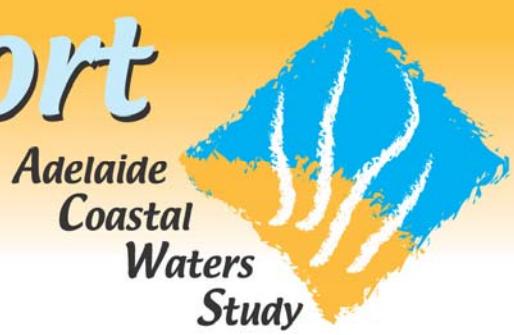


Technical Report



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A review of seagrass loss on the Adelaide metropolitan coastline



Government
of South Australia



A review of seagrass loss on the Adelaide metropolitan coastline

Authors

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Executive Summary

Since the 1940s, approximately 5000 ha of seagrass meadows have been lost from the Adelaide metropolitan coast. Degradation and loss of seagrass meadows is a cause of concern for coastal managers due to the importance of these systems to near-shore productivity, stability and biodiversity.

Primary causes of seagrass decline are poorly understood, particularly for the Adelaide metropolitan coast where seagrass loss has mainly occurred in shallow water close to shore from where it has advanced to seaward. Elsewhere in the world, anthropogenic seagrass loss has generally occurred in deeper water offshore, with later progression shorewards. Thus, the pattern and perhaps the primary causal mechanism(s) of seagrass loss on Adelaide's coast appear to be different or in some way modified from those described and inferred for other areas. Importantly, initial losses appear to have led to further losses via erosion and fragmentation of remaining meadows.

The following review summarises the nature of the seagrass community along the metropolitan coast of Adelaide in terms of individual species, meadow composition and maintenance, and the associated flora and fauna. The information on losses is also summarised, followed by a review of the potential loss mechanisms that can be linked to anthropogenic activities: nutrients, sedimentation and/or turbidity, toxicants, and salinity changes.

Based on the review, no single factor can be identified as the likely primary cause for Adelaide's unusual seagrass decline. Rather it is likely that a combination of factors is responsible for the near-shore seagrass loss. Research into the mechanisms for seagrass loss on the Adelaide coast should thus focus on the interaction of different factors rather than considering each in isolation.

1. Introduction

1.1. Background

Seagrasses evolved from a variety of land-based flowering plants with possibly six different invasions of the sea during the Cretaceous period (120 – 65 MA; Larkum and den Hartog 1989). Seagrass communities play a key role in terms of primary production, nutrient cycling, sediment stabilisation, modification of wave energy gradients and provision of “nursery” habitat for fishes and invertebrates (e.g. Ducker *et al.* 1977, Greenwood and Gum 1986, Howard *et al.* 1989, Short and Wyllie-Echeverria 1996, EPA 1998). Short and Wyllie-Echeverria (1996) suggest that seagrass systems rank with mangroves and coral reefs in terms of primary production, whilst Duarte and Chiscano (1999) estimated seagrass production to be responsible for up to 15% of the ocean’s annual net carbon production. Any loss of seagrass is thus cause for concern, particularly given the very slow rate of recovery observed for many species, in particular *Posidonia* spp. (Kirkman 1998, Meehan and West 2000).

Declines in water quality due to coastal urbanisation and development within river catchments have resulted in the reduction in health of near-shore marine systems worldwide, particularly seagrass communities that often dominate the estuaries and anchorages where cities tend to evolve (Shepherd *et al.* 1989, Gabric and Bell 1993, Seddon 2000, Ralph *et al.* in press). Increased nutrient loads in near-shore systems are most frequently identified as the cause for seagrass decline (Short and Wyllie-Echeverria 1996, Ralph *et al.* in press). The nutrient model argues that plants become starved of light under the pressure of higher phytoplankton, macroalgae and/or epiphyte loads (e.g. Shepherd *et al.* 1989, Dixon 1999, Wear *et al.* 1999, Deegan *et al.* 2002, Ralph *et al.* in press) such that the depth at which meadows can survive is reduced (Figure 1). Light is the key factor that limits the natural depth of many seagrass populations (Duarte 1991a, Cambridge and Hocking 1997). Seagrass losses due to nutrients are thus expected to occur first in deeper areas and to progress shallower over time. There are numerous examples in support of this model: Botany Bay (New South Wales; Larkum 1976, Larkum and West 1990), Princess Royal Harbour (Western Australia; Bastyan 1986, Hillman *et al.* 1990), Plateau des Chèvres, (France; Pergent-Martini and Pergent 1996), Tampa Bay (Florida; Dixon 1999) and Chesapeake Bay (Virginia/Maryland, Orth and Moore 1983).

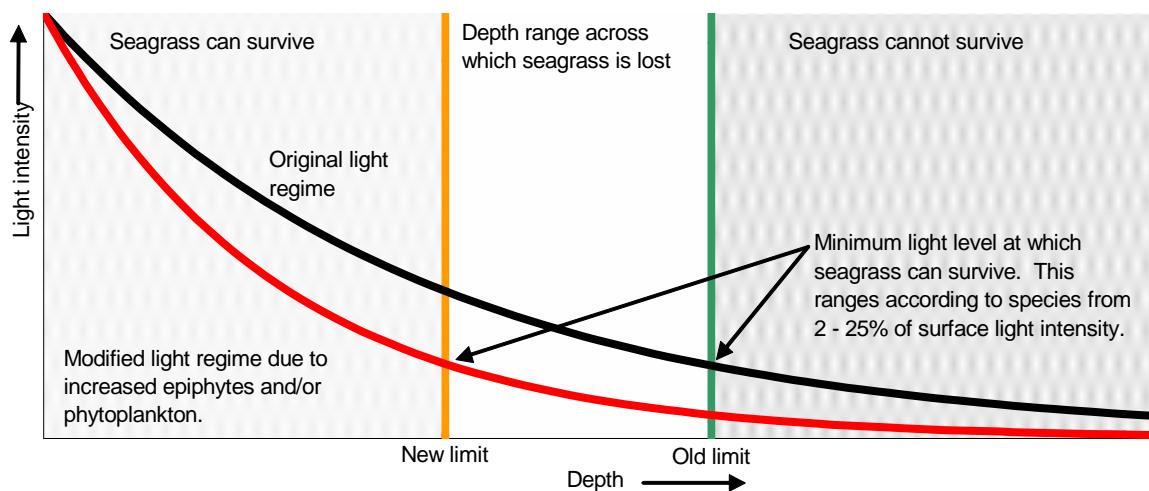


Figure 1. Model of the decline in maximum viable depth for seagrasses due to increased nutrient loads in the water column.

Historically, increased nutrient loads have been considered the major cause for seagrass decline on the Adelaide metropolitan coast (e.g. Shepherd *et al.* 1989, Steffensen *et al.* 1989, EPA 1998); however, the pattern of most of this loss is not consistent with the nutrient load model

because meadow decline has largely occurred in shallow areas close to shore (see below). This difference suggests that alternative mechanism(s) for seagrass decline have operated on the Adelaide metropolitan coast or that increased nutrients are, in some manner, constrained such that off shore seagrasses remain unexposed. The following discussion summarises what is known of the seagrasses and seagrass losses on the Adelaide metropolitan coast, and reviews the potential mechanisms that may be responsible for meadow degradation.

1.2. Seagrass Loss on the Adelaide Metropolitan Coast

Loss of seagrass on the Adelaide metropolitan coast was first observed in 1968 near the Patawalonga outlet and the Glenelg wastewater treatment plant outfall (Figure 2; Shepherd 1970). Since that time, seagrass decline on the Adelaide coast has been well documented (Butler *et al.* 1997), with at least six reports exploring both the extent and potential causes of large-scale losses spanning the period of coastal development from 1949 to 2002 (EWS 1975, Shepherd *et al.* 1989, Steffensen *et al.* 1989, Hart 1997, EPA 1998, Cameron 2003). All of the summaries present estimates of seagrass loss based on irregularly obtained aerial photographs, generally spanning the coast from Outer Harbour to Marino (EWS 1975, Shepherd *et al.* 1989, Steffensen *et al.* 1989) with some as far south as Aldinga (EPA 1998, Cameron 2003).

Estimates of the total seagrass loss from Adelaide's coast range from 4,000 to 5,000 ha (EWS 1975, Shepherd *et al.* 1989, Steffensen *et al.* 1989, Hart 1997, EPA 1998, Cameron 2003). Some of the variability in this range stems from differences in defining the extent of the Adelaide metropolitan coast but there are also differences in the spatial extent of aerial photographs and differences in the interpretation of what constitutes bare sand. These losses have mainly occurred in a 1 – 2 km wide strip, parallel to the shore of Holdfast Bay (Outer Harbour to Brighton), with smaller areas located around the Port Adelaide sludge outfall (operational from 1978 – 1993; Figure 2) and at the dredge spoil-dumping ground off Outer Harbour. Seagrass loss has also been recorded for areas further north (St Kilda to Port Gawler; e.g. Shepherd *et al.* 1989) as well as in deeper water off Pt Malcolm that do not show up on aerial photographs (Butler *et al.* 1997), thus highlighting the limitations of aerial images in determining seagrass decline. The spatial and temporal pattern of seagrass losses adjacent to Adelaide broadly correlates with the pattern of coastal development and anthropogenic inputs into coastal waters (Steffensen *et al.* 1989, EPA 1998).

Apart from the uneven spatial spread, seagrass loss has also been temporally variable, with peak losses observed between 1970 and 1977 along the northern metropolitan coast (Hart 1997, EPA 1998). There are also differences in the rate of loss between species, with *Amphibolis antarctica* appearing to be more sensitive to declines in water quality than *Posidonia sinuosa* or *P. angustifolia* (Steffensen *et al.* 1989), possibly through greater sensitivity to high epiphyte loads or even nutrient toxicity (see below). More recently, the rate of decline has decreased (Hart 1997, EPA 1998) possibly due to the decommissioning of sludge outfalls at Glenelg and Port Adelaide (EPA 1998) and recent improvements in wastewater treatment and catchment management (Butler *et al.* 1997). However, seagrass loss is continuing on the Adelaide coast, largely through the expansion of “blowouts” and increased fragmentation of meadows in southern Holdfast Bay (Figure 3; Clarke 1987, Hart 1997, Seddon 2002).

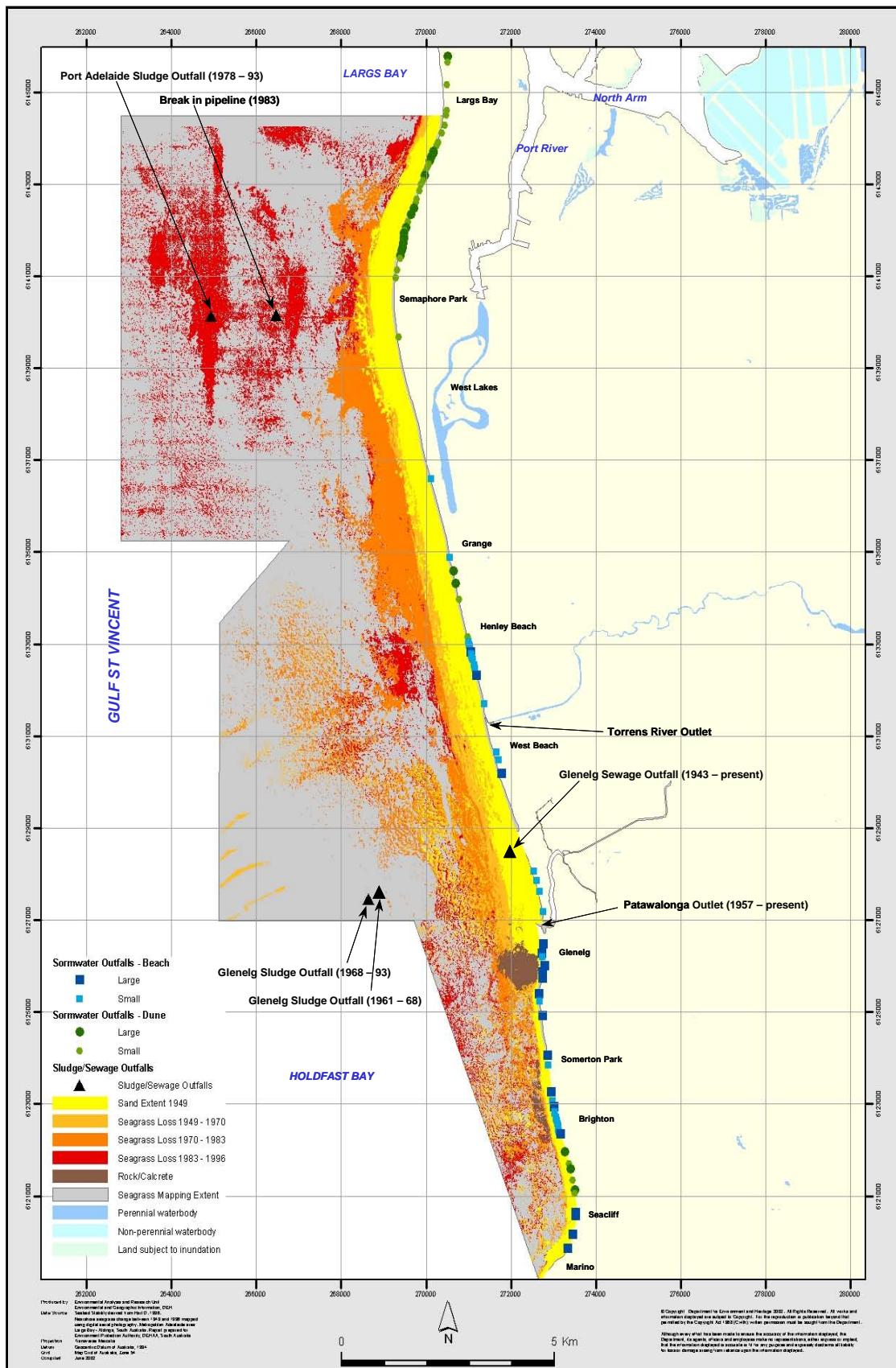


Figure 2. Map of the Adelaide metropolitan coast showing the accumulated loss of seagrasses from 1949 to 1996 between Largs Bay and Marino. The location of input sources is also indicated. Image from Seddon (2002) constructed by Tim Noyce care of the South Australian Department of Environment and Heritage. Reproduced with permission.

Blowouts are naturally occurring gouges that slowly migrate within seagrass beds due to erosion and seagrass loss on one edge and seagrass colonisation on the opposite edge (see Clarke and Kirkman 1989). Individual blowouts may migrate at a rate of 0.5 m per year (Clarke 1987). It appears, however, that the natural process of colonisation is no longer occurring in Holdfast Bay, such that blowouts are increasing in size and seagrass beds are becoming increasingly fragmented (Clarke 1987, Seddon 2002). In these situations, it has been argued that the importance of coastal inputs may have declined relative to the influence of increased sediment re-mobilisation and the exposure of sand due to the decline of seagrass meadows (Larkum and West 1983, Seddon 2002, Townsend 2002).



Figure 3. Edge of a "blow-out" with seagrass debris and some colonising *Amphibolis antarctica*. Photograph: Simon Bryars.

The first detailed summary of seagrass losses on the Adelaide coast suggested that turbidity and/or sedimentation due to stormwater inputs was the key factor in seagrass decline (EWS 1975). However, most other studies since that time have been firm in their opinion that excessive nutrients (from both wastewater treatment plant outfalls as well as stormwater) have had a major detrimental effect through increased epiphyte loads (e.g. Shepherd *et al.* 1989; Steffensen *et al.* 1989; EPA, 1998). Notwithstanding this, there is little if any research on the direct causal mechanisms for seagrass losses in Australia or elsewhere (Short and Wyllie-Echeverria 1996, Seddon 2000, Ralph *et al.* in press) and Adelaide's seagrass losses appear to be atypical. Studies of seagrass declines are usually conducted well after significant losses have occurred (Seddon 2000) making identification of the cause(s) more problematic. Such is definitely the case on the Adelaide coast.

1.3. Adelaide's Seagrass Community

1.3.1. Components of seagrass meadows

There is a relatively high level of endemism among southern Australian seagrasses, with at least a third of species living nowhere else (Shepherd and Robertson 1989). The waters of Adelaide's coastline support up to 13 species of submerged marine angiosperms, belonging to seven different genera (Table 1), including species of *Ruppia* and *Lepilaena* that are often not considered as seagrasses as they occur in salt marsh and hypersaline lakes up to ten times the salinity of seawater (Robertson 1984). In terms of biogeography, the species found on the Adelaide coast have affinities ranging from cool temperate to warm temperate (Shepherd and Robertson 1989). Almost all of them are perennial and flower in the spring and summer, grow across various depth ranges from the intertidal to 40 metres and vary in size from 5 cm to 120 cm in length (Table 1; Robertson 1984). This diversity encompasses a wide array of morphologies and life histories and thus a range of responses to disturbance (see Duarte *et al.* 1997). There are an estimated 15,000 km² of seagrass beds in southern Australia (Greenwood and Gum 1986) with 5000 km² in South Australia; 3,700 km² in Spencer Gulf and 1,530 km² in Gulf St Vincent (Shepherd and Robertson 1989). Seagrass communities in South Australia are considered by Shepherd *et al.* (1989) to be amongst the largest and most diverse in the world.

Shepherd and Robertson (1989) provide a broad description of seagrass communities on the Adelaide metropolitan coast in which they describe two different community types. The first occurs in the shallower areas northwards of Outer Harbour (Barker Inlet to Port Gawler; Figure 4, Zone 1) comprising mixtures of *Zostera muelleri*, *Z. mucronata*, *Ruppia* and *Lepilaena* on broad intertidal mudflats backed by mangroves and samphire swamps, with *Heterozostera tasmanica* and *Posidonia australis* occurring across gently sloping subtidal sediments.

