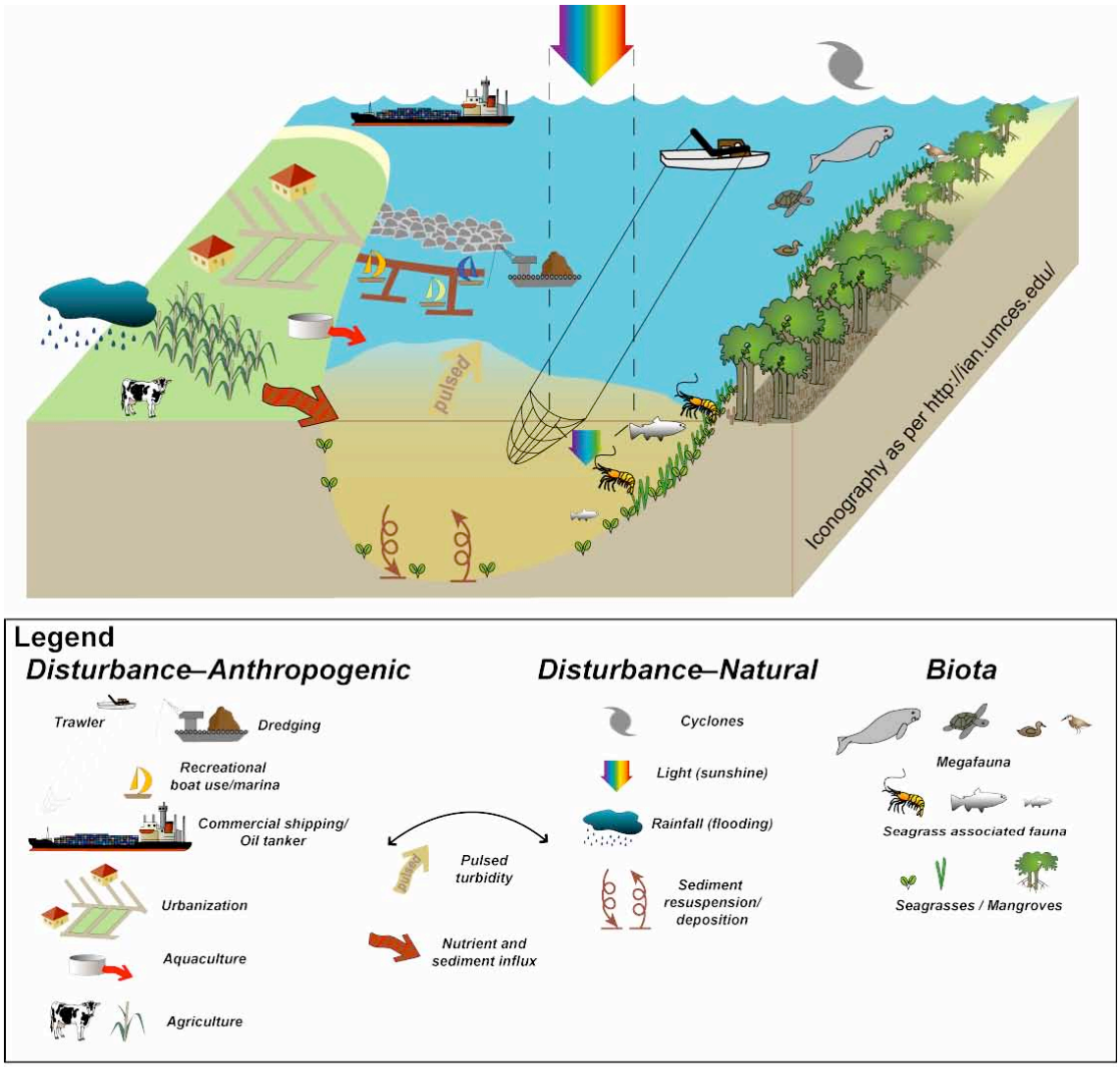
Chapter 1 General introduction



Conceptual diagram representing accepted causes of disturbance in seagrass meadows in the central region of the Great Barrier Reef World Heritage Area.

1.1 Seagrass biology

Seagrasses are angiosperms that have become adapted to life in the marine environment. They inhabit shallow coastal waters throughout the world, except at polar latitudes. The term seagrass is a functional grouping, not a taxonomic one. Evolutionary studies using DNA sequences have revealed that the present seagrass diversity arose from at least three separate lineages (Waycott and Les 1996, Les *et al.* 1997). Despite the group as a whole having different ancestries, they have evolved a set of common/convergent morphological and physiological characteristics (Walker *et al.* 1999). All species of seagrass are rhizomatous, clonal plants with their leaves and roots produced via rhizome extension, and have evolved mechanisms to reproduce in the marine environment (den Hartog 1970, Waycott and Les 1996, Les *et al.* 1997). Because they live in the marine environment and are angiosperms, seagrasses also require sufficient immersion in seawater, an adequate rooting substrate, and enough nutrients and illumination to maintain growth (Arber 1920). They also require an underwater irradiance generally in excess of 11% of that incident at the water surface, a requirement that typically sets their depth limit (Dennison and Alberte 1985). As a consequence of these shared biological characteristics it has been assumed that all seagrass meadows usually function in similar ways.

