varied seasonally with higher rates in winter (1.49 μ mol P.g⁻¹ DW.h⁻¹) and lower rates in spring

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(0.70 µmol $P.g^{-1}$ DW.h⁻¹) for *Amphibolis* and highest in winter (2.09 µmol $P.g^{-1}$ DW.h⁻¹) and least in spring (0.14 µmol $P.g^{-1}$ DW.h⁻¹) for *Posidonia*. Low biological uptake rates of inorganic phosphorus could be attributed to carbonate sediments and particulates in the water column binding inorganic phosphorus, limiting its availability for biological uptake. From an environmental perspective, seagrass beds in the Adelaide coastal waters account for the assimilation of only 5.4 % (19.53 t yr^{-1}) of the total anthropogenic inputs of phosphorus.

Keywords Seagrass · Posidonia · Amphibolis · Epiphytes. Phosphorus uptake . South Australia

Introduction

Estimates of seagrass loss along the Adelaide metropolitan coast have been reported to exceed nearly 5000 ha since the 1940s (Neverauskas [1987a](#page-8-0), [b](#page-8-0), [c](#page-8-0); Hart [1997;](#page-7-0) Shepherd et al. [1989\)](#page-8-0). Previous studies have established relationships between seagrass degradation along this coast with a number of possibilities, including elevated nutrients, increased turbidity due to suspended particulates, toxicants, decreased salinity due to storm water inputs and substrate instability (e.g. Johnson [1981;](#page-8-0) Clarke [1987;](#page-7-0) Shepherd et al. [1989;](#page-8-0) Steffensen et al. [1989;](#page-8-0) Edyvane [1996;](#page-7-0) Seddon [2002](#page-8-0); Nayar et al. [2012](#page-8-0)). The work of Shepherd [\(1970\)](#page-8-0) was the first to link elevated nutrient levels from sewage effluent to degradation of seagrasses along the Adelaide metropolitan coast.

Nutrient sources in nearshore coastal systems include oceanic waters, terrigenous inputs, nutrient recycling within the system and atmospheric fixation (Mann [1982](#page-8-0)). In coastal environments, such as the Adelaide coastal waters, human activities contribute significantly to the nutrient loading (Nixon [1993\)](#page-8-0), stimulating phytoplankton and macroalgae (Short [1987\)](#page-8-0), often leading to eutrophication (Waycott et al. [2009](#page-9-0)). Nutrients such as phosphorus are dispersed through the system by a number of nutrient cycling processes in the water column and sediments (McMahon and Walker [1998\)](#page-8-0). These nutrients eventually become available to primary producers through columnar water, pore water and sediments (Lavery et al. [1993;](#page-8-0) McMahon and Walker [1998](#page-8-0)).

Phosphate $(PO₄³)$ is the common form of phosphorus in seagrass beds. Seagrasses take up phosphorus by active transport through the root-rhizomes, although in some species, both the leaves and root-rhizomes play a role in the uptake of phosphorus (Brix and Lyngby [1985\)](#page-7-0). The uptake of phosphorus by seagrass depends on factors such as diffusion between pore and column waters, seagrass species and environmental conditions (Lee and Dunton [1999;](#page-8-0) Brix and Lyngby [1985](#page-7-0)). However, dissolved inorganic phosphorus has low solubility and is readily adsorbed to carbonate rich sediments (McRoy et al. [1972;](#page-8-0) Jensen et al. [1998\)](#page-8-0), limiting its availability for biological uptake (Fourqurean et al. [1992](#page-7-0); Touchette and Burkholder [2000\)](#page-9-0). The redox potential of the sediments and the sediment water interface also plays an important part in dictating nutrient bioavailability. Oxic sediments may act both as a sink (Bostrom and Petterson [1982](#page-7-0)) and a source (Bortelson [1971\)](#page-7-0) of phosphorus. However, under anoxic conditions, these sediments act as a source of phosphorus. When phosphorus, in the form of orthophosphate ions $(HPO₄²-, H₂PO₄⁻)$ and organic compounds is available, phytoplankton has evolved mechanisms to sequester it from water. This subsequently results in water column concentrations often below the limits of analytical detection (<0.3 μ g.L⁻¹), making them unavailable to macrophytes such as seagrass. These processes are particularly significant from the viewpoint of seagrass meadows off the Adelaide metropolitan coastline, where oxic carbonate sediments make phosphorus cycling in the water column, pore water and sediments a complex process—a challenge for seagrasses in acquiring these nutrients from the system.