Recently, *Zostera muelleri* and *Z. mucronata*, as well as *Z. novazelandica*, have been combined with *Zostera capricorni* (Green and Short 2003) and it is thus likely that the differences between these (sub) species are environmentally driven. Both *Zostera muelleri* and *Z. mucronata* will be considered under the name of *Z. capricorni* throughout this review. In addition, *Heterozostera tasmanica* has been placed into the *Zostera* genus (as *Zostera tasmanica*; Green and Short 2003). However, owing to its different environmental role (intertidal for *Zostera* spp. versus subtidal to 40 m depth for *Heterozostera*) as well as the plethora of literature under its original name, it has been decided to retain the use of *Heterozostera* in this review.

Seagrass losses from this northern zone have mostly been *Heterozostera* and *Posidonia*, which have been ascribed to the opening of the Bolivar wastewater treatment plant outfall in 1967 (Shepherd *et al.* 1989).

Prior to losses, the seagrass community southwards of Outer Harbour (Holdfast Bay; Figure 4, Zones 2 & 3) was thought to comprise overlapping bands of *P. australis*, *P. sinuosa* and *P. angustifolia* meadows, interspersed with patches of *Amphibolis antarctica* (Shepherd and Robertson 1989). *Heterozostera tasmanica* and *Halophila australis* occur throughout, often as an understorey component to larger species, although *Heterozostera* may occur more densely in deeper areas (Shepherd and Robertson 1989). At the time of Adelaide's settlement (1836), this community is thought to have dominated the soft-bottom coastline within Holdfast Bay with a distribution from within a few 10s to 100s of metres from shore to a depth of ~ 15 – 20 m (Shepherd and Sprigg 1976, Shepherd *et al.* 1989). Over time, this zone has suffered major seagrass losses such that the nature of the near-shore system, particularly the presence of *P. australis* close to shore has been inferred based on what has been observed in Spencer Gulf (Shepherd and Robertson 1989, Seddon 2000), and limited observational evidence (see Thomas and Clarke 2002). Certainly, there have been substantial losses of *P. sinuosa*, *P. angustifolia*, *A. antarctica* and *Heterozostera tasmanica* in this zone (Shepherd *et al.* 1989).

Table 1. Species of seagrass reported in Adelaide coastal waters by Robertson (1984), Cambridge and Kuo (1984) and Shepherd *et al.* (1989), roughly in order of their spatial extent. Biogeographical ranges reported from Shepherd and Robertson (1989); most other data from Robertson (1984) with information on *P. coriacea* from Cambridge and Kuo (1984) and Campey *et al.* (2002). Depth ranges indicate either subtidal (0 m +) or intertidal. Heights are maximal common length rather than canopy height.

Species	Habit	Sexes	Biogeographical range	Depth range (m)	Max length (cm)	Flowering and fruiting *
<i>Posidonia sinuosa</i>	Perennial - Rhizoids	Monoeious	Warm temperate	0 - 15	120	August – January
<i>Posidonia australis</i>	Perennial - Rhizoids	Monoeious	Warm temperate	0 - 15	45	October – December
<i>Posidonia angustifolia</i>	Perennial - Rhizoids	Monoeious	Warm temperate	2 - 35	120	November – February
<i>Posidonia coriacea</i>	Perennial – Rhizoids	Monoeious	Warm temperate	1 - 30	120	December
<i>Amphibolis antarctica</i>	Perennial - Lignified rhizoids	Dioecious	Warm temperate	0 - 23	100	Flowers September – February Fruits July – December
<i>Amphibolis griffithii</i>	Perennial - Lignified rhizoids	Dioecious	Warm temperate	0 - 40	100	Flowers February - March Fruits September – February
<i>Heterozosteria tasmanica</i>	Perennial - Rhizoids	Monoeious	Intermediate	0 – 30+	85	September – March
<i>Zostera capricorni</i>	Perennial - Rhizoids	Monoeious	Intermediate	Intertidal	60	August – February
<i>Halophila australis</i>	Perennial - Stolons	Dioecious	Cool temperate	0 - 23	7	October – January
<i>Lepilaena marina</i>	Annual – Rhizoids	Dioecious	Intermediate	Intertidal	10	September – March
<i>Ruppia megacarpa</i>	Perennial - Rhizoids	Monoeious	Intermediate	0 - 2	25	October – March
<i>Ruppia tuberosa</i>	Annual or short-lived perennial – Rhizoids	Monoeious	Intermediate	0 - 1	10	September – November

* Both species of *Amphibolis* are viviparous (i.e. fertilised seeds germinate and grow while attached to the parent for 7 – 12 months).



Figure 4. Map of the Adelaide metropolitan coastline showing 5 m (yellow), 10 m (green), 15 m (orange) and 20 m (red) depth contour lines. Zones 1 – 4 represent the broad-scale study areas that have been selected for the Adelaide Coastal Waters Study. Full species names are listed in Table 1. Shaded areas on land roughly indicate the level of urbanisation with very blue for the central business district (CBD), pale green for inner suburbs, darker green for outer suburbs and the city fringe (darkest).

Southwards of Hallett Cove (Figure 4, Zone 4), the seagrass community has been less clearly described but it is likely to have been similar to that of Holdfast Bay, although the subtidal profile is steeper and there are more reefs (Figure 4; Shepherd and Sprigg 1976, Womersley and Thomas 1976). For these reasons, the seagrass meadows in this zone appear to be patchier, and it would seem unlikely that the shallow water *P. australis* would have been present in any numbers. However there may be a greater abundance of *P. angustifolia*, which favours deeper water (Shepherd *et al.* 1989). *Posidonia coriacea* has also been found in the deeper southern coast (Cambridge and Kuo 1984, Shepherd and Robertson 1989). This area would appear to be the least altered section of the metropolitan coast, due to fewer terrigenous inputs (Steffensen *et al.* 1989).

1.4. Individual Species

Information on each of the taxa known to occur on the Adelaide metropolitan coastline is varied in terms of its completeness; particularly biomass allocations and productivity (see Table 2). *Posidonia*, *Amphibolis* and *Heterozostera* are well studied in Australia, although the bulk of the information appears to derive from either Western Australia or New South Wales. In the case of *Halophila australis* and *Z. capricorni*, there is substantial research on other species in the same genera (e.g. *Halophila ovalis* and *Z. marina*), but its applicability to the South Australian context is uncertain. *Ruppia* spp. and *Lepilaena marina* are poorly known but given their broad range of salinity tolerances, there are likely to be substantial differences within species in biomass, nutrient allocation and productivity that are dependant on local water quality. Neither *Ruppia* nor *Lepilaena* are considered significant within the context of the Adelaide Coastal Waters Study.

Table 2. Estimates of biomass distribution and maximum primary productivity for species of seagrass that occur on the Adelaide metropolitan coast. † indicates data obtained from Paling and McComb (2000), ‡ indicates data from Cambridge and Hocking (1997), §§ data from Bulthuis and Woelkerling (1983), § estimated from Brock (1982), otherwise figures were obtained from a summary by Duarte and Chiscano (1999). Note: there are no data at all for *Posidonia coriacea*, *Halophila australis* or *Lepilaena marina*. NA = no data available for this parameter.

Species	Biomass (g DW m ⁻²)		Productivity (g DW m ⁻² d ⁻¹)	
	Above	Below	Above	Below
<i>Posidonia angustifolia</i>	471.4	840	3	NA
<i>P. australis</i>	453 †	658 †	2.5 ‡‡	0.32 †
<i>P. sinuosa</i>	575	468 †	3 ‡‡	0.17 †
<i>Amphibolis antarctica</i>	1005	297 †	6.2	0.03 †
<i>A. griffithii</i>	737	NA	NA	NA
<i>Heterozostera tasmanica</i>	173 §§§	NA	4.2 §§§	NA
<i>Zostera capricorni</i>	191	176	1.9	0.44
<i>Ruppia megacarpa</i>	164 §	119 §	NA	NA
<i>R. tuberosa</i>	24 §	83 §	NA	NA

1.4.1. *Posidonia*

Large, meadow-forming species of *Posidonia* are the dominant seagrass species on the Adelaide metropolitan coast in terms of cover/abundance (Shepherd and Robertson 1989), particularly within Holdfast Bay (Clarke 1987). *Posidonia* is a cosmopolitan genus, with at least four species represented in Adelaide waters (*P. sinuosa*, *P. angustifolia*, *P. australis* and *P. coriacea*; Table 1; Figure 5). *Posidonia* spp. are characterised by their relatively large size (Duarte 1991b) and strap-like blades that extend from a sheath at the base of the plant.

The distribution of *Posidonia* species varies in terms of depth, water movement and successional status. *Posidonia australis* is thought to act as a climax species (Shepherd and Robertson 1989) and tends to occur in sheltered, shallow subtidal areas. It is thus common in Barker Inlet and along the fringes of tidal flats further north. *Posidonia sinuosa* and *P. angustifolia* are difficult to distinguish, but occur across different, albeit overlapping, depth ranges (Table 1; 0 – 15 m for *P. sinuosa*, 2 – 35 m for *P. angustifolia*; Robertson 1984, Shepherd and Robertson 1989).

Posidonia meadows have only modest rates of production but a substantial standing crop (Cambridge and Hocking 1997), with three species similar in terms of productivity and above ground biomass (Table 2 – note there does not appear to be analogous data for *P. coriacea*). *Posidonia angustifolia* has a relatively higher below ground component than *P sinuosa* or *P.*

australis (Table 2), although this is probably traded off against a slower rate of growth. The ability to store large quantities of carbon may be a benefit in terms of enabling the plant to tolerate extended periods of sub-optimal light (e.g. Burke *et al.* 1996, Alcoverro *et al.* 2001, Holmer and Bondgaard 2001) but a high below ground biomass poses a substantial oxygen demand that cannot be assuaged by dissolved oxygen in the water column (Hemminga 1998). A loss of photosynthetic capacity may result in profound root anoxia and even the production of poisonous sulphides (Hemminga 1998). *Posidonia sinuosa* has the lowest below ground biomass, but a slightly higher above ground component (Table 2), which may suggest a capacity to grow faster than the other *Posidonia* species (through having a greater photosynthetic area) but also suggests a more limited carbon reserve. *Posidonia australis* would appear to be intermediate in terms of biomass allocation (Table 2).



Figure 5. *Posidonia australis* from the Adelaide coast.

Annual nitrogen and phosphorus uptake by *P. sinuosa* and *P. australis* in south-western Australia ranges from 9 – 17 g N m⁻² yr⁻¹ and 1.1 – 1.7 g P m⁻² yr⁻¹, respectively; however, retention of nutrients is lower than expected for a low nutrient environment with losses of 5 – 9 g N m⁻² yr⁻¹ and 0.4 – 0.7 g P m⁻² yr⁻¹ (Cambridge and Hocking 1997). This supports the notion of a high detrital load in *Posidonia* meadows (Klumpp and van der Valk 1984).

Clarke and Kirkman (1989) stated that species of *Posidonia* (and *Amphibolis*) are those that have suffered the greatest losses on the Adelaide Coast.

1.4.2. *Amphibolis*

Amphibolis, as a genus is confined to southern Australia with both species (*A. griffithii*, and the more common *A. antarctica*) occurring in the Adelaide region (Shepherd and Robertson 1989). *Amphibolis* grows into sizeable plants (up to 1 metre; Figure 6) across a wide range of depths, from the intertidal down to 20 to 40 m. However, Robertson (1984) reports that *A. griffithii* grows under lower light conditions and higher wave energy than *A. antarctica* and is thus largely restricted to southerly areas of the Gulf. *Amphibolis antarctica* is more common on the Adelaide coast, occurring in shallower areas (<12 m depth; Shepherd and Robertson 1989) along the fringes of *Posidonia* meadows (Shepherd *et al.* 1989). *Amphibolis* is said to readily

recolonise areas after disturbance (Shepherd and Womersley 1981, Clarke and Kirkman 1989, Marbá and Walker 1999) and is frequently observed in blowouts (Figure 3).

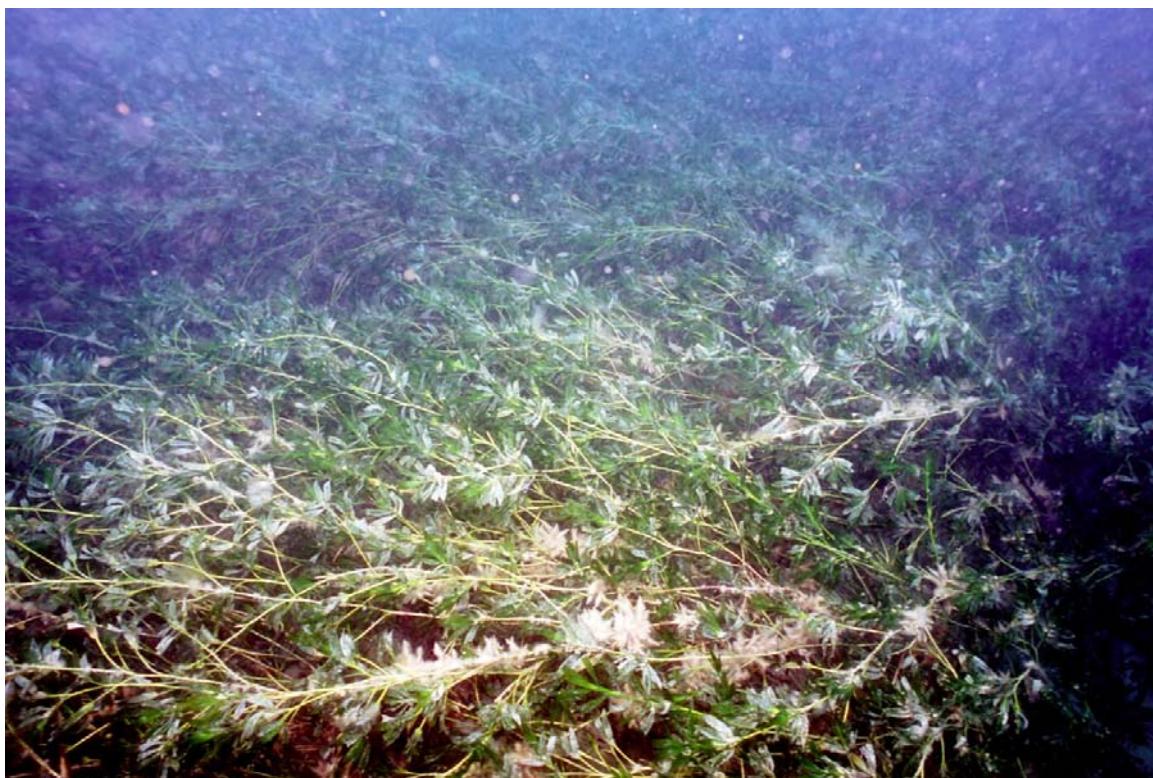


Figure 6. *Amphibolis antarctica* from the South Australian coast. Photograph: Simon Bryars.

Amphibolis antarctica is highly productive relative to other seagrasses in the Gulf, with a strong bias toward above versus below ground biomass (Table 2). *Amphibolis griffithii* also has a high above ground component relative to other seagrasses (Table 2), but this is lower than *A. antarctica*, possibly because of slower growth in its deeper habitat (Table 1). This highly skewed biomass allocation suggests a limited below ground carbon storage, although the above ground biomass is twice that of many other species. Lower below ground biomass might suggest a reduced capacity to tolerate high-energy environments, however, *A. antarctica* is considered an early successional species (Clarke and Kirkman 1989) and readily colonises bare substrate (Figure 3).

Although both species produce flowers at roughly the same time as other seagrasses (spring and summer), they are viviparous, with seedlings maintained on the parent throughout much of the year (i.e. July to December for *A. antarctica*; Table 1). Nitrogen uptake in an *A. antarctica* meadow has been estimated at $18.2 \text{ g N m}^{-2} \text{ yr}^{-1}$ while phosphorus has been estimated at $1.3 \text{ g P m}^{-2} \text{ yr}^{-1}$ (Walker and McComb 1988). Similar levels have been observed for *Posidonia* species (see above), although the mechanism for nutrient uptake is rather different in *Amphibolis* relative to other seagrasses in that most absorption is through the leaf blades rather than the roots. In this respect, *Amphibolis* acts more like a macroalga (Paling and McComb 1994) than a seagrass as it has the ability to colonise rocky substrate (Pedersen *et al.* 1997). However, uptake of most nutrients through leaves may increase the susceptibility of *Amphibolis* to high nutrient loads, in particular to nutrient toxicity (see below).

1.4.3. *Heterozostera*

Heterozostera tasmanica is widespread within Australia, ranging along the southern coast from Western Australia into New South Wales and Tasmania (Shepherd and Robertson 1989). Whilst it can occur at much greater depths (Table 1), it is often a major component of seagrass assemblages from the intertidal zone to around 8 m depth (Robertson 1984). Relative to

Zostera (see below), these broader depths offer a wider range of potential habitats, and a larger suite of species with which it can interact. Whilst longer than *Zostera*, the blades are relatively fine, averaging only a few millimetres in width (Figure 7).



Figure 7. *Heterozostera tasmanica* from the Adelaide coast. Photograph: David Miller.

Heterozostera has relatively fast growth rates, but its biomass is low relative to other species (Table 2), which may be indicative of its pioneer status (Kirkman 1989, Marbá and Walker 1999). Fast growth may enable the plant to cope with smothering of its leafage, but it may react poorly to prolonged periods of increased turbidity. Estimates of nitrogen and phosphorus levels in the above-ground biomass (based on data from Klumpp and van der Valk 1984) are lower than other species ($5.1 \text{ g N DW m}^{-2}$ and $0.7 \text{ g P DW m}^{-2}$, respectively).