Seagrasses have been ranked as one of the most valuable ecosystems in the biosphere, due to the important ecosystem services they provide (Costanza *et al.* 1997). There are five major ecological functions attributed to seagrass meadows (McRoy and Helferrich 1977, Thayer *et al.* 1984, Fonseca 1985, Phillips and Meñez 1988, Larkum *et al.* 1989, Zieman and Zieman 1989, Duarte and Chiscano 1999):

> *(1)* ***High productivity and growth.*** *Seagrasses exhibit high net productivity and are amongst the most productive ecosystems in the biosphere;*
>
> *(2)* ***Food and trophic pathways.*** *Two trophic pathways have been recognized: (i) direct grazing of seagrass and organisms on the living plant material, and (ii) detrital pathways utilizing decaying seagrass material;*
>
> *(3)* ***Shelter.*** *Seagrass beds provide shelter and refuge for (i) the juveniles of a variety of finfish and shellfish of commercial and recreational importance, and (ii) resident and transient adult animals;*
>
> *(4)* ***Sediment Stabilization.*** *Seagrasses stabilize the sediments in two ways: (i) the leaves slow and retard current flow to reduce water velocity near the sediment-water interface promoting sedimentation of particles as well as*

inhibiting re-suspension of both organic and inorganic material and (ii) the roots and rhizomes form a complex interlocking matrix which binds the sediment and also inhibits re-suspension and retards erosion; and

(5) ***Nutrient Source.*** *The production of detritus and the promotion of sedimentation by the leaves of seagrasses provide organic matter for the sediments and maintain an active environment for nutrient recycling.*

These ecosystem functions have been attributed to seagrass meadows generally, even though they were based on studies of a few species of seagrass: *Zostera marina* in the north Atlantic, *Thalassia testudinum* in the Caribbean and *Posidonia oceanica* in the Mediterranean (McRoy and Helferrich 1977, Thayer *et al.* 1984, Phillips and Meñez 1988, Larkum *et al.* 1989, Zieman and Zieman 1989, Duarte and Chiscano 1999). This geographically and phylogenetically restricted interpretation has influenced our perspectives on seagrass ecology. This influence is still perpetuated, as most current literature is based on the study of seagrasses in the Caribbean, Mediterranean and the north Atlantic (Duarte 1999). Whilst the output of Australian seagrass studies has increased (Duarte 1999), most studies have been concentrated in temperate and sub-tropical regions and are focussed on species that are essentially structurally large. This thesis aims to redress this imbalance by focusing on structurally small seagrass species in the tropics.

1.2 Seagrass form and function

In keeping with general marine ecological concepts, seagrass species were historically classified according to their distribution, as either tropical or temperate. However, in recent years an alternative model for classifying seagrasses has been formulated that categorizes seagrass on the basis of growth form (Walker *et al.* 1999). Seagrass growth forms range from small plants with thin leaves (e.g. *Halophila, Halodule*) to large plants with thick leaves (e.g. *Thalassia, Enhalus, Posidonia*). Smaller growth forms may be able to take advantage of improved environmental conditions faster and more dramatically than larger seagrasses. Conversely, larger seagrasses survive longer under adverse environmental conditions than smaller seagrasses. For example, small seagrasses only survive periods of weeks when deprived of light (e.g. Preen *et al.* 1995, Longstaff and Dennison 1999), yet have the ability to recover rapidly from disturbance via seed banks where a healthy seed bank is available (Birch and Birch 1984, Inglis 2000, Mellors and Waycott unpublished data). In contrast, survival rates for extreme

light deprivation are longer for structurally large seagrasses (e.g. > 148 days for *Posidonia sinuosa* see Gordon *et al.* 1994) and recovery rates can be very slow (e.g. decades see West *et al.* 1989).

The hypothesized gradient from structurally small to large genera as described by Walker *et al*. (1999) in their model is presented in Figure 1.1 (all Figures and Tables are grouped together at the end of each chapter). I believe an extension of the gradient presented above will also be reflected in differences in the ecological functions of seagrass meadows. At present the ecological functioning of seagrass meadows is based on structurally large seagrass meadows that are persistent and of high biomass. This study will redress this imbalance by assessing the ecological functioning of small, ephemeral seagrass meadows of low biomass.

1.3 Queensland seagrasses

The coastline of Queensland is approximately 9800 km long covering tropical and subtropical regions (Fig. 1.2). A significant feature of the Queensland coast is the 2600 km long Great Barrier Reef (Hopley *et al.* 1991). While the Great Barrier Reef World Heritage Area is well known for its coral reefs, reefs actually only occupy six per cent of the area (Wachenfeld *et al.* 1998). Estuaries, lagoons, mangroves, salt marsh and seagrass habitats also occur in this region. An estimated 3000 km^2 of coastal seagrass habitats exist within the Great Barrier Reef World Heritage Area (Lee Long and Coles 1997, Carruthers *et al.* 2002). There are approximately 68 species of seagrass found globally (Les *et al*. 1997), of these 15 species have been recorded from Queensland waters (Lee Long *et al*. 2000). Small and diminutive species belonging to the genera *Halodule* and *Halophila* comprise the majority coastal inshore seagrass meadows within the central region of the Great Barrier Reef World Heritage Area (GBRWHA) (Lee Long *et al.* 1993). These meadows are significant as nursery areas for economically important fisheries (Coles *et al.* 1987, Coles *et al*. 1989, Poiner *et al.* 1989), and as a food resource for the threatened fauna *Dugong dugon* and the green turtle *Chelonia mydas* (Lanyon *et al.* 1989).