Different seagrass species have different nutrient requirements. Unfortunately, few published works exist that report relative nutrient uptake rates from temperate waters. This is of significance for *Posidonia* and Amphibolis, two dominant seagrass taxa found in South Australian waters (Westphalen et al. [2005](#page-9-0)). To manage nutrient inputs into the future, there is a need for better understanding of the fate of nutrients, particularly their biological uptake in this system. Management of nutrient inputs are critical in preventing further losses of seagrasses in the gulf waters of South Australia as seagrass loss has wide ranging ecological and economic implications (e.g. Touchette [2007](#page-8-0)). McArthur and Boland [\(2006](#page-8-0)) estimated the economic contribution of seagrass habitats in the gulf waters to be in the order of AUS\$114 million per annum. A decline in 16 % of seagrass cover from this area was estimated to result in a loss in production of around AUS\$ 235,000 per annum. Recognising the value of seagrass and seagrass mats as a carbon sink, Moore and Westphalen ([2007](#page-8-0)) estimated that a loss of approximately 260 km^2 of seagrass in the southern temperate waters of Australia to be worth in excess of A\$500 million.

This study represents an attempt to quantify some of the seasonal uptake rates of the biotic components of the seagrass ecosystem. In the following investigation, total phosphorus uptake rates were quantified in Posidonia (Posidonia angustifolia) and Amphibolis (Amphibolis antarctica) dominated seagrass beds. A simple modelling approach quantified the assimilative capacity of seagrass in relation to anthropogenic inputs of phosphorus in the Adelaide coastal waters.

Materials and methods

Description of the sampling equipment

The benthic chambers used in this study comprised six identical cylindrical units made of clear perspex, each with an overall volume of 13.5 L (Fig. [1\)](#page-2-0). Each chamber had an inflow and an outflow connection onto which a pump line was connected to recirculate water contained within the chamber. The pump line consisted of a fibre-reinforced PVC hose linking the intake of a submersible inline pump (LMV Amazon) through a flow control valve. The outlet of the pump was connected through a hose to a pressure compensator. The pressure compensator was a collapsible bag that compensated for the reduction in the volume of water contained in the chamber as a result of samples being drawn by syringes. It provided pressure relief and prevented pore water from being drawn into the chamber

Fig. 1 Close-up of the in situ chambers deployed over an Amphibolis antarctica bed to quantify uptake rates of phosphorus. Three chambers each were deployed simultaneously over Posidonia angustifolia and Amphibolis antarctica beds. The chambers were bolted on to stainless steel cutters deployed on the seagrass bed 24 h prior to the experiment. The water in the chamber was circulated with a submersible inline pump through a pressure compensator. Sampling ports on the chamber facilitated spiking of nutrients and collection of water samples

due to syringe sampling. The outlet of the compensator fed through a hose into the outflow spout of the chamber. The pumps were powered by a 6 V DC, 144 Ah underwater battery pack. The chambers had sampling straws glued on, serving as sampling ports for pore water and chamber water collections using a syringe. These sampling ports were terminated with a two-way valve that isolated the chamber from the surrounding water. A pore water sampler made with an air stone diffuser was hooked to the pore water sampling straw with a tygon tube internally in the chamber. The stainless steel cutters to which the chambers were bolted had a sharp cutting edge with a square platform. Rubber washers were glued on to the platform to provide a tight seal between the chamber and the cutter after the chamber is bolted down. Each cutter has a volume of 4.5 L and covered an area of 0.0453 $m²$ when pushed into the sediment. Detailed description of the sampling equipment can be obtained from Nayar et al. [\(2006\)](#page-8-0).