1.4.4. *Zostera*

Despite the widespread distribution of the *Zostera* genus (Bearlin *et al.* 1999), and indeed *Z. capricorni* along the Queensland coast (Green and Short 2003), the population on the Adelaide metropolitan coast (Table 1) is rather poorly known. There are certainly differences in morphology related to position along the coast, and there is an estuarine form (originally within *Z. muelleri*; Robertson 1984), that presumably has different light requirements and salinity tolerances to the open-water forms. Burns (1992) found substantial responses of *Z. capricorni* (under the name of *Z. muelleri*) to increased nutrients with major changes in plant morphology, biomass, epiphyte cover and associated fauna relative to the proximity of the Bolivar wastewater treatment plant outfall. Estimates of nitrogen levels in *Z. capricorni* by Burns (1992) showed a substantial difference between above- and below-ground levels ($3.6 \text{ g N DW m}^{-2}$ and $11.8 \text{ g N DW m}^{-2}$ respectively) with significantly higher above-ground levels in plants nearer the Bolivar wastewater treatment plant outfall ($5.0 \text{ g N DW m}^{-2}$).

1.4.5. *Halophila*

While other species of *Halophila* are known to occur in South Australia, the genus appears to be represented on the Adelaide coast only by *Halophila australis* (Robertson 1984). With a

geographic range similar to that of *Heterozostera tasmanica*, *Halophila australis* also exists across a broad depth range, from the intertidal to 23 metres (Robertson 1984), generally as a sporadic component of other seagrass meadows (*sensu* King and Hodgson 1986). *Halophila australis* has an almost prostrate habit with a wide spatulate (paddle – like) blade rather than the straplike leaf exhibited by most other species (Figure 8). Although *Halophila australis* is dioecious (Table 1), apomixis (seed formation without pollination) has been suspected for the *Halophila* genus (McMillan and Williams 1980).



Figure 8. *Halophila australis*, image courtesy of Edgar (1997) copied with permission.

There is no apparent information on biomass or nutrient allocations for *Halophila australis*, although for *Halophila ovalis* the total levels ranged from 60 – 120 g DW m⁻² in the Swan/Canning Estuary (Western Australia) with 30 – 50% of this allocated below ground depending on season (Hillman *et al.* 1995). *Halophila* populations are characterised by low biomass relative to other seagrasses (Duarte and Chiscano 1999). *Halophila ovalis* appears to have very fast leaf turnover, which enables this seagrass to act as a pioneer (Vermaat *et al.* 1995). Although it is thought to be sensitive to shading (Vermaat *et al.* 1995), it also has very low light requirements (Duarte 1991b) and can grow to considerable depth.

1.4.6. *Lepilaena*

As a genus, *Lepilaena* has a broad range of salinity tolerances and frequently occurs in estuaries, coastal lakes and hypersaline environments that are not classed as marine (Robertson 1984). For this reason, *Lepilaena* is frequently not regarded as a seagrass, although *Lepilaena marina* has been reported at Port Gawler (Shepherd and Robertson 1989), where it is commonly associated with *Z. capricorni* in the intertidal (Robertson 1984). Plants of this species are dioecious, probably annuals, with flowers and fruits produced between September and March (Robertson 1984).

1.4.7. *Ruppia*

Like *Lepilaena*, *Ruppia* is a genus that is not generally considered a seagrass for the same reasons (i.e. the environments in which it can occur are often not classed as marine; Robertson 1984). Two species are known in South Australia, *Ruppia tuberosa* and *R. megacarpa*. Both species occur in Western Australia, South Australia and Victoria, with *R. megacarpa* extending into New South Wales and New Zealand (Robertson 1984). On the Adelaide coast, they co-

occur with *Zostera* in the intertidal mangrove areas throughout Barker Inlet and to the north, although both species are small and easily overlooked (Shepherd and Robertson 1989). *Ruppia megacarpa* also occurs in West Lakes (Robertson 1984).

1.5. Maintenance and Growth of Seagrass Meadows

The maintenance of a seagrass meadow is dependent upon the rate of growth and/or reproduction outstripping the rate of loss (Larkum 1976). Tomlinson (1974) suggests that persistence in seagrass meadows is mostly dependent upon vegetative (ramet) growth irrespective of the level of flowering. However, seagrass meadows may also expand via the production of genets through sexual reproduction (Duarte and Sand-Jensen 1990). There are large species-specific differences in the rate of clonal growth (Duarte and Sand-Jensen 1990, Duarte 1991b), the density of flowering (Gallegos *et al.* 1992, Cambridge and Hocking 1997, Inglis and Lincoln Smith 1998, Campey *et al.* 2002) and the degree of clonality (Waycott 1995, Waycott *et al.* 1996). These differences suggest that resource allocation to reproduction and somatic growth varies substantially between species (Marbá and Walker 1999).

While variation in growth rate, flowering intensity and population genetics is broadly accepted, there would appear to be little agreement as to the balance of genet and ramet production as the primary means for meadow maintenance in many seagrass species. In particular, there seems to be little consistency in levels of flowering. For example, Orth and Moore (1982) found significant differences in flowering density amongst years for *Z. marina* in Chesapeake Bay, and Inglis and Lincoln Smith (1998) found a 400-fold difference in *P. australis* flowering shoot density between sites in New South Wales. Similarly, Waycott *et al.* (1996) found that *A. antarctica* flowering ranged from 11 – 50% of shoots across six sites in Western Australia. On the Adelaide coast, there has been substantial variability in *Posidonia* spp. flowering between years (Seddon *et al.* in prep).

Similarly, there is little agreement as to the importance of flowering relative to somatic growth. Cambridge *et al.* (1983) indicated that fragmentation of the rhizome in *Heterozostera tasmanica* is the primary means for meadow persistence for this species, although Marbá and Walker (1999) suggest that, in addition to rapid growth, *Heterozostera* also has a high level of sexual reproduction to support its role as a pioneer species. *Amphibolis antarctica* also acts as an early coloniser in disturbed areas despite its slow horizontal growth rate (Clarke and Kirkman 1989, Marbá and Walker 1999), which suggests a high level of sexual reproduction. This notion was supported by Waycott *et al.* (1996), who stated that the limited genetic variability observed within an *A. antarctica* population was due to a high level of sexual reproduction within a highly inbred population. However, Marbá and Walker (1999) contradicted these observations and suggested that the low genetic variability in *A. antarctica* was the result of clonal growth of a single or very few genotypes and that the sexual contribution to meadow maintenance was negligible, a view supported by McConchie *et al.* (1982). *Posidonia sinuosa* and *P. angustifolia* are reliant on somatic growth but *P. australis* and *A. griffithii* supplement slow clonal expansion with seedling production (Marbá and Walker 1999). This view was supported for *P. australis* with genetic work by Waycott (1995), who found beds were multi-clonal, indicating a high level of sexual reproduction. Similarly, Campey *et al.* (2002) found that the expansion of *P. coriacea* meadows in southern Western Australia could only be explained through sexual reproduction, but that this varied substantially between years.

Overall, there is no clear understanding as to the contribution that sexual reproduction has to seagrass meadow maintenance. Given the observed differences in evidence, the importance of flowering to the maintenance of meadows would appear to vary between locations, years and species. Sexual reproduction is still likely to be important in the maintenance of some seagrass populations, but the degree to which this relates to species, rather than populations within a species, is uncertain. If sexual reproduction is adversely affected by anthropogenic inputs to the near-shore, the causes for large-scale seagrass losses may differ between populations, depending on the relative importance of flowering in meadow maintenance.

1.6. Associated Flora and Fauna

Seagrasses support a diverse epiphytic community comprising diatoms, encrusting macro- and microalgae, bacteria, fungi and organic debris (Klumpp *et al.* 1989) as well as sedentary invertebrates such as hydroids, ascidians, sponges and bryozoans (Shepherd and Sprigg 1976, Borowitzka and Lethbridge 1989). This diversity suggests that epiphyte composition and cover may vary substantially over small spatial and/or temporal scales, although Borowitzka and Lethbridge (1989) suggest that epiphyte distribution is relatively constant, albeit seasonal (Ducker *et al.* 1977), on an annual basis. Diatoms and bacteria are the first colonisers of a seagrass leaf, but as the leaf ages it becomes increasingly covered with larger algae (Borum *et al.* 1984). It follows that species like *Posidonia*, with slow leaf turnover (140 – 250 days; Marbá and Walker 1999), are thus subject to a more substantial epiphyte load relative to those with much faster leaf turnover (i.e. ~ 74 days for *Heterozostera tasmanica*; Bulthuis and Woelkerling 1983). Borum *et al.* (1984) found up to twenty-four species of algae on *Z. marina* leaves with light attenuation from typically around 19% but as high as 90%.

The bulk of small herbivores within a seagrass meadow will preferentially consume the epiphytes growing on the plant (Klumpp *et al.* 1989, Alcoverro *et al.* 1997), although the impression that few animals will eat seagrasses in large amounts is unfounded (Klumpp *et al.* 1989). Relative to seagrasses, however, epiphyte communities are often more nutritious (Klumpp and van der Valk 1984), faster growing and more readily digested (Klumpp *et al.* 1989). In terms of primary productivity, the epiphyte load is thought to support between 10 and 40% of the system total in temperate areas (Penhale 1977, Borum *et al.* 1984). The range of plant growth forms exhibited by the epiphyte community (i.e. from diatomaceous films to large encrusting macroalgae) can also support a broader array of feeding habits than seagrasses alone. There is also substantial flexibility in feeding in some herbivore groups, particularly the crustaceans (Klumpp *et al.* 1989). Even so, a major biomass change in the epiphyte community is likely to be due to seasonal growth of the host seagrass (Alcoverro *et al.* 1997) and the epiphytes (Borum *et al.* 1984), with local environmental factors, including herbivory, being a secondary, albeit important, influence (Alcoverro *et al.* 1997).

The epiphyte community supports a diverse number of consumers including gastropods, amphipods, isopods, shrimps and other crustaceans, and herbivorous fish (Klumpp *et al.* 1989). The fish community that preys on seagrass herbivores is itself prey to larger animals. In Gulf St Vincent, there are at least 13 species of commercially and recreationally important fish that spend at least a portion of their life cycle within seagrass meadows (Scott *et al.* 2000).

Seagrasses themselves are thought to have relatively low nutritional value (Klumpp *et al.* 1989) but grazing levels in terms of biomass loss are highly variable (Cebrián and Duarte 1998). Nonetheless, a surprising variety of fauna make use of seagrasses, including dugongs, sea turtles, fish, crustaceans, molluscs, polychaetes and sea urchins (Larkum and West 1990, Woods and Schiel 1997, Anderson 1998, Brand-Gardner *et al.* 1999, Gambi *et al.* 2000, Valentine and Heck 2001). Alcoverro *et al.* (1997) stated that herbivores had little influence on *P. oceanica* biomass. Similarly, Kirkman and Reid (1979) estimated that only 3 % of the total biomass loss from *P. australis* meadows in a New South Wales estuary could be attributed to herbivores. The general effect of herbivory on seagrasses is poorly understood (Cebrián and Duarte 1998). This lack of knowledge may be particularly applicable to seagrasses on the Adelaide coast, especially amongst larger species (*Amphibolis* and *Posidonia*).

Shepherd and Sprigg (1976) found tubeworms, ascidians, seastars, sea urchins, crabs and razorfish (*Pinna* spp.) as non-epiphytic components of seagrass meadows in Gulf St Vincent. These species, in particular razorfish, are themselves host to other organisms. Apart from acting as both a food resource and substrate, seagrass meadows also support a large detrital component (Klumpp and van der Valk 1984, Klumpp *et al.* 1989). *Posidonia* species contribute a substantial amount of detritus to seagrass systems in southern Australia (Klumpp and van der Valk 1984), which in turn supports its own community of associated fauna and flora. Seagrass

debris may be transported well beyond the range of the meadow. It is often the dominant component of beach wrack and provides food and shelter to the biota in these environments as well as contributing to the stability of beach sediments (Kirkman and Kendrick 1997).

1.7. Seagrass Loss Mechanisms

A large number of mechanisms have been identified as potential causes for seagrass declines both in Australia and elsewhere (Steffensen *et al.* 1989, Walker and McComb 1992, Short and Wyllie-Echeverria 1996, EPA 1998, Seddon 2000, Ralph *et al.* in press), including:

Natural

- Climate and geological change
- Storms and cyclones
- Grazing and bioturbation
- Disease
- Erosion

Anthropogenic

- Eutrophication
- Sedimentation and turbidity
- Toxicants
- Freshwater
- Physical damage
- Global warming and/or ozone depletion

None of the above is mutually exclusive, and seagrass decline at any one location may thus be due to a number of factors, although the additive or synergistic effects from a combination of stress factors are unknown (Seddon 2002). Natural causes of seagrass decline are not the focus of the current discussion, but there is a need for awareness that not all large-scale seagrass losses have an anthropogenic cause. Seddon (2000) investigated the loss of 12,717 ha of near-shore seagrasses from a 95 km stretch of coast in Spencer Gulf in 1994, and while this study investigated the possibility of anthropogenic origins, it was found that high ambient temperatures during unusually low tides were the most likely cause.

Whatever the cause(s) of seagrass losses from Adelaide's near-shore systems since European settlement, they are unlikely to have a wholly natural basis as they are confined to the metropolitan coast and correlate with the pattern of coastal development (see above). Similarly, physical damage and global warming are not part of the current summary. Physical damage due to trampling, propellers and/or anchors, is notable only at local scales and generally occurs only in very shallow water (Creed and Armado Filho 1999, Eckrich and Holmquist 2000, Bell *et al.* 2002). While fixed moorings may affect areas up to 300 m in deeper areas (Walker *et al.* 1989), there are comparatively few moorings off the Adelaide coast that occur outside harbour facilities. The importance of physical damage to Adelaide's seagrass loss is likely to be negligible relative to the size of the loss, although it may initiate development of blowouts in some areas. Conversely, global warming operates across far larger scales than the observed losses and should result in changes to seagrass systems well beyond the coast of Adelaide (Seddon 2000). However, it may be that local impacts are enhanced by the process of global warming. While physical erosion is contributing to ongoing seagrass loss on some parts of the Adelaide coast, it appears that this is a secondary consequence of initial seagrass loss and repeated recruitment failure. We will not be reviewing these secondary losses, rather, the focus of the present report is on reviewing possible anthropogenic primary causes of seagrass decline. Thus, the next four sections cover the potential stressors of nutrients, sediments and turbidity, toxicants, and freshwater.

2. Effects of Nutrients on Seagrasses

Eutrophication is considered the major cause for seagrass decline in Australia and overseas (e.g. Shepherd *et al.* 1989, Gabric and Bell 1993, Short and Wyllie-Echeverria 1996, Nielsen and Jernakoff 1997, Hall *et al.* 1999, Campbell and Miller 2002, Bryars *et al.* 2003), although the actual mechanism(s) for nutrient effects are unclear (Nielsen and Jernakoff 1997). EWS (1975) indicated that sediment movement was a major factor in seagrass decline on the Adelaide coast but Steffensen *et al.* (1989) stated that this was secondary to the effect of increased nutrients. All other reports on seagrass decline on the Adelaide metropolitan coast have suggested increased nutrient load as being the major cause. An EPA (1998) study that included measurements of epiphyte loads on artificial seagrass, suggested that the central and northern Adelaide coast had poor water quality relative to non-urbanised control sites but nutrient levels were not measured. Clear empirical evidence for the role of increased nutrients in the decline of seagrasses has yet to be observed (Nielsen and Jernakoff 1997). Increased growth of seagrass meadows as a response to higher nutrients has been demonstrated for *Halodule uninervis*, *Cymodocea serrulata* and *Halophila ovalis* on the Great Barrier Reef (Udy *et al.* 1999), although this could not be directly linked to installation of a nearby effluent outfall.

Nutrient inputs are said to promote plankton, epiphyte and macroalgal growth, which in turn reduces light availability and the seagrass depth range (Figure 1; e.g. Larkum 1976, Bastyan 1986, Silberstein *et al.* 1986, Larkum and West 1990, Hillman *et al.* 1990, Dixon 1999, Wear *et al.* 1999, Deegan *et al.* 2002). Although the restriction of light availability appears to be the standard model for explaining seagrass losses in eutrophic environments, some reports suggest that physiological and/or morphological responses to nutrient gradients might also play an important role (Burns 1992, Touchette and Burkholder 2000a). Other detrimental factors associated with increased nutrient loads include higher accumulation of organic matter in sediments, leading to anoxia and production of toxic compounds (e.g. sulphides; Delgado *et al.* 1999). Burkholder *et al.* (1992) reported that high nutrient loads could be toxic to *Z. marina*, with "crumbling" shoot meristems preceding mortality. Although subsequent research, with more ecologically relevant nutrient doses, has failed to observe a similar result (Short *et al.* 1995, Moore and Wetzel 2000), the seagrasses adapted to the oligotrophic waters of Gulf St Vincent (Steffensen *et al.* 1989) may be more sensitive to increased nutrient loads. It has been observed that *A. antarctica* appears to decline more rapidly than other species (e.g. *Posidonia* spp.) in the presence of increased nutrients (Shepherd *et al.* 1989), although the possibility of a toxic response to eutrophication has yet to be explored.

There is a need for a greater understanding of the nutrient dynamics of temperate seagrass systems. Most importantly, the assimilative capacity of seagrasses in terms of nutrient loads appears to be poorly known, particularly in low nutrient environments where comparatively small increases in nutrient loads, in particular nitrogen, may have relatively greater influence than in more mesotrophic systems. An understanding of what nutrient fluxes can be accommodated by a seagrass system will assist coastal managers in the designation of target nutrient loads. Further, without knowledge of the level of nutrients that a seagrass system can accommodate, it is difficult to infer the effect of eutrophication in terms of either direct (i.e. toxic) or indirect (e.g. epiphyte loadings) effects.