Coastal seagrass habitats in the region support both intertidal and subtidal seagrasses with intertidal meadows representing a significant resource. The dynamics of tropical seagrasses along the Queensland coast are heavily influenced by long term weather

patterns and occasional extreme flood and cyclone events resulting in stochastic and cyclic patterns of seagrass abundance (Birch and Birch 1984, Poiner *et al.* 1989, Lanyon and Marsh 1995, Preen *et al.* 1995, Waycott and Mellors, unpublished data) and therefore are significantly influenced by seasonal episodic coastal run-off (Bridges *et al.* 1982). Episodic terrigenous runoff events result in pulses of increased turbidity and nutrients and a zone of reduced salinity in nearshore waters. Consequently, these intertidal seagrass meadows act as an interface between terrestrial habitats and marine habitats, bringing them into contact with outputs from agricultural, industrial and urban areas. Hence their preference for the protected waters of estuaries, leeward margins of islands and north-facing bays along this coastline (Coles *et al.* 1989, Lee Long *et al.* 1993) makes them vulnerable to changing water quality.

Overseas and temperate Australian studies have shown that declining water quality can have an adverse affect on seagrass growth, distribution and morphology (Orth 1977, McComb *et al.* 1981, Kenworthy *et al.* 1982, Shepherd *et al.* 1989, Dennison *et al.* 1993, Short *et al.* 1996). Abal and Dennison (1996) predict that if the amplitude and frequency of anthropogenic disturbance bring greater sediment and associated nutrients into the inshore sections of the Great Barrier Reef region, detectable impacts on seagrass meadows may occur as have been observed in Moreton Bay, where it is estimated that 20% of seagrass areas have been lost since European settlement.

1.4 Disturbance and seagrass

Physical disturbances from waves or turbulence associated with strong storms (Birch and Birch 1984, Poiner *et al.* 1989, Preen *et al.* 1995) and anthropogenic impacts can adversely affect coastal seagrasses. Large scale disturbance such as damage from cyclones (hurricanes), can also lead to major seagrass losses (Poiner *et al.* 1989, Poiner and Peterken 1995, Preen *et al.* 1995). Smaller-scale disturbances, such as that caused by the motion of sand waves in and out of seagrass patches (Marba and Duarte 1995) or caused by large herbivores such as dugongs (Preen 1995) are also natural recurrent events that structure seagrass landscapes.

The most obvious source of human impact to seagrass ecosystems is physical disturbance, caused by human usage of the coastal zone for transportation, recreation and food production. Direct habitat destruction by land reclamation and port

construction is a major source of disturbance to seagrass meadows, due to dredging and landfill activities as well as the consequent reduction in water transparency. The construction of new ports is also associated with changes in sediment transport patterns involving both increased erosion and sediment accumulation along adjacent coasts (Duarte 1999). Such disturbances are now well recognized as a major source of change to seagrass ecosystems. These changes result from direct physical modification or indirectly through impacts on water quality including increased nutrient loads (leading to eutrophication) and increased sediment loads in environments that support seagrass (Short and Wyllie-Echeverria 1996). Thus, by virtue of their proximity to the coast, seagrasses receive the brunt of diverse forms of coastal pollution.

Eutrophication of the coastal zone/water body that seagrasses inhabit has been linked to seagrass loss on a global, regional and local scale (Walker and McComb 1992, Dennison *et al.* 1993, Short *et al.* 1996, Devlin 1999). Whilst the causes of seagrass losses are many, the most common cause observed to date has been the reduction of light availability from three major factors (Walker and McComb 1992):

i. Chronic increases in dissolved nutrients leading to proliferation of light absorbing algae, either phytoplankton, macroalgae or algal epiphytes on seagrass leaves and stems;

ii. chronic increases in suspended sediments leading to increased turbidity; and

iii. pulsed increases in suspended sediment and/or phytoplankton that cause a dramatic reduction of light penetration for a limited time.

Whilst all three of these factors are of concern to all habitats within the inshore waters of the Great Barrier Reef, opinion appears to be divided over the extent of the impact of these factors on inner reef habitats (see Bell 1991, Bell and Gabric 1991, Walker 1991, Bell and Elmetri 1995, Larcombe *et al.* 1996, Furnas 2003). At present we can only hypothesize, rather than predict the affect of such changes on the structurally small seagrass species that colonize the inshore intertidal seagrass meadows within the central region of the Great Barrier Reef World Heritage Area.

1.5 The effect of excess nutrients on seagrass

Because of their higher nutrient uptake rates, micro- and macro- algae respond to excess nutrients more rapidly than seagrasses (Shepherd *et al.* 1989). Thus, coastal eutrophication promotes phytoplankton biomass, reducing water transparency and stimulating the growth of epiphytes and opportunistic macro-algae, which further shade and decrease the light available to seagrasses (Hemminga and Duarte 2000). A consequence of the different nutrient uptake rates between algae and seagrass is that increased nutrient inputs can lead to a shift from nutrient limitation to light limitation for the seagrass (Sand-Jensen and Borum 1991). At the same time, increased pelagic primary production will result in a greater input of organic matter to the sediments, enhancing microbial activity and sediment oxygen deficit. These processes result in the deterioration of the sediment environment to support seagrass, as a consequence of reduced light availability. Other negative effects of eutrophication occur when high nitrate and ammonium concentrations are toxic to the seagrass plants themselves (e.g. Van Katwijk *et al.* 1997).