Field sampling

Sampling location

The site chosen for the experiment was located off Tennyson (34°52.532′ S, 138°27.797′ E; Fig. [2](#page-3-0)). All deployments were carried out within 100 m radius of this point. The field site comprised beds of P. angustifolia and A. antarctica alongside each other at an average water depth of about 8 m during high tide.

Chamber deployment and sample collection

All field deployments were carried out at around 10 am in the morning on the day of the trial. The dates for the studies were 5 August 2005 (winter), 29 November 2005 (spring) and 21 February 2006 (summer). Stainless steel cutters were driven into seagrass beds by SCUBA divers at least 48 h prior to the experiment to allow for stabilisation of the sediments and recovery of seagrass. Three of these cutters were driven into A. antarctica and the remaining three into *P. angustifolia*. Care was taken to ensure minimal damage to seagrass, at the same time ensuring that the cutters were driven at least 10 cm into the sediment.

On the day of the trial, approximately 1.5 L of water sample was collected in a polyethylene bottle about 0.5 m above the seagrass bed for qualitative and quantitative analysis of phytoplankton and measurement of ambient water quality. Water quality parameters, viz., water temperature, dissolved oxygen (DO), salinity and pH were measured using a Hach SensIon 156 multi-parameter probe immediately after collection on board the vessel. The Hach multi-parameter probe was calibrated for DO (sulphite method), salinity (NaCl standard) and pH (pH buffers) in the laboratory adopting the procedures outlined in the operating manual [\(http://www.hach.com/asset-get.](http://www.hach.com/asset-get.download.jsa?id=7639982446) [download.jsa?id=7639982446\)](http://www.hach.com/asset-get.download.jsa?id=7639982446). The resolution and accuracy of the various parameters are also detailed in the operating manual. Upon taking the ambient water quality measurements, approximately 100 mL of the water samples were fixed with Lugol's iodine for qualitative and quantitative phytoplankton analysis.

Stock nutrient solution of 1000 mg. L^{-1} for spiking was prepared from AR grade salt of KH_2PO_4 and loaded into 20-mL syringes. These syringes were sealed with an end cap. Each chamber was then spiked with the stock solution carried in syringes to yield a final concentration of 1 mg. L^{-1} of the nutrient in each chamber. Samples for initial concentrations of phosphorus in pore water (C_{ip}) and columnar water (C_i) were collected in 60-mL syringes and sealed immediately with an end cap. The samples were filtered immediately after collection through a 0.45-μm pore size membrane cartridge filter (Millipore) into a 60-mL polyethylene bottle pre-rinsed with deionised water and some of the sample. The bottles were then stored in ice under dark conditions.

Fig. 2 Map showing location of chamber deployment. All chamber deployments were carried out within a 100 m radius of the point marked off Tennyson

Chambers were incubated for 2 h. Pore water (C_{fp}) and chamber water samples (C_f) , constituting final concentrations, were collected and processed the same way as'initial samples'. About 120 mL of water sample from each chamber was collected along with two ambient samples for water quality measurements. Water quality parameters were measured as above. At the termination of the experiment, seagrass samples from each of the six chambers were cored out and transported to the laboratory for biomass analysis. Data for photosynthetically active radiation (PAR) was obtained from an Odyssey light logger deployed on site set to log data every 6 min.

Water samples collected and filtered aboard the vessel were stored in sample bottles and frozen at −20 °C until they could be analysed. Concentrations of phosphorus (as $PO₄$) in the chamber water and pore water were analysed for soluble reactive phosphorus. Similarly, ammonium (NH4) and total oxidised nitrogen (NO_x) concentrations in the chamber water at the end of the incubation was determined. Dissolved inorganic nutrients (NH_4 , NO_x and PO_4) were measured by flow injection analysis using a Lachat QuickChem 8000 automated FIA following standard protocol.