Seagrass meadows can act as sources or sinks of nutrients (Dudley *et al.* 2001) and thus changes in seagrass cover and/or species composition induced by anthropogenic stress has the potential to alter nutrient cycling in coastal areas (Larned 2003). Un-vegetated sediments are generally sources of ammonium (NH_4^+) due to organic matter remineralization (Herbert 1999) while seagrass meadows most often act as sinks for nutrients from the water column (Larned 2003). Dissolved nutrients leach from both living and decaying seagrass tissues much slower than the rate of uptake required for plant metabolism (Buchsbaum *et al.* 1991, Enriquez *et al.* 1993). An increase in nutrient concentrations due to eutrophication can lead to the loss of seagrass

meadows that will in turn aggravate the problem by reducing the capacity of the environment to assimilate the increased nutrient load.

Seagrasses derive nutrients (except carbon) mainly from sediment porewater but also from the water column (Maier and Pregnall 1990, Lee and Dunton 1999), particularly in the case of *Amphibolis* (Pedersen *et al.* 1997). Physiological responses vary widely amongst species depending on adaptations to nutrient-depauperate or nutrient-enriched conditions. In nutrient-poor waters, seagrasses may be nitrogen-limited in sandy/organic sediments and phosphorus-limited in carbonate sediments (Short 1987, Short *et al.* 1990, Williams 1990, Kenworthy and Fonseca 1992). Adelaide's metropolitan coast is considered to be a predominantly carbonate sedimentary province (Shepherd and Sprigg 1976) and so, are probably phosphorus limited. Many species respond well to a low to moderate nitrogen and/or phosphorus enrichment (Udy and Dennison 1997a, Udy *et al.* 1999) but excessive nutrients may have a negative effect not only by reducing light availability but for some species, there may be a toxic affect as well (Touchette and Burkholder 2000a). It has been suggested that, in some cases, pulses of high nutrient levels may be more detrimental to seagrasses than long-term chronic contamination (Moore and Wetzel 2000).

2.1. Uptake Mechanisms

2.1.1. Nitrogen

Seagrass uptake of nitrogen relies primarily on inorganic forms (i.e. ammonium NH_4^+) and to a lesser degree nitrate (NO_3^-) but at least some seagrasses can assimilate organic forms such as amino acids and urea (McRoy and Goering 1974, Bird *et al.* 1998). Seagrasses rely on an active uptake system for NO_3^- , while assimilation of NH_4^+ may involve two separate transport systems: a low-affinity system where NH_4^+ is passively transported through membrane channels and a high-affinity system that relies on the production of a protein responsible for transmembrane transport (Figure 9; Ourry *et al.* 1997). The latter may induce a feedback mechanism by decreasing uptake rates when NH_4^+ reaches high levels in plant tissues (Lee and Ayling 1993). By this mechanism, the capacity for uptake decreases from nitrogen-depauperate to nitrogen-replete plants (Short and McRoy 1984, Thursby and Harlin 1984).

Uptake kinetics vary from classic Michaelis-Menten models to linear uptake, depending on species and environmental conditions. *Amphibolis antarctica* seedlings show a sustained linear uptake relative to ambient concentrations, assimilating nitrogen primarily through the leaves with little root development until maturity, suggesting an adaptation to maximize nitrogen uptake from pulses in the water column (Paling and McComb 1994). Similarly, *Z. marina* growing in sediments depauperate in nitrogen shows linear uptake when the water column becomes nitrogen-enriched. Under these conditions, assimilation is higher than in plants growing in nitrogen-enriched sediments, which also respond with a linear uptake (Roth and Pregnall 1988).

Nitrogen uptake affinities are highly variable and generally higher for NH_4^+ in comparison to NO_3^- : e.g. leaf uptake rates range from 5 - 270 $\mu\text{mol g}^{-1}$ DW h^{-1} for NH_4^+ and from 3 - 75 $\mu\text{mol g}^{-1}$ DW h^{-1} for NO_3^- (Touchette and Burkholder 2000a). In pristine marine habitats, total nitrogen in the water column during the day is normally less than 3 μM (Touchette and Burkholder 2000a). Nitrate assimilation generally occurs by leaf uptake from the water column (Lee and Dunton 1999), except when groundwater inputs are high (Maier and Pregnall 1990). Sediments in seagrass habitats are usually hypoxic or anoxic and NH_4^+ is considered the dominant form of nitrogen with levels in the range of 1 - 180 μM in sediment porewaters (Touchette and Burkholder 2000a). NH_4^+ concentrations in porewaters and in the water column increase at night because of reduced uptake by plankton and other biota, lower oxygen levels and organic matter breakdown (Henriksen and Kemp 1988).

Young roots have a primordial role in nitrogen assimilation but the pathway of nutrient uptake (roots versus leaves) can vary with nutrient concentration. Plants have been observed to change their uptake of nitrogen from NH_4^+ in the sediments to NO_3^- in the overlying water with increasing water column enrichment (Figure 9). Uptake of nitrogen by the roots can be limited by diffusion from porewaters, which reduces the capacity of the roots to supply the nutrient requirements of the plant (Lee and Dunton 1999). In some environments, such as those with a rock substrate (as in some *A. antarctica* systems), almost all nutrient requirements are met through leaf uptake (Terrados and Williams 1997). Uptake from the water column thus varies with environmental conditions in the range 30-90% of total nitrogen requirements (Touchette and Burkholder 2000a). The high nutrient-uptake affinity of the leaves may reflect a response to the low levels of NH_4^+ in the water column in comparison to sediments, but also an adaptation to maximize nutrient assimilation in oligotrophic environments (Burkholder *et al.* 1994, Lee and Dunton 1999). In *Z. marina*, NH_4^+ leaf uptake is independent of NH_4^+ availability in sediment porewaters, but root uptake is seriously affected by water column concentrations perhaps because of higher shoot to root (basipetal) in comparison to root to shoot (acropetal) translocation of nutrients (Thursby and Harlin 1982). The inverse mechanism is reported for *Ruppia maritima* in that leaf uptake is strongly affected by NH_4^+ availability to the roots, maybe because of acropetal translocation of nutrients or root uptake being independent of NH_4^+ levels in plant tissues (Thursby and Harlin 1984). Acropetal and basipetal translocations of nutrients are thus species dependent and might change according to nutrient availability in different environmental compartments (sediments versus water column). It is generally believed, however, that seagrasses are more tolerant of sediment than water-column nutrient enrichment possibly due to lower uptake by the roots (dependent on diffusion) among other factors (Ralph *et al.* in press).

Ammonium uptake is followed by assimilation in the plant tissues by the glutamine synthetase (GS)/glutamate synthetase (glutamine-oxoglutarate amido-transferase or GOGAT) biochemical cycle (Figure 9; Goodwin and Mercer 1983). For some species, NH_4^+ toxicity can occur at concentrations in the range 3 - 220 μM in the water column and 500 - 1600 μM in the sediments (Santamaria *et al.* 1994, van Katwijk *et al.* 1997). Because of its toxicity, NH_4^+ is not allowed to accumulate in plant tissues but is rapidly incorporated into glutamate for use in the production of amino acids and other organic compounds (Figure 9; Touchette and Burkholder 2000a). Due to the need of carbon skeletons for the production of amino acids and hence for the assimilation of NH_4^+ , it has been suggested that plants growing in muddy sediments (where carbon reserves are higher) are less susceptible to NH_4^+ toxicity than plants growing in sandy sediments (van Katwijk *et al.* 1997, Ralph *et al.* in press). Glutamate synthetase activity is strongly dependent on environmental conditions and is higher in seagrass leaves in comparison to roots, confirming the importance of aboveground tissues in nitrogen incorporation (Kraemer *et al.* 1997). Plants growing in deeper waters have been reported to show higher GS activity, probably as a mechanism to maintain NH_4^+ assimilation rates in environments with reduced light availability and longer periods of root anoxia (Pregnall *et al.* 1987, Kraemer *et al.* 1997).

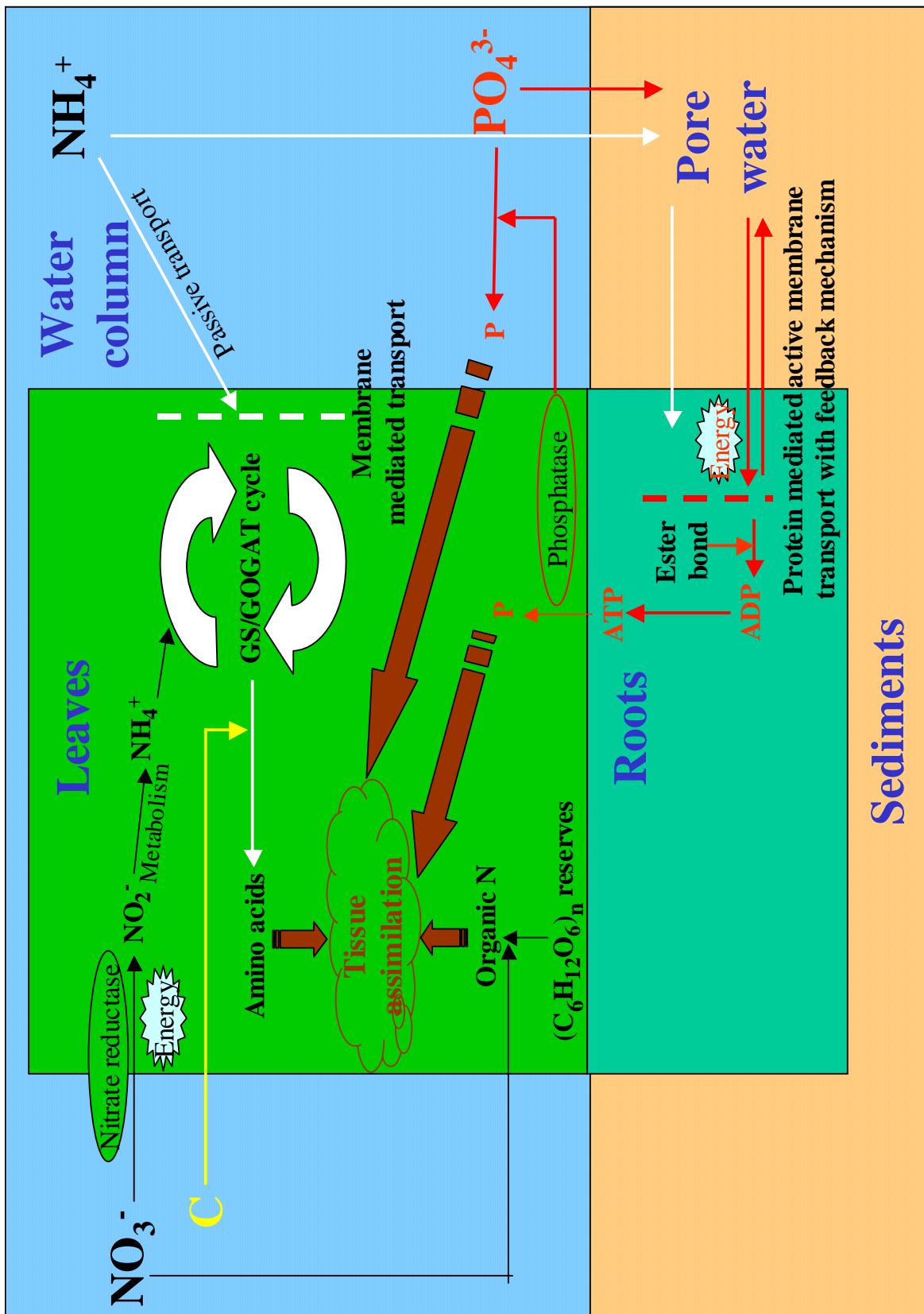


Figure 9. Schematic of nitrogen and phosphorus uptake pathways for a typical seagrass. See text for a detailed explanation.

Nitrate assimilation by seagrass tissues is an energy-demanding process involving reduction of nitrate to nitrite and regulated by the enzyme nitrate reductase (NR; Figure 9; Ferrario-Mery *et al.* 1997). Nitrate reductase activity is generally higher during periods of high photosynthetic activity when metabolic energy is at its maximum (Layzell 1990). The increased supply of carbon skeletons (carbohydrates) and reductants during light periods favours the assimilation of NO_3^- (Turpin *et al.* 1991). Nitrate uptake stimulates the synthesis of NR (Figure 9; Beevers and Hageman 1983). With a half-life of only a few hours, NR activity quickly responds to changes in NO_3^- concentrations (Hewitt *et al.* 1976). The product of nitrate reduction, nitrite, is toxic to plants and thus quickly metabolised to NH_4^+ , which is subsequently assimilated into amino acids through the GS/GOGAT cycle detailed above (Figure 9). These processes occur mainly in aboveground tissues as NO_3^- is preferentially translocated to the leaves for storage and reduction (Touchette and Burkholder 2000a). For *Z. marina*, NR activity is lower in plants growing at depth, further confirming the role of light availability in regulating NR (Roth and Pregnall 1988). Nitrate uptake in *Z. marina* can be sustained throughout a diel cycle by maintaining NR activity during dark periods (Touchette and Burkholder 2000a). This can occur when NO_3^- is enriched in the water column and carbohydrate reserves are plentiful. This adaptation to assimilate inorganic forms of nitrogen in both darkness and light can be particularly useful in oligotrophic environments where nutrient supply might occur mainly as pulses (e.g. storm events; Lee and Dunton 1999).

For both *Z. marina* and *Halophila decipiens*, sustained high NO_3^- concentrations ($>3 \mu\text{M}$) combined with no product feedback inhibition can lead to a negative physiological response (Bird *et al.* 1998, Touchette and Burkholder 2000a). In this scenario, plants are unable to shut off NO_3^- uptake, using their carbohydrate reserves to metabolise NO_3^- into organic forms of nitrogen and ultimately reaching a situation where growth is compromised by the internal limitation in carbon supplies (Roth and Pregnall 1988, Burkholder *et al.* 1992, Touchette and Burkholder 2000a). Product feedback inhibition is not apparent for many other seagrass species, which are actually stimulated by NO_3^- enrichment (Burkholder *et al.* 1994, Lee and Dunton 1999). In a few extreme cases (e.g. *Halophila stipulacea*), plants have adapted to environments extremely depauperate in NO_3^- and show very low NR activity independent of environmental concentrations (Dodrema and Howari 1983).

2.1.2. Phosphorus

Phosphorus in seagrass habitats occurs mostly in the form of phosphate (PO_4^{3-}) with concentrations $< 2 \mu\text{M}$ in the water column and $< 20 \mu\text{M}$ in sediment porewaters (Figure 9; Touchette and Burkholder 2000a). Higher PO_4^{3-} concentrations occur at night, especially during summer, as a result of organic matter breakdown and sediment release under lower oxygen levels. Carbonate sediments in tropical and subtropical regions are phosphorus-limited because PO_4^{3-} in the sediments becomes trapped by the formation of calcium complexes (Stumm and Morgan 1996).

Inorganic phosphorus uptake affinities and rates are lower than for NH_4^+ but comparable to those reported for NO_3^- (Touchette and Burkholder 2000a). Similar to nitrogen, inorganic phosphorus uptake varies with the plant nutritional status, species and environmental conditions. Some plants do not follow the Michaelis-Menten kinetics model of uptake. For example, *Zostera noltii* shows an initial phase of rapid uptake followed by a steep decline, indicative of internal regulation mechanisms such as product inhibition feedback (Figure 9; Perez-Llorenz and Niell 1995).

Seagrass uptake of phosphorus relies on active transport (as for nitrate) and occurs mainly through the roots because inorganic phosphorus has low solubility and readily adsorbs to particulates (Figure 9; McRoy *et al.* 1972, Touchette and Burkholder 2000a). As with nitrogen, uptake of phosphorus is thus dependent on diffusion from sediment porewaters (Lee and Dunton 1999). Also similar to nitrogen, the preferential uptake by roots vs. leaves can change according to species and environmental conditions (Brix and Lyngby 1985). Phosphorus availability

seems to be a determining factor, with leaf uptake dominating in plants growing in phosphorus-depauperate sediments and where the water column is enriched with phosphorus (Thursby and Harlin 1984). Uptake by the leaves is faster than uptake by the roots and in eutrophic environments can correspond to several times the phosphorus requirements for optimal growth (Figure 9; Thursby and Harlin 1984, Brix and Lyngby 1985, Perez-Llorenz and Niell 1995). However, the minimum phosphorus concentration for uptake to occur may be higher for leaves in comparison to roots (Thursby and Harlin 1984, Stapel *et al.* 1996). *Zostera marina* has been reported to rely heavily on leaf uptake with sediments playing a role only when phosphorus concentrations in the water column are extremely low (Brix and Lyngby 1985). Light can also influence phosphorus uptake in seagrasses with some species showing highest leaf uptake during photosynthetic periods while root uptake seems to be mostly unaffected (McRoy *et al.* 1972, Brix and Lyngby 1985). Following uptake, phosphorus is translocated to other tissues and some release from the leaves into the water column might occur, which can increase phosphorus availability to epiphytes (Figure 9; McRoy and Barsdate 1970, Penhale and Thayer 1980, Brix and Lyngby 1985, Perez and Romero 1993).