Research on the effects of eutrophication on seagrass meadows has focused on the effects of reduced light quality (Hemminga and Duarte 2000). Nonetheless, the deterioration of the sediment conditions may also play a critical role in enhancing the loss of seagrasses. Seagrass sediments are typically rich in organic materials due to enhanced particle deposition and trapping under seagrass canopies (Terrados and Duarte 1999, Gacia and Duarte 2001) compared to adjacent bare sediments. Microbial processes are therefore stimulated in the seagrass rhizosphere which, if sufficiently intense, leads to the depletion of anaerobic metabolism and release of by-products such as sulphide and methane, that may be toxic to seagrasses (Terrados *et al.* 1999). These concepts are primarily based on studies that have dealt with the loss of structurally large seagrasses in temperate regions (e.g. Shepherd *et al.* 1989, Hemminga and Duarte 2000). These systems tend to be detritus driven and are ‘closed’ systems with respect to nutrient cycling. Low biomass seagrass meadows of structurally small seagrass species (Walker *et al.* 1999) that are prevalent within the central region of the Great Barrier Reef World Heritage Area are predicted to be open systems with respect to nutrient cycling.

1.6 Nutrients in the Great Barrier Reef Lagoon (GBRL)

Sources of nutrients into the Great Barrier Reef Lagoon (GBRL: the body of water between the mainland and reefs) include terrestrial run-off, upwelled outer shelf waters, precipitation, resuspension of sediments caused by strong winds, inputs from atmospheric fixation by cyanobacteria and point source discharges (Walker and O'Donnell 1981, Wolanski *et al.* 1981a, Ullman and Sandstrom 1987, Cosser 1988, Baldwin *et al.* 1988, Bell 1991, Walker 1991, Hunter 1992a, Furnas and Mitchell 1997, Mitchell and Furnas 1997). Aquaculture ventures are another potential nutrient input source to the near shore zone (Linden 1990, Brodie 1995a).

Terrestrial inputs of nutrients may be introduced to the receiving coastal waters from either a point source or non-point/diffuse source. The biological significance of point rather than non-point/diffuse sources depends on location and the differences in quantities and form of the nutrient involved, areal loading characteristics, and temporal distribution of loading (Gabric and Bell 1993). For example, as a point source, sewage discharge has low biological significance in a regional context but is of high significance in a local context due to its high areal loading.

In terms of overall inputs to the GBRL, point sources like sewage are trivial, contributing 1% of the total discharge (Brodie 1995b). Diffuse sources, which contribute 85% of contamination are clearly dominant (Chittleborough 1983, Rasmussen 1990, Bell 1991, Walker 1991, Yellowlees 1991, Moss *et al.* 1992, Brodie *et al.* 1995, Furnas *et al.* 1995, Mitchell and Furnas 1997, Wasson 1997, Furnas 2003). Terrestrial run-off is mainly from catchments where agriculture (both grazing and sugar cultivation) is practised (Hunter and Rayment 1991, Yellowlees 1991, Moss *et al.*1992, Blake 1996, Furnas 2003*)*. Grazing is a bigger contributor of nutrients and sediments in river discharge (80%) than sugar cane cultivation (15%), by virtue of its being the dominant land-use in GBR catchments (Moss *et al.* 1992, Rayment and Neil 1997, Wasson 1997, Furnas 2003). Nutrients lost under sugar cane cultivation are derived from both natural soil nutrients and added fertilizer (Prove and Hicks 1991). In the case of grazing land, most nutrients are lost from soils, as distinct from added fertilizer (Brodie 1995a). The principal cause of this loss is the removal of natural vegetation and overgrazing, both of which increase erosion. It therefore becomes difficult to differentiate between the impacts of turbidity/sedimentation and excess nutrients on

nearshore habitats, because the principal source of nutrients, particularly phosphate, is sediment (Perez-Llorens *et al.* 1993).

Nutrients and sediments run off land under natural conditions, making detection of unnatural increases difficult to detect. Land-use has increased along the Queensland coast since European settlement (Pulsford 1991, Moss *et al.* 1992, Furnas 2003). This has resulted in higher rates of erosion (Arakel 1991, Hunter 1992b) associated with deforestation, over-grazing (Walker 1991, Gabric and Bell 1993) and large increases in fertilizer usage associated with expansions in crop cultivation (Brodie 1992, Brodie 1995a). The sediment load in this region is estimated to have increased by a factor of four since European-settlement (Moss *et al.* 1992, Brodie *et al.* 1995). In addition, there has been a huge increase in added nutrients. For example, the total amount of fertilizer applied to crops from European settlement to 1940 equalled the amount of fertilizer applied during 1990 (Pulsford 1991, Furnas 2003).

Rivers are the major conduit of nutrient and sediment input and thus have a profound influence on tropical coastal ecosystems (Birkeland 1987, Brodie 1992, 1995a, Furnas 2003). River flow in tropical Queensland is highly variable due to seasonal (wet vs dry), inter-annual and cyclone-related rainfall (Walker and O'Donnell 1981, Wolanski *et al.* 1981a, Furnas and Mitchell 1995, Mitchell and Furnas 1996, 1997). Superimposed on this variable flow are large regional differences between rivers of the Wet Tropics (the coastal belt between Paluma, north of Townsville to the Daintree north of Cairns) and those of the Wet-Dry Tropics (Townsville to Rockhampton) (Fig. 1.2).