The seagrass samples collected in the field were processed in the laboratory immediately upon arrival. The samples were rinsed in clean seawater and cleaned of dead leaves, debris and sand. Wet weights of the total biomass of above- and below-ground biomass of seagrass collected from each of the six chambers were measured. The moisture content of a sub-sample $(\sim 5$ g wet weight) of each biomass component was measured gravimetrically by freeze-drying the samples. The moisture content of the samples was then used to work out the dry weight of the total biomass (W) contained in each chamber.

Total biotic phosphorus (as phosphate) uptake rate (P), a consolidated value for the uptake rates of seagrass above ground biomass, below ground biomass and epiphytes, was calculated using the formula:

$$
P(\mu mol \ P.g^{-1}DW.h^{-1}) = \frac{[(TIC - TFC) \cdot 1000]}{W \cdot t \cdot 0.3262 \cdot A}
$$

where

'P' is the uptake rate of phosphorus (μ mol P.g⁻¹) $DW.h^{-1}$

TIC or total initial concentration (mg) is calculated using the formula

$$
TIC(mg) = [(C_{\text{fc}} \times V_{\text{c}}) + (C_{\text{ip}} \times V_{\text{p}})]
$$

TFC or total final concentration (mg) is calculated using the formula

$$
TFC(mg) = [(C_{fc} \times V_c) + (C_{fp} \times V_p)]
$$

 $V_{\rm C}$ ' is the volume of water column contained in the chamber, 13.5 L

 V_P is the volume of pore water contained in the steel cutter of the chamber, 1.211 L

 ${}^{\circ}C_{\text{fc}}$ is the final chamber water phosphorus concentrations $(mg.L^{-1})$

 ${}^{\circ}C_{\text{in}}$ is the initial pore water phosphorus concentrations $(mg.L^{-1})$

 ${}^{\circ}C_{\text{fp}}$ is the final pore water phosphorus concentrations $(mg.L^{-1})$

 W' is the total biomass in (g DW)

't' is the duration of incubation (h)

0.3262, the phosphorus conversion factor

'A' the atomic weight of phosphorus (30.97371)

Data for phosphorus uptake was analysed using a twoway analysis of variance (ANOVA) with Tukey's pairwise comparison post hoc tests to determine significant differences between seasons. The assumption of homogeneity of variance was tested using Levene's test and was met. The statistical analysis was carried out using Minitab Ver. 13.2 with a significance level of $\alpha \leq 0.05$.

Results and discussion

Mean values of ambient and chamber water quality for various physicochemical parameters measured during chamber deployments for the three seasons are summarised in Table 1. Seasonal differences were very pronounced for most parameters, with the exception of salinity and pH. The differences between ambient levels and levels in the chamber were insignificant, with the exception of dissolved oxygen where mean concentrations ranged from 6.6 to 10.3 mg. L^{-1} in ambient and 5.9 to 6.9 mg. L^{-1} in chamber water. Details of the seasonal variations in biological parameters in P. angustifolia and A. antarctica beds monitored during the study are

Table 1 Ambient and chamber water quality during deployments in winter, spring and summer. All values are means±standard error of means

summarised in Table [2.](#page-5-0) Above- and below-ground biomass for both species registered a peak in spring and a reduction in summer. Epiphytes registered highest loading in summer (P. angustifolia 0.57 ± 0.04 g.g⁻¹; A. antarctica 5.03±0.88 $g.g^{-1}$). Phytoplankton abundance was highest in winter $(29.3 \pm 0.7 \text{ cells.mL}^{-1})$ and least in spring $(5.0 \pm 2.5 \text{ cells.mL}^{-1})$.