Assimilation of inorganic phosphorus is believed to depend on proteins that transport PO_4^{3-} across cellular membranes (Muchhal-Umesh and Raghothama 1999). The PO_4^{3-} incorporation pathway occurs mainly through the formation of ester bonds to Adenosine Diphosphate (ADP) to produce Adenosine Triphosphate (ATP; Figure 9; Taiz and Zeiger 1991). The activity of phosphatases (PAs) increases under low phosphorus concentrations (or high phosphorus demand) to maximize the use of internal phosphorus by releasing it from phosphorus-containing compounds (Vincent and Crowder 1995). Under these conditions, PAs may also be released extra-cellularly into the environment to maximize the use of phosphorus from environmental sources (Lapointe *et al.* 1994). Phosphatase activity will vary with phosphorus availability, environmental conditions, tissue age and epiphyte cover (Figure 9; Touchette and Burkholder 1999). It has been suggested that the presence of epiphytes will reduce the capacity of the plant to assimilate phosphorus from the water column and therefore older leaves with higher epiphyte coverage will have higher PA activity (Touchette and Burkholder 2000a).

Phosphorus uptake and assimilation is directly related to carbon and nitrogen metabolism by affecting energy transfer pathways (e.g. ATP cycle), forming metabolic intermediates (e.g. starch and sucrose synthesis and degradation) and regulating enzymatic activity (e.g. protein phosphorylation and dephosphorylation). In environments where phosphorus is not limiting, PA activity may increase for periods of high carbon metabolism (e.g. when carbohydrate reserves are low or sucrose demands are higher; Touchette and Burkholder 1999).

2.2. Indicators of Nutritional Status

The C:N:P ratio of seagrass tissues is highly variable according to environmental conditions, species and age but values of 474:21:1 have been reported as representative of 27 seagrass species (Duarte 1990). Tissue C:N:P content can be used as an integrative indicator of environmental conditions and flag nutrient perturbations (Fourqurean *et al.* 1992, Fourqurean *et al.* 1997). Low leaf nitrogen content, for example, has been linked to nitrogen-limitation in some species while values >1.8% suggest uptake in excess of growth requirements in eutrophic environments (Duarte 1990, Campbell and Miller 2002).

2.3. Nutrients and Loss of Light

The relationship between eutrophication and seagrass degradation argues that nutrients lead to increased epiphyte loading and/or increased turbidity and/or production of excessive macroalgae (Figure 1; e.g. Bastyan 1986, Steffensen *et al.* 1989, Hillman *et al.* 1990, Gabric and Bell 1993, Nielsen and Jernakoff 1997, EPA 1998, Hauxwell *et al.* 2001, Bryars *et al.* 2003, Ralph *et al.* in press). The effect of all three responses is primarily a reduction in light availability, although higher epiphyte loads and smothering macroalgae may also restrict gas exchange (Borowitzka and Lethbridge 1989, Hillman *et al.* 1990) and nutrient uptake (Hauxwell *et al.* 2001). The

extra weight of macroalgal smother may cause the seagrass to lie flat, which could ultimately lead to anoxic conditions. Sediment and water-column anoxia as a result of excessive nutrients has also been identified as a threat to seagrass systems (Gabric and Bell 1993). Whatever the mechanism, high epiphytic loads are said to result in reduced growth, leading to shoot thinning, reduced above-ground biomass and ultimately death (Silberstein *et al.* 1986, Short *et al.* 1995, Bryars *et al.* 2003). Nonetheless, such symptoms are not always evident in seagrasses exposed to increased nutrient loads in the field (McMahon *et al.* 1997).

Nielsen and Jernakoff (1997) reviewed the effects of nutrients on seagrasses and found that water-column nutrients generally had no direct effect on seagrass shoot production. Rather there was often a negative effect on above-ground seagrass biomass, which may be attributed to loss of light due to increased epiphyte growth and turbidity. However, the link between eutrophication and seagrass decline is still largely based on correlation (Short and Wyllie-Echeverria 1996, Seddon 2000, Ralph *et al.* in press).

Bastyan (1986) and Hillman *et al.* (1990) investigated the loss of seagrasses from Princess Royal Harbour and Oyster Harbour in Western Australia. In both surveys, losses of large areas of *Posidonia* (*P. australis* and *P. sinuosa*) and *Amphibolis* were attributed to high epiphyte loads and/or smothering by macroalgae as an indirect effect of eutrophication. Losses of *Posidonia*, *Amphibolis* and *Heterozostera* (Shepherd *et al.* 1989) on the Adelaide coast have largely been attributed to the same factors (Shepherd *et al.* 1989, Steffensen *et al.* 1989, Hart 1997, EPA 1998, Cameron 2003). However, as stated earlier, the loss of seagrass from the Adelaide metropolitan coast has largely occurred in shallow water close to shore and progressed to seaward (Figure 2). The mechanism for seagrass decline along the Adelaide coast does not therefore support the simple eutrophication-light restriction model.

Gulf St Vincent has very low natural nutrient levels due to a high level of oceanic flushing and lack of significant freshwater inputs (Steffensen *et al.* 1989). Thus, the seagrass community within the Gulf should be adapted to cope with oligotrophic conditions. *Amphibolis antarctica* grows relatively well in low nutrient environments (Walker and McComb 1988) and may be highly sensitive to eutrophication, either through high epiphyte loads (Shepherd *et al.* 1989) or nutrient toxicity (*sensu* Burkholder *et al.* 1992). However, seagrasses show significant differences in nutritional responses, and inferences based on studies on a few other temperate species can not *a priori* be applied to the species found in South Australian waters. The nutritional characteristics of the species found along the Adelaide metropolitan coastline have not been established.

3. Sedimentation and Turbidity

3.1. General Effects

Turbidity and sedimentation have been identified by many authors as important factors associated with seagrass loss (e.g. EPA 1998, Orth and Moore 1983, Carruthers *et al.* 1999, Ralph *et al.* in press). While Shepherd *et al.* (1989) identified the primary cause for human-induced seagrass loss as a lack of light getting to the photosynthetic surface of the plant, this attenuation may occur in different ways. For example, increased water-column turbidity restricts light availability before it reaches the plant (Bulthuis *et al.* 1984b, Longstaff and Dennison 1999, Cabello-Pasini *et al.* 2002, Ruiz and Romero 2003). Conversely, sedimentation coats the leaves with silt, reducing the light at the leaf surface (Tamaki *et al.* 2002, Shepherd *et al.* 1989) or burying the plant in more extreme cases (Clarke 1987, Duarte *et al.* 1997, Mills and Fonseca 2003). In this latter case, the situation can be exacerbated by the fact that photosynthesis may no longer produce enough oxygen for aerobic decomposition of a heavy organic load, resulting in sediment anoxia, which can also be detrimental to seagrasses (e.g. Clarke 1987, Duarte *et al.* 1997, Mills and Fonseca 2003, Holmer and Bondgaard 2001, Tamaki *et al.* 2002).

In general, it is difficult to separate the effects of turbidity and sedimentation in field studies (Ralph *et al.* in press), because under relatively low energy conditions, seagrass beds act as depositional environments as they slow water movement beneath the canopy (Gacia *et al.* 1999, Heiss *et al.* 2000). However, under high-energy conditions (Clarke 1987), re-suspension of sediment within a seagrass bed will add to turbidity and leaf smothering, particularly within degraded meadows. It is also important to recognise that there may be a biological dimension to the level of turbidity in a system due to excessive planktonic growth (Steffensen *et al.* 1989, Hall *et al.* 1999) which may have resulted from increased nutrient levels (e.g. Steffensen *et al.* 1989, Ralph *et al.* in press). Whilst the cause(s) may differ, the result for the plant is a reduction in light availability.

In very simple terms, lower light energy limits photosynthetic capacity, resulting in lower carbon fixation (Russell-Hunter 1970). In the first instance, this may result in a slowing of growth rate, but if a plant receives less light than is required to balance its metabolic requirements and loss processes, it will eventually die. It is generally accepted that seagrasses require 5-20% of the incident surface irradiance in order to survive (Dennison *et al.* 1993). However, this may vary considerably, even within a species (e.g. 4.4% - 29.4% for *Z. marina*; Abal *et al.* 1994). In reality, the situation is more complicated as seagrasses live in a light environment that fluctuates naturally on several temporal scales (Larkum 1981, Abal *et al.* 1994, Ruiz and Romero 2003). Variations in light occur due to lensing caused by the sea surface, day/night changes, tidal changes and seasonal changes amongst others (Touchette and Burkholder 2000b). The influence of shading by other individuals and self-shading can also be important (Olesen *et al.* 2002). Seagrasses (like other plants) are able to store excess energy in the form of non-structural carbohydrate reserves and starch, which can be drawn upon during periods of low light intensity (Burke *et al.* 1996, Alcoverro *et al.* 2001, Holmer and Bondgaard 2001). Furthermore, they are able to adapt their photosynthetic apparatus to increase photosynthetic efficiency at lower light levels (Goodman *et al.* 1995, Vermaat *et al.* 1997). However, there are limits to this adaptability (Abal *et al.* 1994, Goodman *et al.* 1995, Burke *et al.* 1996) and the oxygen demand created by increased biomass required for carbon storage may actually become a burden under low light conditions (Hemminga 1998). Alcoverro *et al.* (2001) modelled annual carbohydrate reserves in *Posidonia oceanica* and demonstrated that the plant may actually have a carbon deficit for several months under normal circumstances. However, they also showed that decreasing light levels may cause a net annual carbon loss to which they attributed a decline observed in *P. oceanica* in the field.

3.2. Sedimentation

Complete burial of seagrasses is likely to induce a response similar to an extreme level of turbidity (e.g. Cabello-Pasini *et al.* 2002). The consequences for the plant depend on several factors such as the depth of burial and the life history of the species involved (Duarte *et al.* 1997, Mills and Fonseca 2003). *Zostera marina* responded similarly to burial in either sand or silt (Mills and Fonseca 2003) but the survival of smothered *Posidonia* species was highly truncated under anaerobic versus aerobic sediment (Clarke 1987). Plants may respond to burial by changing morphology (elongation, branching) to increase the amount of photosynthetic tissue above ground (Duarte *et al.* 1997, Vermaat *et al.* 1997, Mills and Fonseca 2003), but the energy expended to do this must be recouped before carbon reserves become too depleted.

Larger species are likely to resist burial, as they will have a greater emergent photosynthetic area than a species of shorter stature. Indeed, Duarte *et al.* (1997) reported that in a mixed community of tropical seagrasses, it was the largest species which best coped with burial. Smaller species will be smothered by relatively less sediment and are unlikely to have large carbohydrate reserves to maintain them over periods of minimal light.

Shepherd *et al.* (1989) stated that lack of light provides a unifying mechanism for seagrass loss, although this ignored the effect of burial on gas exchange. A critical difference between seagrasses and their terrestrial counterparts is the medium in which they live. The boundary layer around the leaves, through which gases must diffuse, is several orders of magnitude thicker in the aquatic environment, and consequently gaseous diffusion is orders of magnitude slower (Abel and Drew 1989). While some gases are lost through seagrass roots via the lacunar system (Moriarty and Boon 1989), carbon appears to be primarily supplied through the leaves (Larkum *et al.* 1989). An increase in the thickness of the boundary layer, as would be caused by sedimentation on the leaves, decreases the rate of diffusion, potentially limiting carbon fixation. This effect is exacerbated in that, unlike terrestrial plants, seagrasses do not have stomata to improve gas exchange. It is worth noting that only seagrasses in very low-energy environments are likely to retain a significant load of sediment on their leaves for a prolonged period. Unfortunately, whilst the theoretical framework is present, there is little published empirical evidence as to the impact of sediment on seagrass leaves (Ralph *et al.* in press).

Seagrasses are also likely to be affected by the nature of the sediments that are deposited, which may bring with them pollutants, such as herbicides and petrochemicals, or a high nutrient load. These have varying levels of influence on seagrass growth and survival, which are described elsewhere (see below). However, it is worth touching on two important features:

1. The redox state of the sediments may be altered if there is a high organic load; and
2. The relative rates of erosion and sedimentation will physically act to change the depth of the substrate beneath the surface of the water.

Sediment conditions play an important role in the abundance and growth of seagrass (Terrados *et al.* 1999, Halun *et al.* 2002), although they may be less important than temperature, salinity and depth constraints (Livingston *et al.* 1998). Sediment anoxia is common to many seagrass meadows (Moriarty and Boon 1989, Terados *et al.* 1999), although under normal conditions an oxygenated zone of up to 1 mm thick exists around the roots, caused by diffusion of oxygen through the lacunar system (Moriarty and Boon 1989, Terrados *et al.* 1999). Terrados *et al.* (1999) indicated that seagrass species differ in their capacity to cope with sediment anoxia. However, where oxygen is denied to the sediment because photosynthesis has been inhibited, the resulting anaerobic conditions lead to interference in the cycle of nitrogen metabolism (Pregnall *et al.* 1984), resulting in the production of sulphides (Moriarty and Boon 1989, Delgado *et al.* 1999, Halun *et al.* 2002). Elevated sulphide levels are associated with stress and mortality in a variety of species (Goodman *et al.* 1995, Carlson *et al.* 1994, Terrados *et al.* 1999, Seddon 2000, Ralph *et al.* in press); which is exacerbated as sulphides are able to diffuse

through the seagrass rhizosphere (zone within the sediment influenced by the roots), thus affecting the roots (Erskine and Koch 2000). Furthermore, decreased seagrass photosynthesis decreases sulphide reoxidation, cycling back to yet further loss in photosynthetic capacity (Carlson *et al.* 1994).

Often there is a dynamic balance between rates of sediment accumulation and erosion (Clarke and Kirkman 1989). If sedimentation rates are greater than erosion, material will build up, resulting in depth changes, which in shallower areas, where many seagrass species occur (Table 1), may result in a drastic change in physical environment. Whilst the shallower depth brings with it a greater quantity of light, in very shallow areas, seagrasses adapted to occasional periods of exposure to air will be more at risk of desiccation and prolonged high UV levels (Bulthuis 1983, Adams and Bate 1994a, Seddon 2000, Ralph *et al.* in press).

Seagrass meadows are known to demonstrate “autocatalytic” behaviour (Larkum and West 1983), meaning that loss of seagrass through one factor has the effect of weakening the structure of the seagrass bed, making it more vulnerable to other factors (such as sediment erosion) and further loss. Whilst Clarke (1987) concluded that no substantial ill effects were caused by moderate levels of disturbance around the roots of *Posidonia* and *Amphibolis*, the “blowout” behaviour described by many authors (e.g. Shepherd *et al.* 1989; Kirkman 1985; Davison 1987) as typical of seagrass beds is a clear indication that erosion may become a problem. Suffice to say, influences such as turbidity and sedimentation can weaken the bed and make it more susceptible to other factors.

3.3. Turbidity

Although it is clear that some broad distinctions can be drawn in terms of critical light limits at which seagrass may grow, the level of variability within a given species is high (see *Z. marina*; Table 3), making interspecies differences difficult to determine. This variation is further complicated by the fact that estimates are drawn using different methods. In some cases, laboratory experiments quantify the amount of light required for a positive carbon balance, ignoring fluctuating *in situ* light regimes and carbon storage capacity (see Cabello-Pasini *et al.* 2002 for the importance of these factors). Otherwise, depth limits are associated with light attenuation coefficients to produce a result which ignores the possibility that the depth limit may be imposed by factors other than light (e.g. Duarte 1991a, Cambridge and Hocking 1997).

Duarte (1991a) summarised data on the maximal depth of various seagrass species from around the world and, where possible, the attenuation coefficient (*k*) of the waters where they were found. Using this information, and making the assumption that light was the depth-limiting factor, the minimum percentage of sub-surface light required (Table 3) can be calculated using the formula:

$$I_d = I_0 e^{-kd}$$

where I_d is irradiance at a given depth, d ; I_0 is the light immediately sub-surface and k is the attenuation coefficient.

Table 3. Minimum light requirements for some species (or congeners) of seagrass found on the Adelaide coast in terms of surface light intensity. Taken from Duarte (1991a).

Species	% Surface intensity
<i>Heterozostera tasmanica</i>	2 – 7.2
<i>Posidonia angustifolia</i>	6.1
<i>P. coriacea</i>	8
<i>Ruppia</i> sp.	8.2
<i>Z. marina</i>	4.7 – 43.8

Whilst minimal light requirements are important, it is an oversimplification to assume that light attenuation alone determines plant response to increased turbidity and sedimentation. Also of importance is the length of time that different species can survive at low light levels. Temporary fluctuations in turbidity or sedimentation may be accommodated by the plant depending on the nature of the species and the period of sub-minimal light. In general, it is considered that smaller, faster-growing genera (such as *Halophila*) have a faster acclimation to low light regimes than larger slow-growing genera (such as *Posidonia* and *Amphibolis*). However, when light levels are below photosynthetic compensation levels, it is the larger species that have the necessary carbohydrate reserves to withstand longer periods of sub-minimal light. *Posidonia sinuosa* survives longer at sub-compensation light levels than *Heterozostera tasmanica*, which in turn survives slightly longer than *Z. marina*, while *Halophila ovalis* coped with sub-minimal light for the shortest period (Cheshire *et al.* 2001). Whilst these results used different methodologies and measurements to determine survival, it is clear that species with larger below-ground biomass are better adapted to longer periods of sub-minimal light.

3.3.1. *Posidonia*

Whilst *Posidonia* has been the subject of a number of studies concerning minimum available light, these have focussed on *P. oceanica*, which requires 10-16% of sub-surface light to survive (Dalla Via *et al.* 1998, Ruiz and Romero 2001, Ruiz *et al.* 2001). *Posidonia coriacea* is known to require at least 8 % surface light intensity (Table 3), but although the depth ranges are known for *Posidonia* species on the Adelaide coast, the related physical data (specifically the attenuation level) are poorly known. Because of their larger size, *Posidonia* species are able to store considerable amounts of non-structural carbohydrate. This feature enhances its tolerance to moderate periods of burial or variable light quantity (Alcoverro *et al.* 2001). In a shading study of *P. sinuosa* and *P. angustifolia* off the Adelaide coast, Neverauskas (1988) found a loss of leaves but retention in shoot density over the first six months, whereafter the community declined.