The overall variability in discharge to the GBRL is largely driven by year to year differences in discharge from two of the rivers in the Wet-Dry Tropics; the Burdekin and Fitzroy, which drain the two largest catchments adjacent to the Great Barrier Reef (Hausler 1991, Brodie 1996, Woolfe *et al.* 1996, Mitchell and Furnas 1997, Wasson 1997, Furnas 2003). For example, in 1979, the Burdekin River flow was 28 times higher than in 1982 (Mitchell 1992). Considering such variability, it is not surprising that the bulk of sediment and peak nutrient inputs to the GBRL occurs during flood events, particularly the very large floods following cyclones and monsoonal rain depressions (Alongi 1988, Mitchell *et al.* 1991, Mitchell and Furnas 1996, 1997).

Flood events mobilise dissolved nutrients through ground water flow and the surface transport of dissolved and particulate nutrients via erosion and sheet flow (Mitchell 1992). Concentrations of dissolved nutrients show both positive (concentration) and negative (dilution) relationships with river flow, while levels of particle-associated nutrients show strong positive relationships with flow (Mitchell *et al.* 1991, Mitchell 1992, Hunter 1992b, Mitchell and Furnas 1993, Mitchell and Furnas 1996). Australian studies have shown that most nutrients are in particulate (sediment and nutrients) form and are mostly transported during flood events (Chittleborough 1983, Gabric and Bell 1993, Eyre 1993, 1994), reflecting an increase in surface flow erosion, and mobilisation of stream bed sediments (Mitchell *et al.* 1991, Mitchell 1992).

Dissolved and particulate nutrient concentrations are, in general, low through the Great Barrier Reef region. Latitudinally, the lowest mean concentrations of many nutrient species are observed in waters adjoining the remote north Cape York Peninsula, while the maximum concentrations are most commonly found in remote Torres Strait and in the more anthropogenically impacted central region of the Great Barrier Reef (16–20°S (Furnas and Mitchell 1995). Longitudinally, the distribution of dissolved nutrients and sediment is characterized by weak cross-shelf gradients, while concentrations of particulate species are consistently highest in the shallow (<20 m) nearshore band (Baldwin 1988, Arakel 1991, Pailles *et al.* 1993, Hamilton 1994, Furnas and Mitchell 1995, Furnas 2003). Particulate nutrients brought to the coast by rivers tend to stay nearshore (Belperio 1983a, b, Arakel 1991, Wolanski *et al.* 1981b, Hamilton 1994, Brodie 1995a, Wasson 1997, Furnas 2003) because:

i. sand is deposited at river mouths because of a drop in river velocity and further movement is halted by onshore wave action; and

ii. drift is predominantly northwards in response to prevailing south-easterly weather.

The south-easterly winds constrain the muddy plumes along the coast of northern Queensland (Fig. 1.3). The sediment from these plumes then settles out of the water column. Over geologic time, this phenomenon has resulted in the formation of a wedge of terrigenous sediment in the nearshore zone tapering over a distance of 10 km (Johnson and Carter 1988, Hopley *et al.* 1991, Carter *et al.* 1993, Larcombe and Woolfe

1996, Furnas 2003) (Fig. 1.3). Consequently, nearshore sediments are expected to be nutrient rich as the plumes act as a nutrient source.

While riverine flux may be episodic, the processes of sedimentation and regeneration/resuspension, even under moderate south-easterly winds, serve to distribute these biologically available nutrients throughout the year (Walker and O'Donnell 1981, Ullman and Sandstrom 1987, Baldwin 1988, Furnas 1988, Furnas and Mitchell 1997, Furnas 2003). Once in the water column, nutrients tend not to be dispersed, diluted or exchanged with Coral Sea waters because flushing of the Great Barrier Reef Lagoon is limited by the enclosure formed by the main reef (Wolanski 1994, Brodie *et al.* 1995, Furnas 2003). Consequently, residence time for nutrients in the lagoon, while not precisely known, may be prolonged (Wolanski 1994, Furnas 2003). The combination of increased nutrients reaching the lagoon and the possibility of accumulation within the lagoon as a result of poor circulation has led to concern about the impact of declining water quality on the maintenance of coastal ecosystems (Clark 1992, Hunter and Rayment 1991, Furnas 2003) and the vitality of coral reefs (Rasmussen 1988, Kinsey 1988a, b, Furnas 2003) within the Great Barrier Reef World Heritage Area.

The consequence of this highly variable local environment is that there are often dramatic differences between locations at fine spatial scales. Differences between years and even seasons may also be large. Thus, it is important to consider, this spatial and temporal variability when studying the seagrass communities of the region. Consequently, my thesis looks at patterns and processes within intertidal seagrass meadows within the Great Barrier Reef World Heritage Area, over meso-spatial scales (c. >550km) and fine temporal (intra-annual) scales.

1.7 Seagrass and nutrients

Seagrass meadows are usually nutrient limited (Duarte 1999). Thus increased nutrient inputs are expected to enhance seagrass primary production. As nutrients are seen both as limiting, and as the cause of significant seagrass declines, it is crucial that our understanding of the nutrient environment of seagrasses is improved. There is significant debate world wide as to whether seagrasses are nitrogen (N) or phosphorus (P) limited. This is considered to be dependent on the type of sediment that seagrass

inhabits. Short (1987) noted the importance of sediment geochemistry in seagrass beds in determining nutrient limitation of seagrass growth. He concluded that seagrasses growing in temperate, terrigenous environments are more typically nitrogen limited, whereas seagrasses occurring in tropical, carbonate environments generally experience phosphorus limitation. However, porewater nitrogen availability lower than 100 µM has been shown by Dennison *et al*. (1987) to be insufficient for seagrass growth (at least for *Zostera marina*). If this value is used as a baseline, many seagrasses around the world, do not meet this criterion on the basis of published porewater nutrient levels (Table 1.1). The 100 µM 'rule' must be imprecise at best. Phosphorus limitation for P is expected to occur in seagrass meadows when values for porewater P are below 10 µM (Erftemeijer *et al*. 1994). However, like N porewater levels observed in the literature, most of the studies record levels below this (Table 1.1). Nutrient levels are variable and critical levels not universal (Moody 1985). In Australia, recent studies have suggested that seagrasses are limited by N rather than P in a variety of locations and sediment types (Udy and Dennison 1996,1997a, b, Udy *et al.* 1999).