Total uptake of spiked inorganic phosphorus by biological components was negligible during the study, never exceeding 0.5 % of the total resource (Table [3\)](#page-6-0). Similarly, there was no limitation of inorganic nitrogen in the chambers during the deployments. In carbonaterich sediments, dissolved inorganic phosphorus is retained by the sediments (Jensen et al. [1998](#page-8-0); Ziegler et al. [2004\)](#page-9-0), limiting its availability for biological uptake (Fourqurean et al. [1992;](#page-7-0) Touchette and Burkholder [2000\)](#page-9-0). Sediments of the Adelaide metropolitan coast are predominantly carbonate (Shepherd and Sprigg [1976](#page-8-0)), limiting the bioavailability of phosphorus. Also, inorganic phosphorus uptake affinities and rates for seagrass are often much lower (Hocking et al. [1981](#page-8-0)) than ammonium and depend on the nutritional status of the plant and the prevailing environmental conditions (Touchette and Burkholder [2000\)](#page-9-0). This is consistent with the low biotic uptake rates recorded in our study. In their extensive review, Touchette and Burkholder [\(2000\)](#page-9-0) reported maximal phosphorus uptake rates ranging from 0.014 to 43 µmol $P.g^{-1}$ DW.h⁻¹ in seagrasses, much lower than those reported for ammonium, but comparable to the rates for nitrate. Furthermore, in oligotrophic temperate marine environments such as the study area, nitrogen is often limiting, further supporting the observations made in this study on lower phosphorus uptake. Highest uptake rates occurred in winter (1.49±0.4 µmol $P.g^{-1}$ DW.h⁻¹; mean±SE of

Table 3 Percent uptake of total resource by the biotic components at the end of the incubation. The data shows adequate availability of phosphorus, ammonium and nitrate and that there was no limitation of nutrients in the chamber at the termination of the experiment. Values represent mean \pm standard error of means (n=3)

Resource	Species	Winter	Spring	Summer
$PO4-P$	P. angustifolia	0.16 ± 0.04	0.02 ± 0.01	0.01 ± 0.00
	A. antarctica	0.11 ± 0.03	0.05 ± 0.03	0.09 ± 0.07
NH_4-N	P. angustifolia	5.8 ± 0.1	8.6 ± 0.2	4.0 ± 0.1
	A. antarctica	51.1 ± 3.7	85.2 ± 0.6	21.8 ± 0.3
$NO3-N$	P. angustifolia	$1.8 + 3.8$	8.7 ± 0.3	0.3 ± 0.0
	A. antarctica	4.9 ± 1.4	17.2 ± 0.5	1.4 ± 0.0

means) and lowest in spring $(0.7\pm0.4 \text{ \mu mol P.g}^{-1})$ DW.h⁻¹) for *A. antarctica* and highest in winter (2.09 \pm 0.53 µmol $P.g^{-1}$ DW.h⁻¹) and lowest in summer (0.14 \pm 0.02 μmol $P.g^{-1}$ DW.h⁻¹) for *P. angustifolia* (Fig. [2\)](#page-3-0). These uptake rates were similar to the rates reported in A. antarctica by Paling and McComb [\(1994\)](#page-8-0) in Western Australia, but much lower than the maximal uptake rates of 7–43 µmol $P.g^{-1}$ DW.h⁻¹ reported by Perez-Llorens and Niell [\(1995](#page-8-0)) in Zostera noltii. Stapel et al. [\(1996\)](#page-8-0) however reported uptake rates ranging from 2.2 to 3.2 μmol $\overline{P}.\overline{g}^{-1}$ DW.h⁻¹ in tropical seagrass *Thalassia* hemprichii. While there was a significant difference in the seasonal uptake rates, there was no difference in the uptake rates in meadows of the two species (Table 4). Tukey's test revealed significant differences in the uptake rates between winter and spring. Factors such as light and temperature have been reported to play an important role in regulating phosphorus uptake by seagrass (McRoy and Barsdate [1970](#page-8-0); Patriquin [1972](#page-8-0);

Table 4 Results of two-way Analysis of Variance (ANOVA) for phosphorus uptake rates in Posidonia angustifolia and Amphibolis antarctica beds

Source	Degrees of F freedom		\boldsymbol{D}	Tukey's pair wise comparison
Seasons	2	4.29	0.04	$\overline{W} > Su$ > Sp
Species		0.47	0.51	
Season × species	\mathcal{L}	141	0.28	

Results of Tukey's pair-wise comparison are arranged in the ascending order of their means. Lines drawn over groups indicate 'seasons' that are not significantly different from each other ($p>0.05$). Figures in ital are statistically significant at $p\leq 0.05$