Clarke (1987) undertook a series of field-based burial experiments, which demonstrated that, under aerobic conditions, the degree of burial correlated with the level of decreased growth of *P. angustifolia* most likely due to the corresponding loss in photosynthetic area, but even complete burial did not cause mortality within 4 months, indicating a substantial store of non-structural carbon. In contrast, if complete burial occurred under anaerobic conditions, *P. angustifolia* mortality occurred within 2 weeks. Clarke (1987) did admit, however, that the results were unlikely to relate to the natural setting owing to a high degree of sediment stability observed in seagrass beds such that sand level changes are generally temporary and those capable of burying a 60 cm long seagrass were unlikely. Nonetheless, it is worth noting that this is not the case where large anthropogenic loads of (potentially anoxic) sediment are dumped on the plants, as may occur during dredging operations or major storm events.

As *P. australis* is found growing up to the intertidal zone, the issue of depth changes for this species becomes more relevant. In the intertidal zone, significant increases in the height of the bed are possible with correspondingly greater possibility of increased exposure to air resulting in death. Seddon (2000) demonstrated that *P. australis* was susceptible to the effects of high temperature when exposed at extreme low tides, and that regrowth from rhizomes might be completely inhibited.

It has been suggested that turbidity is the primary cause of the widespread loss of *P. oceanica* in the Mediterranean (Peres 1984, cited by Shepherd *et al.* 1989), although there is evidence to suggest that this species has some ability to photoacclimate (Ruiz and Romero 2003). Despite this adaptation, *Posidonia* beds in turbid areas demonstrated reduced productivity levels and lower carbohydrate reserves. However, Ruiz and Romero (2003) concluded that loss of productivity was not responsible for the observed level of mortality and that other factors must be involved. This is a common theme across much of the research directed at finding the causes

of seagrass decline in that it is rare that a single cause can be identified. Rather it is the combined influence of two or more effects that can be more detrimental than the sum of each factor in isolation (Ralph 1999).

3.3.2. *Amphibolis*

No data were obtained from the literature on the minimum light requirements of *Amphibolis*. Bearlin *et al.* (1999) mentions *Amphibolis* as a taxon whose root structure makes it relatively tolerant of sediment disturbance and contrasts it with other more delicate species such as *Halophila*. Clarke and co-workers (see Clarke 1987) investigated the likely causes of loss of seagrasses (particularly *Posidonia* and *Amphibolis*) from the Adelaide metropolitan coastline. Experimentation demonstrated that, as long as the sediments remained aerobic, *Amphibolis* was unaffected in terms of its growth rate by burial by up to 10 cm of sediment. This was contrasted with *Posidonia*, which demonstrated an inverse relationship between growth and depth of burial, unless conditions were anaerobic (Clarke 1987). The reason for this tolerance to burial was hypothesised as being that the long wiry stem on which the blades of *Amphibolis* are attached acted to ensure that the photosynthetic surfaces of the plant are kept above the levels of burial typically seen in this environment. Clarke (1987) concluded that burial was unlikely to be a significant factor in the major loss of seagrasses along Adelaide's coast because the tolerance demonstrated by the plants was well in excess of the movement of sand measured in the area (see Davison 1987). Furthermore, Clarke (1987) stated that natural burial that did occur was temporary and within the capacity of the plant's tolerance limits.

Shepherd *et al.* (1989) lists several cases of *Amphibolis* losses off the metropolitan coast for which turbidity and sedimentation can be at least partially blamed: pre 1949 loss south of the Outer Harbour breakwater; 1978-1982 loss at the Port Adelaide sludge outfall (now closed); the 1968-1982 loss around the Glenelg sludge outfall (now closed); and the 1935-85 loss in the inshore regions from Brighton to Semaphore. However, it is noteworthy that in all cases other factors have also been implicated. The work of Neverauskas (1985a, 1985b, 1987a, 1987b, 1987c, 1988) suggests that the principal cause of seagrass loss off the metropolitan coast in the vicinity of the Port Adelaide sludge outfall, has been increased epiphytic growth due to excess nutrient loading of the water.

3.3.3. *Heterozostera*

Heterozostera tasmanica appears to have a relatively low minimum light requirement, with only 2 - 9% sub-surface irradiance required for this species (Table 3; Bulthuis 1983, Campbell *et al.* 2003; Note that Campbell *et al.* 2003 reported under the name *Zostera tasmanica*). However, in spite of this tolerance, *Heterozostera tasmanica* is vulnerable to high deposition environments as the leaves are quickly coated with sediment (Clarke and Kirkman 1989). Shepherd *et al.* (1989) reported this as a cause of *Heterozostera* decline in Westernport Bay (along with *Zostera* – see above), but Clarke and Kirkman (1989), on the basis of information provided by Bulthuis (1983) and Bulthuis *et al.* (1984a), went further to claim that *Heterozostera* was far less tolerant to sedimentation in the intertidal. Perhaps the combination of the decreased light and the stresses of the intertidal zone are too much for *Heterozostera*, whereas *Zostera*, which is almost entirely intertidal, is better adapted. It is worth noting that Shepherd *et al.* (1989) raises the possibility that the loss of 445 ha of *Heterozostera* in the northern Adelaide waters between 1965 and 1985 was due to sediment accretion.

3.3.4. *Zostera*

It has been reported that *Z. marina* (a northern hemisphere species) has highly variable light requirements (Table 3; Burke *et al.* 1996, van Katwijk *et al.* 1998, Abe *et al.* 2003), although with limited capacity to deal with the decreased light found in turbid environments (Moore and Wetzel 2000, Cabello-Pasini *et al.* 2002). By contrast, *Z. noltii* in Spain required only 2% of immediate subsurface light (or 0.8 mol photons m⁻² day⁻¹) for survival at 18.5 °C (Peralta *et al.* 2002).

Zostera capricorni (under the name *Z. muelleri*) was a major component of seagrass losses in Westernport Bay (Victoria) as a result of either sediment settling onto the blades of the plant in combination with the effects of exposure (Shepherd *et al.* 1989) or turbidity from regular dredging and port activities (Bulthuis 1983, Bulthuis *et al.* 1984a). However, Bearlin *et al.* (1999) modelled the impact of turbidity on *Z. capricorni* and suggested that this species was susceptible to physical disturbance because of its delicate hairy root structure.

Burial also results in *Zostera* mortality (Mills and Fonseca 2003). Thus, burial and sedimentation are likely to be significant factors for these smaller species, particularly given their position in the already difficult conditions of the intertidal zone (Clarke and Kirkman 1989, Seddon 2000). Shepherd *et al.* (1989) reported that several species of *Zostera* around the world have suffered serious mortality from lack of light caused by increased turbidity, which had been induced by increased sediment loads in rivers, and human activities in coastal embayments. Estuaries and protected bays, a common habitat for *Zostera*, thus present considerable problems related to turbidity and sedimentation.

3.3.5. *Halophila*

No data are available on the minimum light requirements of *Halophila australis*, although it does occur at more than 20 m depth (Robertson 1984, Tanner 2003), suggesting a relatively low minimum light requirement. Work on *Halophila ovalis* suggests that it has a high light requirement (16%; Schwarz *et al.* 2000) and is particularly vulnerable to short-term light fluctuations (Longstaff and Dennison 1999). *Halophila ovalis* is reported to be relatively opportunistic and poorly adapted to any decline in light (Duarte *et al.* 1997, Longstaff and Dennison 1999, Longstaff *et al.* 1999). Clarke (1987) found that it died more rapidly than *Amphibolis* or *Posidonia* when buried. Bearlin *et al.* (1999) suggested that the root systems of *Halophila* were similarly delicate to those of *Zostera* such that it was also at risk to physical disturbance.

3.3.6. *Lepilaena*

There are no known publications as to the minimum light requirements for *Lepilaena*.

3.3.7. *Ruppia*

Ruppia megacarpa is a species with a relatively high requirement of 24% of sub-surface light to survive (Carruthers *et al.* 1999). Increased turbidity has been directly attributed to either a decline in *Ruppia megacarpa* density in Wilson Inlet in Western Australia (Carruthers *et al.* 1999), or complete loss as in Lake Budgewoi (New South Wales; King and Hodgson 1986). However, species of *Ruppia* from elsewhere (Brazil) have a much lower light requirement (8.2 %; Table 3) and may cope better with increased turbidity.

4. Toxicants

A diverse array of pollutants may influence seagrass health and survival. Ralph *et al.* (in press) described the toxicant load in near-shore systems as a “cacophony”, which suggests that the toxicant load at any one location is difficult to predict. Toxicants relevant to seagrasses can be divided into three groups (heavy metals, petrochemicals and pesticides). The current discussion has been limited to those compounds for which there is at least some literature. For metals, this is restricted to cadmium, copper, lead and zinc. In terms of herbicides, atrazine, diuron, cybutryne (irgarol 1051) and glyphosate will be considered. Petrochemicals comprise a daunting number of compounds, the effects of which are described only in general terms. Note that insecticides have not been considered, largely because they are less likely to have any direct influence on seagrasses, having been designed to leave plants unaffected.

4.1. Heavy Metals

Urbanised coastal environments are subjected to heavy metal contamination via the discharge of stormwater, industrial and treated wastewater discharge, urban and municipal run-off, agricultural and mining activities and atmospheric deposition (Batley 1996, Haynes and Johnson 2000). In addition to anthropogenic contamination, natural weathering and erosion of some types of rocks and soils may also contribute a variety of heavy metals to coastal waters (Batley 1996). While some metals are an essential physiological requirement of many marine plants and animals and occur naturally in seawater, excessive concentrations in the marine environment have been known to detrimentally impact on a variety of species and ecosystems (Langston 1990). The potential threat to marine organisms posed by metal pollution has been recognised for decades (Langston 1990).

Research linking heavy metal contamination to seagrasses began in the late 1970's and focused on the accumulation in plant tissues (e.g. Lyngby *et al.* 1982, Lyngby and Brix 1984, Ward *et al.* 1986, Ward 1987) because they are effective at extracting and incorporating metals from both the water column and interstitial spaces in sediments (Ward *et al.* 1986, Campanella *et al.* 2001). Numerous researchers have suggested the use of seagrasses as bio-monitors, as their tissue heavy-metal content often reflects bio-available water/sediment concentrations. However, there are many factors known to influence the accumulation of heavy metals by seagrasses, including differences between seagrass species, the tissue type (including compartment and age), the heavy metal in question, the concentration of the metal within the sediments and water, as well as various sediment characteristics (composition and/or chemistry; Langston 1990). The presence of freshwater inputs may also make some metals more bioavailable. Hence, while seagrasses may be utilised as bio-monitors of heavy metal contamination, given the large number of factors influencing metal accumulation, it is likely that their use is not possible under all circumstances and that development of generalisations is problematic.

While the use of seagrasses as biological indicators of heavy metals has been extensively studied (e.g. Lyngby *et al.* 1982, Lyngby and Brix 1984, Ward 1987), there is a lack of information on the physiological impacts of heavy metals on seagrasses. The following summarises our level of knowledge on some of the more common heavy metals.

4.1.1. Cadmium

Although cadmium (Cd) can be found in relatively high concentrations in some coastal marine environments, it appears to have limited impact on seagrass physiology. Levels of cadmium as low as $0.11 \mu\text{g g}^{-1}$ may accumulate in some seagrass species (Malea 1994), but physiological impacts are only found following exposures at much higher concentrations (Table 4; Lyngby and Brix 1984, Malea 1994, Ralph and Burchett 1998a, Macinnis-Ng and Ralph 2002). Exposure to cadmium concentrations of 0.56 mg L^{-1} for 19 days was found to reduce the growth of *Z. marina* (Lyngby and Brix 1984), while exposure to 1 mg L^{-1} cadmium for 4 days reduced

the photosynthetic quantum yield in *Halophila ovalis* (Ralph and Burchett 1998a). However, exposure to 1 mg L⁻¹ cadmium for 10 hours failed to exhibit a response in *Z. capricorni* (Macinnis-Ng and Ralph 2002). This lack of response may have been due to the lower exposure period in this study (10 hours compared to 4 and 19 days) natural variation between seagrass species, or the fact that all other studies were laboratory-based. Macinnis-Ng and Ralph (2002) undertook an *in situ* study using chambers attached to the benthos wherein there would have been substantially increased opportunities for biological and chemical interactions that could have dissipated the effect of the treatment. The lowest concentration of cadmium that has been found to negatively impact upon seagrasses was identified by Malea (1994), who found that exposure to 0.1124 mg L⁻¹ cadmium for 16 days caused cellular damage in *Halophila stipulacea* (Table 4; Malea 1994). There is no information on the physiological impact of cadmium on temperate species of seagrass, such as *Posidonia*.

There are a few possible explanations for the limited impact of cadmium on seagrasses. Cadmium is not required for growth or development by plants, and consequently it may be actively excluded by the plant (Ralph and Burchett 1998a). This suggestion may be supported by Malea (1994), who identified a lower uptake of non-required metals relative to essential elements. Alternatively, seagrasses may sequester non-essential metals like cadmium into structural components of the leaf tissue, preventing them from affecting sensitive metabolic processes (Ward 1987).

4.1.2. Copper

Unlike cadmium, copper (Cu) is an essential micro-nutrient, required in a number of enzyme systems linked to Photosystem (PS) II electron transport, mitochondria and chloroplast reactions, cell wall lignification, carbohydrate metabolism, and protein synthesis (Woolhouse 1983, in Ralph and Burchett 1998a). While copper is a natural component of marine environments in low concentrations, elevated copper concentrations consistently produce toxic responses in a range of seagrass species. Elevated concentrations of copper have been reported to inhibit the transport of electrons at the donor and acceptor sites of PS II, leading to a decrease in the quantum yield (Prasad and Strzalka 1999, in Macinnis-Ng and Ralph 2002). Research on the physiological impact of copper on seagrasses suggests that concentrations of 1 mg L⁻¹ can impact on a variety of seagrass species, including *Halophila ovalis*, *Halophila spinulosa* and *Z. capricorni* (Table 4; Ralph and Burchett 1998a, Prange and Dennison 2000, Macinnis-Ng and Ralph 2002, Macinnis-Ng and Ralph 2004b). Furthermore, *in situ* experiments on *Z. capricorni* identified that this species was unable to completely recover after exposure to 0.1 mg L⁻¹ copper for 10 hours (Macinnis-Ng and Ralph 2002). The degree of impact, however, significantly varies between species. In a study by Prange and Dennison (2000), *Halophila spinulosa* was found to be significantly more sensitive to copper exposure than *Halophila ovalis* or *Z. capricorni*, but, in the same study, copper exposure failed to produce a significant photosynthetic response in *Halodule uninervis* or *Cymodocea serrulata*. The lowest concentration of copper that has been experimentally tested is 0.0635 mg L⁻¹, which failed to affect the growth of *Z. marina* after exposure for 19 days (Lyngby and Brix 1984).

4.1.3. Lead

The susceptibility of seagrasses to lead (Pb) appears to be limited. Lead is a non-essential element and, as with cadmium, may be actively excluded or sequestered by seagrasses to minimise the extent of exposure (Ralph and Burchett 1998a). Lead concentrations between 0.1 and 10.36 mg L⁻¹ for various exposure periods appear to have an insignificant impact on the growth or photosynthetic ability of a variety of seagrass species (Table 4; Lyngby and Brix 1984, Ralph and Burchett 1998a, Macinnis-Ng and Ralph 2002).

4.1.4. Zinc

Zinc (Zn) is an essential micro-nutrient in many enzyme systems as well as in the biosynthesis of plant growth hormones (Wahbeh 1984, in Ralph and Burchett 1998a). The responses of seagrasses exposed to zinc at a variety of concentrations appear to be highly variable both

within and between species (Table 4). Variability within the same species had been demonstrated in two different studies undertaken by Macinnis-Ng and Ralph (2002; 2004b). In both of the studies, *Z. capricorni* was exposed to 0.1 and 1 mg L⁻¹ zinc for 10 hours, however, different results were obtained. In one study, both concentrations were found to reduce the photosynthetic efficiency of *Z. capricorni*, although results were highly variable (Macinnis-Ng and Ralph 2002), while in the other, both concentrations failed to significantly affect photosynthetic efficiency (Macinnis-Ng and Ralph 2004b). Lyngby and Brix (1984) assessed the impact of zinc on the growth rate of *Z. marina* and found a significant reduction in growth at concentrations of 3.27 mg L⁻¹.

4.1.5. Summary of heavy metals

Relatively few studies have investigated the physiological impacts of heavy metals on seagrasses. Nonetheless, results do suggest that responses of seagrasses to heavy metal contamination are species-specific and highly dependent on the exposure period and concentration. Furthermore, impacts vary between studies with differences in the seagrass parameters measured and the type of experiment undertaken (e.g. field versus laboratory). In most cases, heavy metals that are required for metabolic processes by the seagrass (e.g. copper and zinc) have greater impacts than those that are non-essential elements (e.g. cadmium and lead; e.g. Ralph and Burchett 1998a, Macinnis-Ng and Ralph 2002). Plants expend energy in mechanisms targeting the uptake of the metals required for biochemical processes (Ralph and Burchett 1998a). However, when exposed to an excessive metal concentration, the uptake level may outstrip metabolic requirements and potentially result in toxic impacts (Ralph and Burchett 1998a). Alternatively, heavy metals that have no biological role may be actively excluded or sequestered to minimise their potential for toxicity (Ralph and Burchett 1998a).

Studies linking heavy metal contamination to seagrasses in South Australia are restricted to those undertaken near Port Pirie (~ 200 km north of Adelaide), adjacent the world's largest lead smelter, which may be one of the most polluted locations in South Australia (Edwards *et al.* 2001). Seagrasses in the local waters (*P. australis*, *P. sinuosa* and *A. antarctica*) have been found to contain higher concentrations of cadmium, lead and zinc relative to their proximity to the smelter (Ward *et al.* 1986; Ward 1987). In addition, Ward (1987) found that the growth rate of *P. australis* was significantly lower close to the smelter compared to the same species located 8 and 16 km distant, although there was no attempt to determine which metal/combination of metals was responsible.