Determining if seagrasses are nutrient limited has been controversial. Early studies utilized the ratio of N:P based on phytoplankton bioassays. This 'Redfield ratio' (16:1::N:P) is inappropriate for seagrasses due to the increased complexity and structural carbohydrate composition of benthic plants compared with phytoplankton (Atkinson and Smith 1983). Atkinson and Smith (1983) devised a macrophyte ratio of 30:1 based on collections from around the world. This ratio included tissue nutrient concentrations from macroalgae as well as seagrasses. Then, Duarte (1990) using literature values from 1975 to 1990 calculated a global N:P ratio for seagrasses 24:1. Using this information, Duarte (1990) suggested tissue nutrient concentrations less than 1.8% for nitrogen (N) and 0.2% for phosphorus (P) implied nutrient limitation to seagrass growth. A comparison of tissue nutrient contents from the literature (Table 1.2) indicate that most Australian seagrasses are nutrient limited, that is they have a N:P ratio less that 24:1.

The only true test of nutrient limitation is to conduct fertilization experiments and see if the seagrasses respond to increases in sediment nutrients (Bulthius and Woelkerling 1981, Perez *et al*. 1991, Fourqurean *et al*. 1992, Erftemeijer *et al*. 1994, Udy and Dennison 1996, 1997a, b, Udy *et al*. 1999). Consequently, I evaluated the response of

Halophila ovalis from two locations, to different levels of N and P fertilizer, at different times of the year to assess nutrient limitation in this region.

1.8 Thesis aims and outline

Along the coastline of the Great Barrier Reef Lagoon, inshore seagrass beds have recruited, grown and evolved in the presence of dynamic freshwater, terrestrial nutrient and sediment inputs (Blake 1996, Brodie 1996). Seagrass meadows in this region are characterized by structurally small species that are low in biomass, ephemeral, short lived, and recruit from seed banks as predicted by the model of Walker *et al.* (1999). As much of the our knowledge on seagrass ecology has been learned by studying structurally large species from the North Atlantic, Mediterranean or Caribbean regions (Duarte 1999), there is a need to re-evaluate the way in which seagrass meadows function in this very different part of the world. In this thesis, I aim to contribute to a deeper understanding of the ways in which structurally small seagrasses interact with their geochemical environment. This will provide valuable information for building a more comprehensive model of seagrass form and function. Given the extent and value (economically and ecologically) of inshore seagrass meadows in the Great Barrier Reef World Heritage Area this study will also aid in defining the overall ecosystem services these meadows of structurally small seagrasses provide.

This thesis, entitled ‘Sediment and nutrient dynamics in coastal intertidal seagrass of north eastern tropical Australia’ is comprised of five main chapters, with two chapters (4 and 5) containing significant subchapter structure to facilitate the presentation of complex datasets.

In this chapter, I have described the general biology and the ecological functions of seagrass meadows and set them in context of structurally large and small seagrasses within the definition of the Seagrass Function and Form Model (Walker *et al.* 1999). I then presented an overview of the sources and impacts of nutrient and sediment based disturbance on seagrasses of this region.

I outline the methodologies common to all aspects of this thesis (Chapter 2) and present a detailed site description and inventory of the species of seagrass and the physical, chemical and biological status of the intertidal meadows (Chapter 3). Chapter 3 also discusses the possibility of nutrient limitation of seagrasses within the central region of

the Great Barrier Reef World Heritage Area based on critical levels and molar ratios of the sediment and seagrass nutrients. In Chapter 4, I reassess the attributes that have become universally ascribed to seagrasses in the literature in three subchapters. Firstly, I investigate the nutrient status and sediment trapping paradigm for these tropical intertidal seagrass meadows within the central region of the Great Barrier Reef World Heritage Area. I do this by comparing nutrient status and sediment structures between seagrass-vegetated areas that were low in biomass, and comprised of structurally small species and adjacent non-vegetated intertidal areas (Subchapter 4.1). The outcomes from Subchapter 4.1 made me question the relevance of three commonly held concepts in relation to sediment trapping within seagrass meadows. These concepts were evaluated for each of the different species and was important for understanding ecological processes within these intertidal seagrass meadows of structurally small species encountered within the central region of the Great Barrier Reef World Heritage Area (Subchapter 4.2). As the preceding two subchapters represented static measures of these meadows (i.e. samples collected at one time of the year), I also required a perspective on the intra-annual dynamics of these meadows in this region. To gain this insight, I investigated the intra-annual variability in growth rates, sediment nutrient status, plant nutrient status and biomass accumulation within two seagrass meadows of *Halophila ovalis* in my study region (Subchapter 4.3).