 W winter, Sp spring, Su summer

Penhale and Thayer [1980;](#page-8-0) Touchette and Burkholder [1999](#page-8-0)). While high nutrient uptake rates in summer might be expected, fine suspended sediments settling on seagrass leaves might have been a reason for reduced uptake during that season. The fine suspended sediments might have originated from nearby dredging operations (within 5 nm). Seagrasses were observed to be in relatively poor condition based on visual observations (Nayar et al. [2009\)](#page-8-0). Under these conditions, seagrass photosynthesis may be lowered, explaining the reduced uptake rates (Patriquin [1972;](#page-8-0) Perez et al. [1994](#page-8-0)).

While nitrogen inputs into the Adelaide coastal waters have been widely attributed to widespread seagrass loss (Nayar et al. [2012](#page-8-0)) and decline in water quality, less attention has been focused on the impact of phosphorus inputs (Fox et al. [2007](#page-7-0)). In an audit conducted on the inputs and concentrations of loads received by the Adelaide coastal waters (Wilkinson et al. [2005](#page-9-0)) and a subsequent report by Gaylard [\(2009\)](#page-7-0), it was determined that around 362 t yr^{$^{-1}$} of phosphorus was discharged into the coastal waters in 2007. These inputs were largely attributed to the three major waste water treatment plants collectively accounting for 93 % (335 t yr^{-1}) of the total load, followed by storm water inputs accounting for 6 % of the inputs (20 t yr^{-1}) and about 1 % from wet fall (4.9 t yr^{-1}) and 0.5 % from dry fall (1.9 t yr^{-1}) .

A simple modelling approach, described in Nayar et al. [\(2012\)](#page-8-0), was adopted to ascertain phosphorus inputs and assimilation in the Adelaide coastal waters. Seasonally, daily uptake of phosphorus registered highest uptake rates in winter followed by spring and least in summer (Figs. 3 and [4\)](#page-7-0). It was estimated that out

Fig. 3 Mean seasonal phosphorus uptake rates in a Posidonia angustifolia and Amphibolis antarctica bed (µmol P g^{-1} DW h^{-1}). The *error bars* denote standard error of means $(n=3)$

Fig. 4 Total daily phosphorus assimilation (kg P. day⁻¹) by Posidonia and Amphibolis beds in Adelaide coastal waters

of the total anthropogenic inputs of phosphorus into the Adelaide coastal waters, only 5.4 % (19.53 t yr^{-1}) was assimilated by seagrass beds, largely by Posidonia beds (19.52 t yr⁻¹; >99 %). This is attributed to the smaller aerial cover of *Amphibolis* sp. (0.17 km^2) and therefore lower biomass, when compared to cover of Posidonia sp. (131 km^2) in the Adelaide coastal waters.

Conclusions

Total uptake of spiked inorganic phosphorus by biological components was negligible in the study, never exceeding 0.5 % of the total resource. Low biological uptake rates of inorganic phosphorus could be attributed to carbonate sediments and particulates in the water column binding inorganic phosphorus (Jensen et al. [1998](#page-8-0); Ziegler et al. [2004\)](#page-9-0), limiting its availability for biological uptake. Highest uptake rates were in winter and lowest in spring. Smothering of the seagrass beds by suspended sediments probably resulted in reduced uptake during summer, as the chamber deployments during that season coincided with dredging operations. Overall phosphorus uptake rates reported in this study for P. angustifolia and A. antarctica beds were comparable to the findings of Paling and McComb ([1994\)](#page-8-0) in Western Australia. From an environmental perspective, seagrass beds in the Adelaide coastal waters accounted for the assimilation of only 5.4 % of the total anthropogenic phosphorus inputs. This signifies the

importance of management plans for phosphorus inputs into the coastal waters where 95 % of the anthropogenic inputs remain unutilised and is potentially bioavailable. Although nitrogen loads into the system have been regarded to be a far greater problem requiring immediate attention, reduction of phosphorus inputs also deserves attention.

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