Table 4. Summary of seagrass responses to various heavy metals. Sources A = Malea (1994), B = Lyngby and Brix (1984), C = Ralph and Burchett (1998a), D = Macinnis-Ng and Ralph (2002), E = Prange and Dennison (2000), F = Macinnis-Ng and Ralph (2004a), G = Macinnis-Ng and Ralph (2004b).

Type	Species	Dose(s) (mg L ⁻¹ unless stated)	Exposure (days / hours)	Response	Source
Cd	Lab <i>Halophila stipulacea</i>	0.1124, 1.124 µg L ⁻¹ 0.1124, 1.124, 11.24	16 d	Cellular damage at concentrations $\geq 0.1124 \text{ mg L}^{-1}$.	A
	Lab <i>Zostera marina</i>	0.01124, 0.0562, 0.562, 5.62	19 d	Growth rate inhibited for ≥ 0.562 and 5.62 mg L^{-1} .	B
	Lab <i>Halophila ovalis</i>	1, 5, 10	4 d	Slight reduction in photosynthetic efficiency in all treatments proportional to dose.	C
	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	None	D
Cu	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	D
	Lab <i>Halophila ovalis</i>	1, 5, 10	4 d	Reduction in photosynthetic efficiency in proportion to dose.	C
	Lab <i>Halophila spinulosa</i>	1	12 d	Leaf senescence after 24 hours.	E
	Lab <i>Halophila ovalis</i>	1	12 d	Reduction in photosynthetic efficiency	E
	Lab <i>Halodule univervis</i>	1	12 d	Reduction in photosynthetic efficiency, although not significant	E
	Lab <i>Zostera capricorni</i>	1	12 d	Reduction in photosynthetic efficiency	E
	Lab <i>Cymodocea serrulata</i>	1	12 d	None	E
	Lab <i>Zostera marina</i>	0.635, 3.177 µg L ⁻¹ 0.3177, 3.177	19 d	Growth rate inhibited $\geq 0.3177 \text{ mg L}^{-1}$ with response proportional to dose.	A
	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	G
	Field <i>Zostera capricorni</i>	5	10 hrs	Reduction in photosynthetic efficiency.	F
	Lab <i>Zostera marina</i>	0.02, 0.1036, 1.036, 10.36	19 d	None	A
	Lab <i>Halophila ovalis</i>	1, 5, 10	4 d	None	C
Pb	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	Slight reduction in photosynthetic efficiency but highly variable.	D
	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	Variable reduction in photosynthetic efficiency proportional to dose.	D
	Lab <i>Zostera marina</i>	0.0065, 0.0327, 0.327, 3.27	19 d	Growth rate inhibited by 3.27 mg L^{-1} .	A
	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	None	F
Zn	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	Variable reduction in photosynthetic efficiency proportional to dose.	D
	Lab <i>Zostera marina</i>	0.0065, 0.0327, 0.327, 3.27	19 d	Growth rate inhibited by 3.27 mg L^{-1} .	A
	Field <i>Zostera capricorni</i>	0.1, 1	10 hrs	None	F

4.2. Herbicides

Herbicides generally enter the marine environment as run-off from agricultural, forestry and municipal applications; however, they can also be directly introduced as biocides from ship hulls (Ralph *et al.* in press). There is a range of herbicides known to enter the marine environment from such uses, the best known/most common of which include atrazine, diuron (DCMU), cybutryne, simazine and glyphosate. While herbicides are generally not considered to have contributed to wide-scale seagrass loss, there has been little research in this area, although various compounds have been found within coastal environments at concentrations likely to impact on seagrass health (e.g. Haynes *et al.* 2000b). These observations suggest that herbicides may play a role in seagrass decline in some areas, and should therefore be considered when assessing the potential mechanisms of seagrass loss. Notwithstanding this, it is important to realise that there is often very little information on herbicide concentrations in the marine environment as well as relatively little information on the physiological impacts of herbicides on seagrasses, particularly in terms of growth and reproduction. The majority of research to date appears to have focussed on acute (i.e. short term) responses to a range of dosages.

4.2.1. Atrazine

Atrazine, a triazine herbicide, is one of the most widely used herbicides in some parts of the world (e.g. Chesapeake Bay catchment; Schwarzschild *et al.* 1994) and is rapidly absorbed by seagrasses through their leaves and roots (Schwarzschild *et al.* 1994). Atrazine inhibits photosynthesis by binding to the second electron receptor (Q_B) protein, inhibiting electron transport (Ralph 2000). Although only a few studies have investigated the impacts of atrazine on seagrasses, all have found that this herbicide does have an effect; albeit one that varies considerably with concentration, exposure period and seagrass species (Table 5; Correll and Wu 1982, Mitchell 1987, Schwarzschild *et al.* 1994, Ralph 2000, Macinnis-Ng and Ralph 2003a). Atrazine concentrations of $\geq 10 \mu\text{g L}^{-1}$ significantly reduced effective quantum yield in *Halophila ovalis* and *Zostera capricorni*, although the exposure levels differed substantially, with 96 hours and 10 hours respectively (Ralph 2000, Macinnis-Ng and Ralph 2003b). Atrazine concentrations less than $10 \mu\text{g L}^{-1}$ were not examined in either study and consequently the impact of such low levels on these seagrasses remains unknown. However, atrazine concentrations as low as $5 \mu\text{g L}^{-1}$ have been shown to reduce plant growth and productivity in freshwater plants after prolonged exposure (five or more weeks; cited in Schwarzschild *et al.* 1994). Longer exposure periods of lower concentrations of atrazine ($< 10 \mu\text{g L}^{-1}$) may thus have the potential to detrimentally affect seagrasses, and with an average half-life of 30 days (PAN 2004); this substance may spread over a large area. The only study to contradict the findings of others is that of Correll and Wu (1982), who found that concentrations of $75 \mu\text{g L}^{-1}$ actually stimulated photosynthesis in the seagrass *Z. marina*.

Simazine, another triazine herbicide related to atrazine, has a similar half-life (average 28 days; PAN 2004) and modes of action and toxicity to atrazine (Tomlin 1994, in Ralph 2000). A detailed review of this herbicide has not been included in this review although one study that investigated the impact of both herbicides to *Halophila ovalis*, found that simazine had a similar but slightly reduced impact relative to atrazine (Ralph 2000).

4.2.2. Diuron

Diuron, otherwise referred to as DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) is a phenylurea herbicide that is extensively used in the Queensland cane industry for pre-emergent weed control (Hamilton and Haydon 1996, in Haynes *et al.* 2000b). However, it is also used as a biocide on boat hulls and can be found in marina sediments (Thomas *et al.* 2000), which may have particular relevance to dredging operations. Diuron reversibly inhibits photosynthetic electron flow to the plastoquinone in Photosystem II (PSII) by blocking the electron transport chain just after the primary electron receptor (Q_A ; Macinnis-Ng and Ralph 2003a). Haynes *et al.* (2000b) examined the response of *Halophila ovalis*, *Cymodocea serrulata* and *Z. capricorni* in a laboratory based trial using 0.1, 1, 10 and $100 \mu\text{g L}^{-1}$ diuron. They found that all three

seagrasses exhibited declines in effective quantum yield in response to diuron exposure, but with some variation between species. *Cymodocea serrulata* was the least impacted, being affected by 10 and 100 µg L⁻¹ diuron. Conversely, *Z. capricorni* and *Halophila ovalis* exhibited photosynthetic stress at all four concentration levels. *Halophila ovalis* was particularly sensitive, as indicated by a reduction in the effective quantum yield at all treatment levels within 24 hours. Chesworth *et al.* (2004) found that exposure to 1 µg L⁻¹ diuron reduced the photosynthetic efficiency of *Z. marina*, while concentrations less than this (0.5 µg L⁻¹) had no impact.

Macinnis-Ng and Ralph (2003b) exposed *Z. capricorni* to 10 and 100 µg L⁻¹ diuron in both laboratory and field environments with similar results in that both concentrations significantly reduced the effective quantum yield. While the exposure time of the two studies varied (5 hours in Haynes *et al.* 2000b and 10 hours in Macinnis-Ng and Ralph 2003a), both found that recovery of photosynthetic ability occurred in most cases.

4.2.3. Cybutryne

Like atrazine and simazine, cybutryne is also a triazine herbicide used in antifouling paints on boat hulls with increasing popularity since the restriction of the use of tributyltin. Cybutryne has a very similar mode of action to other triazines in that exposure reduces plant photosynthetic ability (Scarlett *et al.* 1999b). Significantly, cybutryne is a particularly effective herbicide and has been known to concentrate in *Z. marina* leaf tissues up to 25,000 times higher than values found in the surrounding water (Scarlett *et al.* 1999a), and 30,000 times in freshwater macrophytes (Tóth *et al.* 1996, in Scarlett *et al.* 1999a). However, information on the impact of cybutryne on seagrasses is limited to a few studies on *Zostera* species with results suggesting that concentrations as low as 0.18 µg L⁻¹ can impact on the photosynthetic efficiency of *Zostera* (Scarlett *et al.* 1999a). While Macinnis-Ng and Ralph (2003b) did not investigate concentrations this low, impacts were observed in both laboratory and field samples of *Z. capricorni* exposed to 10 µg L⁻¹; the lowest concentrations used. Similarly, Chesworth *et al.* (2004) identified a reduction in the photosynthetic efficiency in *Z. marina* at the lowest concentration measured (Table 5).

4.2.4. Glyphosate

Glyphosate is the most widely used non-selective herbicide in the world (PAN 2004). Glyphosate acts on various enzyme systems throughout the plant by interfering with amino acid formation (Ralph 2000). Despite its extensive use on terrestrial plants, glyphosate has been classified as relatively non-toxic to aquatic flora (Tomlin 1994, in Ralph 2000). Limited research investigating the impacts of glyphosate on seagrasses is in line with this interpretation, with Ralph (2000) finding that concentrations ranging between 1 and 100 mg L⁻¹ did not affect the photosynthetic capacity of *Halophila ovalis* (Ralph 2000).

4.2.5. Summary of herbicides

There is little information on herbicides and pesticides in Adelaide's metropolitan waters and consequently inferences about the possible physiological impacts of herbicides to South Australian seagrasses cannot be made. The Mt Lofty Catchment Management Board has found detectable levels of atrazine, simazine and hexazinone (another triazine) in a number of reservoirs that service the Adelaide metropolitan area (Mt Lofty Ranges Watershed Protection Office 2000). Based on elevated concentrations of diuron in sediments adjacent to cane growing areas in Queensland (Haynes *et al.* 2000a), and the results of laboratory trials, Haynes *et al.* (2000b) concluded that "exposure to herbicide concentrations present in near-shore Queensland sediments present a potential risk to seagrass functioning". While this is possible in Queensland, the same type of prediction cannot be made in South Australia, as there is no information about the levels of this herbicide in South Australian water or sediments and no experimental data on the way in which South Australian seagrass species respond to diuron.

Cybutryne can be discounted as a threat to near-shore systems, as the majority of seagrass loss off the Adelaide Metropolitan coastline took place during the 1970's when this herbicide was not in use. However, cybutryne is one of a family of herbicides (triazines – similar to atrazine, simazine, etc) for which there may be some relevance. Alternately, glyphosate readily binds with soil particles or otherwise rapidly breaks down into non-toxic forms (PAN 2004) and is therefore unlikely to reach the sea in hazardous levels.

Historically there would appear to be little by way of consistent monitoring of herbicides or pesticides in metropolitan waters. There may be some value in obtaining measurements of some of the broader herbicide groups, in particular the triazides and possibly glyphosate; however, specific testing for the effects of these compounds on seagrasses is considered unnecessary, given the preponderance of other, more likely causes for seagrass loss.

Table 5. Summary of seagrass responses to various herbicides. Sources A = Macinnis-Ng and Ralph (2003b), B = Ralph (2000), C = Correll and Wu (1982), D = Mitchell (1987), E = Haynes *et al.* (2000b), F = Chesworth *et al.* (2004), G = Scarlett *et al.* (1999a), H = Macinnis-Ng and Ralph (2004a).

	Type	Species	Dose(s) ($\mu\text{g L}^{-1}$ unless stated)	Exposure (days / hours)	Response	Source
Atrazine	Field	<i>Zostera capricorni</i>	10, 100	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	A
	Lab	<i>Zostera capricorni</i>	10, 100	10 hrs	Reduction in the photosynthetic efficiency proportional to dose.	A
	Lab	<i>Halophila ovalis</i>	10, 100, 1000	96 hrs	Reduction in photosynthetic efficiency proportional to dose.	B
	Lab	<i>Zostera marina</i>	75 and 650	48 d	75 $\mu\text{g L}^{-1}$ stimulated photosynthesis, while 650 $\mu\text{g L}^{-1}$ inhibited.	C
	Lab	<i>Halodule wrightii</i>	30 ppm	23 d	Reduction in survival of ramets, production of new ramets, above ground biomass and growth.	D
Diuron	Lab	<i>Cymodocea serrulata</i>	0.1, 1, 10, 100	5 d	Reduction in photosynthetic efficiency in $\geq 10 \mu\text{g L}^{-1}$.	E
	Lab	<i>Halophila ovalis</i>	0.1, 1, 10, 100	5 d	Reduction in photosynthetic efficiency proportional to dose.	E
	Lab	<i>Zostera capricorni</i>	0.1, 1, 10, 100	5 d	Reduction in photosynthetic efficiency proportional to dose.	E
	Field	<i>Zostera capricorni</i>	10, 100	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	A
	Lab	<i>Zostera capricorni</i>	10, 100	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	A
Cybutryne	Lab	<i>Zostera marina</i>	0.5, 1, 2.5, 5, 10, 25	10 d	Reduction in photosynthetic efficiency $\geq 1 \mu\text{g L}^{-1}$ proportional to dose. Significant reduction in growth at 3.2 $\mu\text{g L}^{-1}$	F
	Lab	<i>Zostera marina</i>	0.5, 1, 2.5, 5, 10, 25	10 d	Reduction in photosynthetic efficiency proportional to dose.	G
	Field	<i>Zostera capricorni</i>	10 and 100	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	A
	Lab	<i>Zostera capricorni</i>	10, 100	10 hrs	Reduction in photosynthetic efficiency proportional to dose.	A
	Lab	<i>Zostera capricorni</i>	100	10 hrs	Reduction in effective quantum yield	H
Glyphosate	Lab	<i>Zostera marina</i>	0.5, 1, 2.5, 5, 10, 25	10 d	Reduction in photosynthetic efficiency proportional to dose. Significant reduction in growth at 1 $\mu\text{g L}^{-1}$	F
	Lab	<i>Halophila ovalis</i>	1, 10, 100	96 hrs	None	B

4.3. Petrochemicals

Petrochemicals are primarily introduced into marine environments through accidental oil spills, although there are numerous other sources including hazardous materials disposal, leakage from oil facilities, activities in refineries, effluent from non-petroleum industries, boat engines in ports and harbours, and urban (car use) and stormwater runoff (Thorhaug 1992, in Ralph *et al.* in press, Ralph and Burchett 1998b). The majority of petrochemical inputs generally occur within shallow-water environments that are often inhabited by seagrasses, which thus presents a high probability of exposure. However, research investigating the impact of petrochemicals on seagrasses is relatively limited and, while oil spills are generally known to have few long lasting effects, results are highly variable.

Observations of the effects of the *Exxon Valdez* oil spill on *Z. marina* health (Dean *et al.* 1998) showed that seagrasses remained “relatively unaffected”, with impacts on the density of shoots and flowering shoots only significant in the first year after the spill. Other seagrass parameters measured by Dean *et al.* (1998), such as biomass, seed density and germination, were found to be unaffected. Kenworthy *et al.* (1993) noted a similar lack of long-term or acute impacts on *Halodule uninervis*, *Halophila ovalis* and *Halophila stipulacea* following the Gulf War oil spill. Laboratory studies of the impact of short-term exposure to oil on these seagrass species supported the finding of Kenworthy *et al.* (1993), with no significant impacts being found (Durako *et al.* 1993). In contrast, *Thalassia* seagrass beds were severely affected by the *Zoe Colocotronis* spill in Puerto Rico (Nadeau and Berquist 1977, in Dean *et al.* 1998) and the Witwater oil spill in Panama (Jackson *et al.* 1989, in Dean *et al.* 1998).

Variation in the way that seagrasses can be impacted by oil spills is likely to reflect the way in which the oil interacts with the plants. In some cases oil spills can cause direct mortality due to smothering and poisoning, or absorption of dissolved toxins by the seagrass (Zieman *et al.* 1984, in Macinnis-Ng and Ralph 2003b). This type of interaction may explain the loss of seagrasses as a result of oil spills in areas where other research has found minimal impacts on seagrass beds (as in the studies outlined above). It also may explain why, in a study performed by Jackson *et al.* (1989, in Dean *et al.* 1998), intertidal seagrasses perished because of an oil spill while subtidal portions of the seagrass meadow survived. Doerffer (1992) stated that the most damaging effect of oil spills to marsh plants occurs when they are completely covered with oil. It follows that intertidal seagrasses are probably more at risk than those occurring subtidally. The primary phototoxic effect of oil is induced by the absorption of the water-soluble fraction (WSF; Doerffer 1992), which causes a reduction in tolerance to other stress factors such as sublethal quantities of hydrocarbons that are incorporated into tissue (Zieman *et al.* 1984 in Macinnis-Ng and Ralph 2003b).