The final data chapter (Chapter 5) addresses, through experimentation, the responses of sediment, biomass and tissue nutrients of *Halophila ovalis* meadows to nutrient addition. The response of this structurally small seagrass, was tested at different times of the year to varying levels of N, P and N+P enrichment at locations with different sedimentary regimes (mineralogy, sediment nutrients, sediment grain size (Chapter 5)). The experimental site and the methodologies common to all sections of this study, including the experimental design, statistical analyses, the behaviour of Osmocote® in the marine environment are presented in Subchapter 5.0. The different sedimentary regimes (mineral composition and sediment particle size) of the experimental plots (sites within meadows) at the bay scale (between locations), within bay scale (different times of year), the block scale and at the treatment level are assessed (Subchapter 5.1). The responses of the ambient sediment nutrients (porewater and adsorbed) at the two locations (with dissimilar sedimentary regimes) to varying amounts and combinations of N and P Osmocote® at different times of the year are evaluated (Subchapter 5.2) and

the response of *Halophila ovalis* within these meadows to the changed sediment nutrient status is investigated (Subchapter 5.3).

The last chapter (Chapter 6) summarizes and synthesizes the results of my thesis and lists the significant findings of the entire study. It places these results in context and provides comment on the future direction of research and management of these low biomass meadows of structurally small seagrass species that are ecologically and economically important in this region of the Great Barrier Reef World Heritage Area.

A short note on the presentation of this thesis: figures and tables are placed at the end of each chapter and subchapter in which they are first referred. They are separated from the main text by coloured leaves of paper for ease of location. Finally, all coloured graphics are only printed on one side of the page.

Figure 1.1 Seagrass functional form model depicting the existing seagrass genera along a continuum from structurally small seagrass to structurally large species including their hypothesized distribution, ecophysiology and ecological interactions (Walker *et al*. 1999).

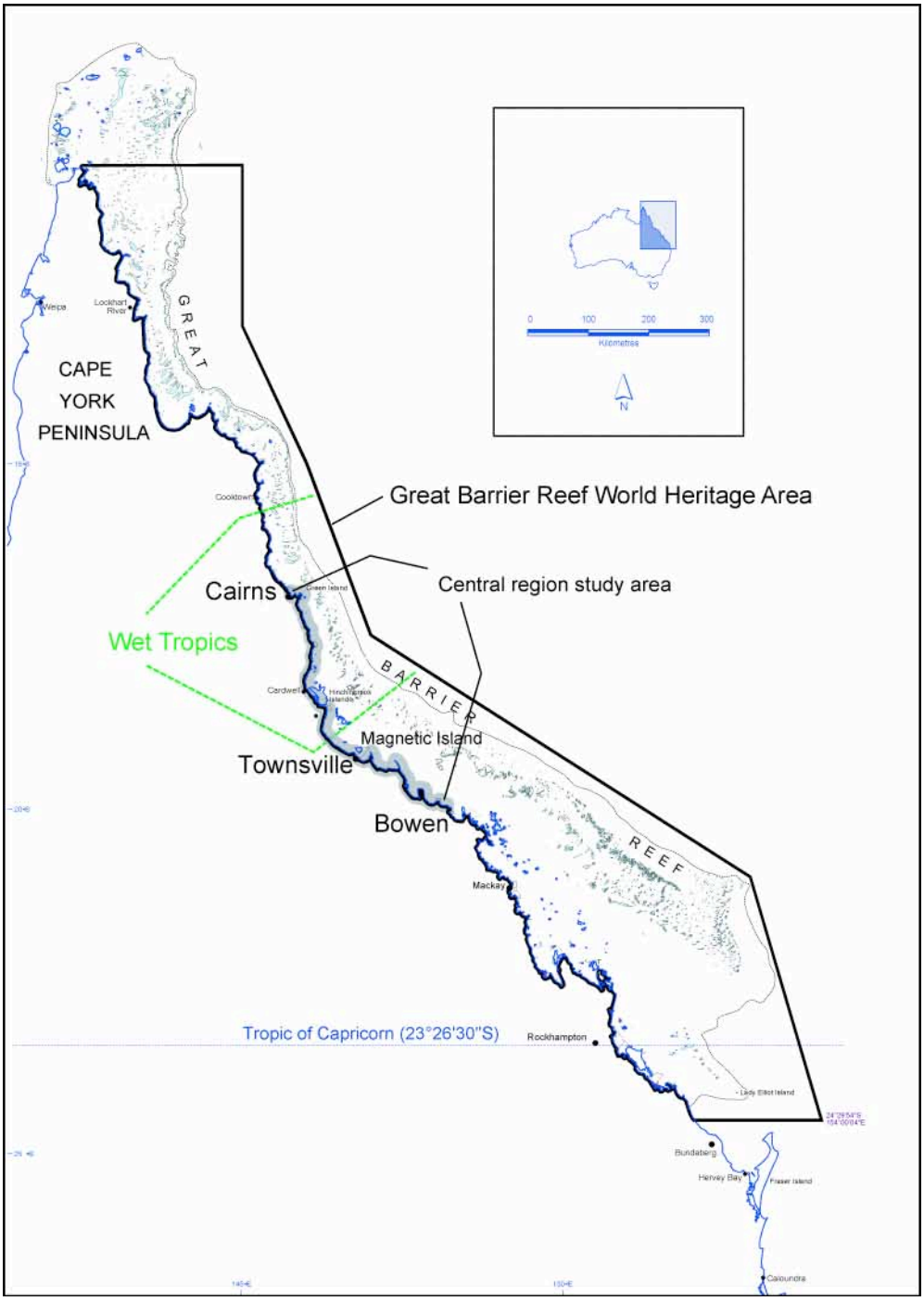


Figure 1.2 A map of Queensland showing the delineation of the Great Barrier Reef World Heritage Area, the location of the Great Barrier Reef and the extent of the Great Barrier Reef Lagoon (Source: www.reefed.edu.au).