The use of dispersants to clean up oil spills offers the benefit of reducing the threat of oiling shorelines and water-surface inhabitants such as marine mammals and seabirds (Wolfe *et al.* 1998). However, dispersants encourage the oil to spread and increase the bioavailable fraction of oil by increasing the concentration of poly-aromatic hydrocarbons (PAH's) in the water column and altering the interaction of these compounds with biological membranes (Wolfe *et al.* 1998). Consequently, dispersants have been found to pose a threat to seagrasses alone or in combination with oils (e.g. Hatcher and Larkum 1982, Thorhaug *et al.* 1986), although results are variable, depending on the response measured. Hatcher and Larkum (1982) and Thorhaug *et al.* (1986) both identified that dispersed oil had more impact on a variety of seagrass species (*P. australis*, *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme*) than oil or dispersant alone. These findings contradict those of Ralph and Burchett (1998b) who identified that *Halophila ovalis* was equally impacted by oil and an oil and dispersant mixture, as well as Macinnis-Ng and Ralph (2003a), who identified no response to oil and dispersant treatment, but a significant effect to oil exposure alone. Both Ralph and Burchett (1998b) and Macinnis-Ng and Ralph (2003a) used chlorophyll fluorescence as a measure of impact, whereas Hatcher and Larkum (1982) used oxygen production and leaf turnover rates and Thorhaug *et al.* (1986) examined growth, mortality and seagrass “health”. Further differences between these studies

are likely to reflect not only differences between species, but also the type of dispersant and oil used. Comparisons between studies are thus problematic, but while it appears that petrochemicals may impact the short-term health of some seagrasses, there are few longer-term impacts (Connolly and Jones 1996). Consequently, it is unlikely that petrochemicals have resulted in the extensive seagrass losses observed along Adelaide's metropolitan coastline, particularly in the absence of any major spill events. The only oil spill of any note in South Australia was the *Era* in Spencer Gulf in 1992, for which no impact on local seagrass communities could be identified (Connolly and Jones 1996), although Wardrop *et al.* (1992) found some impact on nearby mangroves.

5. Salinity Changes

Freshwater inputs into marine systems are likely to be turbid with increased levels of nutrients (Gillanders and Kingsford 2002). While nutrients are widely considered to be detrimental to seagrasses, there is little research on the direct effect of freshwater / lower salinity. Most research on salinity changes with respect to seagrasses has focused on estuarine species such as *Z. marina* (e.g. van Katwijk *et al.* 1999; Kamermans *et al.* 1999; Hellblom and Bjork 1999). Estuaries may have a far more varied salinity regime relative to exposed coasts and even in areas of high terrestrial runoff, the difference in densities between fresh and saline water means that the former will tend to float (i.e. stratification). The exposure of seagrasses in any but the shallowest of circumstances may be limited. While Gulf St Vincent is considered to have relatively minor freshwater inputs and a high level of oceanic flushing (Steffensen *et al.* 1989), seagrass recession to seaward along the Adelaide coast correlates with the completion of stormwater outfalls in the 1960's (Figure 2; Seddon 2002). Therefore, there would seem to be some merit in investigating reduced salinity as a possible cause for seagrass decline along the Adelaide metropolitan coast. Such studies may be particularly pertinent, as freshwater inputs also carry high sediment, nutrient and toxicant loads and it could be that the effect of these pollutants is enhanced at reduced salinities (Ralph *et al.* in press).

5.1.1. *Amphibolis* and *Posidonia*

As *Amphibolis* and *Posidonia* inhabit coastal areas, one might suspect that they would not normally be exposed to salinities other than that of normal seawater (35 ppt). Nonetheless, in some coastal embayments where evaporation rates are high, they do occur at elevated salinities. For example, Walker (1985) found *A. antarctica* growing at 57 ppt in Shark Bay, Western Australia, and both *Amphibolis* and *Posidonia* occur in upper Spencer Gulf and upper Gulf St Vincent (Edyvane 1999) where salinities are > 40 ppt during summer (Nunes and Lennon 1986; de Silva Samarasinghe and Lennon 1987). Walker and McComb (1990) also showed that seedlings of *A. antarctica* collected from Shark Bay had maximum leaf production rates at 42 ppt but were unable to survive at 65 ppt.

Amphibolis and *Posidonia* can also be exposed to lowered salinities in areas adjacent major freshwater inputs. For example, Hillman *et al.* (1990) reported *Posidonia* growing in Oyster Harbour in south-west Western Australia, where salinities are known to vary seasonally between about 25 and 37 ppt due to freshwater inputs in winter (Hillman *et al.* 1991). Indeed, Tyerman *et al.* (1984) found the growth of *P. australis* to be unaffected at salinities down to 13 ppt. Nonetheless, while vegetative growth of *P. australis* may continue at lowered salinities, seed germination may have a different response (Tyerman 1989). Unfortunately, no information could be found on the tolerance of *Amphibolis* to reduced salinities.

5.1.2. *Zostera* and *Heterozostera*

The only truly estuarine system on the Adelaide coast is the tidal section of the Onkaparinga River, an area known to support *Z. capricorni* (Shepherd and Robertson 1989). While substantial work has been done on the response of *Z. marina* to changes in salinity, the results are varied, leading to the conclusion that the impact is dependent on the longer-term history of the individuals involved. Hellblom and Bjork (1999) failed to demonstrate any effect on photosynthesis and respiration of *Z. capricorni* when salinity was altered from 33 to 0 ppt on a short-term basis (over 4 hours). However, Kamermans *et al.* (1999) with an estuarine population of *Z. capricorni*, showed that shoot, leaf and below-ground biomass production were greater in a population kept at 22 ppt than at 32 ppt. Furthermore, van Katwijk *et al.* (1999) showed that the effect of higher nutrients was positive only when salinity was kept low. However, they concluded that ecotypes existed within the species, which defined their response to salinity level. *Zostera capricorni* in eastern Australia exhibited lower seed germination rates at 30 ppt than at 15 ppt, but only under aerobic conditions. Conversely, under anaerobic conditions, there was no effect of salinity (Brenchley and Probert 1998).

Other species of *Zostera* also tend to demonstrate a preference for lower salinities. For example, *Z. novazelandica* had markedly greater flower production at 17 ppt than at 33 ppt, and failed to flower at all at 70 ppt, although interestingly it did survive at this exposure (Ramage and Schiel 1998). Vermaat *et al.* (2000) also showed that *Z. noltii* was unable to survive at the salinity of seawater (35 ppt). In contrast, Adams and Bate (1994b) found that *Z. capensis* had maximum growth at salinities of 15 and 35 ppt in the laboratory, with field observations by both Adams and Bate (1994b) and Adams *et al.* (1992) showing that it can be common in parts of estuaries characterised by marine conditions.

Although information on *Heterozostera tasmanica* is limited, in West Lakes, South Australia, this plant appeared to thrive during prolonged (3 months) exposure at salinities as low as 15 ppt (Westphalen pers. obs.). Given that both *Z. capricorni* and *Heterozostera tasmanica* can occur in the intertidal (Robertson 1984) as well as within estuaries (Kamermans *et al.* 1999), it may be anticipated that both taxa have mechanisms enabling tolerances to altered salinity regimes.

5.1.3. *Halophila*

Halophila ovalis demonstrates the high likelihood of ecotype differentiation within seagrass species. Benjamin *et al.* (1999) showed that individuals from a marine population were unable to tolerate 20 ppt salinity, whilst estuarine plants were able to cope with 10 ppt. In contrast, Ralph (1998) found that *H. ovalis*, which had been cultured at 35 ppt was able to tolerate rapid transfer to both 9 ppt and 52 ppt. They died, however, at the extremes of 0 ppt and 70 ppt.

5.1.4. *Ruppia* and *Lepilaena*

While there is no information specific to *Ruppia megacarpa*, Murphy *et al.* (2003) have demonstrated a higher quantum yield for *R. maritima* under a salinity range from 10 - 20 ppt than from 0 ppt - 40 ppt. Murphy *et al.* (2003) also noted that there was a degree of acclimation to the differing salinities. La Peyre and Rowe (2003) found that it was the change in salinity rather than the steady state values, which were most detrimental to *R. maritima*. Fourqurean *et al.* (2003) predicted that an increase in freshwater runoff into the Bay of Florida would have substantial effects on the species composition of the seagrass beds, with *R. maritima* taking over habitat from *Thallasia testudinum* as a result of its greater tolerance to freshwater. Both *Ruppia* and *Lepilaena* are known to tolerate a range of salinities (Robertson 1984). For example, Adams and Bate (1994b) found that *R. cirrhosa* was able to continue growth at salinities between 0-75 ppt in the laboratory. However, the field distribution of *R. cirrhosa* suggests a preference for brackish estuarine conditions (Adams *et al.* 1992,), possibly related to a lack of seed germination at salinities > 35 ppt (Adams and Bate 1994b).

6. Conclusions

Coastal Adelaide has been used as a dumping ground for urban runoff almost since the time of settlement in 1836. Inputs to the metropolitan coast have included a diverse array of treated wastewater outfalls, stormwater drains and vastly altered riverine inputs (Figure 2; Steffensen *et al.* 1989, EPA 1998). However, all these sources are fundamentally freshwater inputs that contain varying levels of nutrients, heavy metals, petrochemicals, pesticides and herbicides, as well as sediments. Possibly the major difference is that wastewater treatment plant outfalls operate(d) throughout the year and thus act(ed) as a variable but constant presence whereas stormwater and riverine inputs are substantially more seasonal, having little or no direct influence in dry periods. The magnitude and dispersion of pulse events on the Adelaide coast needs to be quantified (Butler *et al.* 1997), as does their potential impact on seagrass health.

Eutrophication, sedimentation, turbidity and salinity changes are common to virtually all land-based inputs to Gulf waters. Toxicants are likely to be spatially variable depending on the catchment, with lead, cadmium and petrochemicals derived from road runoff into stormwater, while pesticides and herbicides relate more to agriculture. Given the doses required to affect seagrass health, it would seem unlikely that toxicants are a significant factor in large-scale declines of seagrass on the Adelaide coast.

Seagrass loss off the Adelaide metropolitan coast has most frequently been attributed to eutrophication (e.g. Shepherd *et al.* 1989, Steffensen *et al.* 1989, EPA 1998), but the pattern of most of the decline does not comply with the nutrient-loss model as it is currently understood (e.g. Shepherd *et al.* 1989, Dixon 1999, Wear *et al.* 1999, Ralph *et al.* in press). Determining the reasons why Adelaide's seagrass decline is different should be a primary goal of investigations into loss mechanisms on the metropolitan coast. Temperature, depth and salinity levels are thought to be the primary factors controlling seagrass growth, but light, sediment and nutrient characteristics become more important when the former are not limiting (Livingston *et al.* 1998). Gulf St Vincent is a large inverse estuary 70 km wide and 160 km long that has an unusual tidal regime (Butler *et al.* 1997), along with substantial gradients in wave energy, turbidity, temperature and salinity (Shepherd and Robertson 1989). The near-shore thus covers a broad range of physiological and morphological tolerances that has been known to support a number of different species of seagrass. The primary causal mechanisms for seagrass decline on the Adelaide metropolitan coast are thus likely to be a complex interaction of factors (nutrient loads, salinity changes, loss of light through turbidity and/or sedimentation) that vary both spatially and temporally in both composition and magnitude.

Studies investigating multiple factors that potentially cause seagrass loss appear to be relatively few. The existing literature has tended to consider two very similar factors such as two toxicants (Chesworth *et al.* 2004, Macinnis-Ng and Ralph 2004a, Macinnis-Ng and Ralph 2004b). Alternately, field studies often provide an integrated measure of the effect of changes in water quality. For example, Campbell *et al.* (2003) measured the responses of *Heterozostera tasmanica* and *Z. capricorni* to high levels of water-column chlorophyll *a*, nutrients and suspended material. However, while their study provides the integrated response to a number of stresses, we have little understanding of the relative importance of individual factors. In contrast, Hellblom and Bjork (1999) considered the combined and isolated effects of decreased salinity and organic carbon and osmolality on photosynthesis in *Z. marina*, with carbon having more influence than other factors. In another study of *Z. marina*, van Katwijk *et al.* (1999) investigated the effect of salinity changes combined with increased nutrients and found a complex series of interactions based on salinity responses and whether the plants were estuarine or marine. Whilst shading trials have frequently been employed in determining the effect of reduced light availability on seagrasses (e.g. Neverauskas 1988), loss of light due to epiphytes and/or sedimentation may have a different affect relative to seagrass decline caused by increased turbidity, as the former causes may also interfere with gas exchange (Borowitzka and Lethbridge 1989, Hillman *et al.* 1990). It is difficult to differentiate the effects of increased

turbidity and sedimentation or smothering (Ralph *et al.* in press), particularly in the field setting. However, carefully controlled experiments employing multiple factors are required, particularly in the context of losses on the Adelaide metropolitan coast.

The bulk of the seagrass loss on the Adelaide metropolitan coast has occurred in Holdfast Bay (Figure 2). Although there are few data on the composition of the system prior to major decline, it may be inferred from elsewhere along the coast (see above) that *P. sinuosa* and *A. antarctica* were the most likely dominants nearshore and thus comprised the bulk of the loss along with understorey/meadow-fringing species (*Halophila australis* and *Heterozostera tasmanica*). Additional loss of *P. angustifolia* from deeper areas is also likely. *Posidonia australis* may also have been lost from very shallow water in Holdfast Bay as Thomas and Clarke (2002) found it in shallow water in northern Holdfast Bay during the mid-1980's.

Large-scale losses of seagrass meadows result in an alteration of the system to one where phytoplankton are the dominant primary producers, with no habitat available for most of the original fauna, culminating in a dramatic loss in biodiversity (Clarke and Kirkman 1989, EPA 1998). Energy via water movement is increased while stability of sediment is reduced, resulting in substantial sand movement (Bulthuis *et al.* 1984b, Clarke and Kirkman 1989, Walker and McComb 1992, EPA 1998). This may affect any remaining seagrasses in a self-perpetuating cycle of decline (or feedback loop) meaning that, whatever the mechanism for the initial loss, once damaged a meadow is at high risk of further degradation (Larkum and West 1983, Seddon 2002). Indeed physical erosion of seagrass meadows and increased sedimentation/turbidity loads because of increased sediment resuspension, rather than terrigenous inputs of nutrients, sediments, and freshwater, are likely to be the cause for current losses on the Adelaide metropolitan coast (Seddon 2002). It is therefore important to be aware of the historical versus current mechanisms for seagrass loss and that the amelioration of historical causes may not affect the ongoing rate of decline. It is thus important to obtain an understanding of the spectrum of decline mechanisms. This information will feed our understanding of the tolerances of seagrass systems that can be used in management models for both the maintenance of the extant population as well as developing amelioration or restoration strategies.

There have been substantial improvements in inputs into Adelaide's near-shore, in particular the closure of both the Glenelg and Port Adelaide sludge outfalls in 1993, but also recent improvements in wastewater treatment and catchment management (Butler *et al.* 1997). Despite these changes, there is still no understanding of what nutrient levels can be tolerated by the seagrass community, even though current water quality for the Gulf is less likely to affect seagrass health than historical levels. Any investigation of loss mechanisms may thus need to consider historical levels of nutrients, turbidity and salinity. Given that current losses are more likely due to sedimentation/turbidity and physical erosion triggered by initial seagrass loss and repeated recruitment failure, it may be that improvements in terrigenous inputs have little benefit for seagrass health. Rather there may be a need to discover more of what encourages seagrass recruitment/succession thereby slowing water movement and promoting sediment stabilisation.

There can be no hope of any large-scale seagrass recovery without removing or reducing the factors responsible for losses (Paling 1995 in Paling and van Keulen 2002). This in itself may take a prolonged period, with processes such as the leaching of nutrients from enriched sediments taking several years (Seddon 2002). Bryars and Neverauskas (2002) found a small level of natural re-establishment of *Posidonia* near the Port Adelaide wastewater treatment plant sludge outfall off Semaphore that was decommissioned in 1993. In the absence of secondary impacts such as excessive sand movements or sedimentation, amelioration of terrigenous inputs may thus have positive results without the need for intervention. However, it is more likely that large-scale recovery of seagrass meadows on the Adelaide coast will require assistance, either in the form of provision of appropriate settlement substrate for seedlings, transplanting of mature stock or the harvesting and planting of germinated seedlings (Seddon *et al.* 2004). The South

Australian seagrass restoration research and development program is a longer-term project that will run over at least nine years, working in collaboration with the Department of Environment and Heritage. At this point in time, there has been feasibility research looking at transplant of adult material (Seddon *et al.* 2004) and planting of germinated seedlings (Seddon *et al.* in press).

Natural seagrass losses are generally not permanent, as the causal factors (e.g. storms, floods, disease, or abnormal tides) are rarely prolonged (Seddon 2000), although there may be substantial alteration in species composition and abundance within a disturbed area. Seddon (2000) found that lost areas of *A. antarctica* and *P. australis* in the upper Spencer Gulf were readily colonised by species of *Zostera*, *Ruppia* and *Lepilaena*. The community that develops may thus be substantially different to that of the pre-disturbed state, owing to either the need for successional processes to run their course or that the disturbance instigated some alteration to some aspect of the system that prevents the re-establishment of some species. On the Adelaide coast, substantial levels of sand movement have altered depth regimes or exposed the underlying clay (Fotheringham 2002), both of which may prevent the recruitment of some, if not all seagrass species, irrespective of improvements to water quality and strategies aimed at increasing seagrass recovery. Even where it is possible, recovery of seagrass systems from either natural or anthropogenic disturbance is widely considered very slow (Kirkman 1998, Meehan and West 2000) especially for *Posidonia* species. Seagrass management thus requires a long-term perspective, although an immediate focus of both water quality changes and restoration strategies should be the prevention of further losses.

7. References

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