Figure 1.3 A conceptual model of the interactions between wind stress, wind-driven coastal currents, the inner lagoon, frontal zone (the zone characterized by the depth limit of wind driven resuspension and cross-shelf distribution of terrigenous sediments that constrain and produce the nutrient rich sediment layer within the inshore region of the Great Barrier Reef Lagoon (redrawn from Furnas 2003).

Table 1.1 Values for porewater nutrients in seagrass beds around the world.

Location	Sediment type	Seagrass species	Porewater nutrients		Source
			NH_4^+ (µM)	PO_4^{3-} (µM)	
Tropical/subtropical					
Alfacs Bay, Spain	terrigenous	*Cymodocea nodosa*	200–400	4–30	Perez *et al.* 1994
Green Island, N Qld Aust	carbonate	*Halodule uninervis (w)* *Cymodocea serrulata*	5.6	1.3	Udy and Dennison 1996
Moreton Bay, SE Qld, Aust	terrigenous	*Halodule uninervis (w)*	7.1	4.7	Udy and Dennison 1996
S. Sulawesi, Indonesia	carbonate	*Thalassia hemprichii* *Enhalus acoroides*	38.8–117.6	4.1–13.1	Erftemeijer 1994
S. Sulawesi, Indonesia	terrigenous	*Thalassia hemprichi* *Syringodium isoetifolium* *Cymodocea serrulata*	19.2–27.l	7.7–10.1	Erftemeijer 1994
S. Sulawesi, Indonesia	terrigenous	*Enhalus acoroides*	44.8–88.4	2.9–8.7	Erftemeijer 1994
San Salvador Is, Bahamas	carbonate	*Syringodium filiforme*	100	2	Short *et al.* 1985
Moreton Bay, SE Qld Aust	terrigenous	*Zostera capricorni* *Cymodocea serrulata*	15–60		Boon 1986
Florida, USA	carbonate	*Halodule wrightii* *Thalassia testudinum*	98–160	0.5–3	Fourqurean *et al.* 1992
Florida, USA	carbonate	*Thalssia testudinum* *Halodule wrightii*	191	0.8	Powell *et al.* 1989
Texas, USA	terrigenous	*Halodule wrightii*	100–350	10–20	Pulich 1985
Temperate					
Western Port Bay, SE Aust	terrigenous	*Heterozostera tasmanica*	200–1700	3–60	Bulthius & Woelkerling 1981
Port Phillip Bay responded to enrichment	terrigenous	*Heterozostera tasmanica*	11–19	6–8	Bulthius *et al.* 1984
Massachchusetts, USA	terrigenous	*Zostera marina*		75	McRoy *et al.* 1972
Alaska, USA	terrigenous	*Zostera marina*	30–130	6–25	Short 1983
Massachusetts, USA	terrigenous	*Zostera marina*	180–300	-	Dennison *et al.* 1987
NE Japan	terrigenous		300		Iizumi and Hattori 1982

Table 1.2 Values of seagrass tissue nutrients for leaf, rhizome and root taken from the literature (ambient values only used).

	Species	Location	%N	%P	$N:P_{(atomic)}$	Source
Leaf	*Halophila ovalis*	Cockle Bay, MI, N Qld, Aust	0.72	0.16	10:1	Birch 1975 (combined data)
	Halophila ovalis	Townsville , N Qld, Aust	1.57	-	-	Lanyon 1991
	Halophila ovalis	global average n = 2	0.7	0.18	9:1	from Duarte 1990
	Zostera marina	various USA	1.8–4.5	0.33–0.45	12–30	Thayer *et al.* 1984
	Syringodium filiforme	San Salvador, Bahamas	1.29	0.061	47:1	Short *et al.* 1985
	Syringodium isoetifolium	Green Island, N Qld, Aust	1.6	0.21	17:1	Udy *et al.* 1999
	Zostera capricorni	global average n= 7	1.5	0.26	13:1	from Duarte 1990
	Zostera capricorni	Moreton Bay, SE Qld, Aust	1.6	0.2	18:1	Udy and Dennison 1997b
	Halodule uninervis	Green Island, N Qld, Aust	2.4	0.26	20:1	Udy *et al.* 1999
	Halodule uninervis	Moreton Bay, SE Qld, Aust	2.4	0.24	22:1	Udy and Dennison 1997b
	Halodule uninervis	Magnetic Island, N Qld, Aust	0.92	0.15	14:1	Birch 1975
	Halodule uninervis	Townsville, N Qld, Aust	1.91	-	-	Lanyon, 1991
	Halodule uninervis	global average n = 15	2.4	0.19	27:1	from Duarte 1990
	Cymodcea nodosa	Spain	1.9–2.3	0.11–0.14	38–39:1	Perez *et al.* 1991
Rhizome	*Zostera capricorni*	Moreton Bay, SE Qld, Aust	0.43	0.07	14:1	Udy and Dennison 1997b
	Syringodium isoetifolium	Green Island, N Qld, Aust	0.9	0.23		Udy *et al.* 1999
	Syringodium filiforme	San Salvador, Bahamas	0.59	0.27	49:1	Short *et al.* 1985
	Halodule uninervis	Magnetic Island N Qld, Aust	1.14	0.18	14:1	Birch 1975
	Halodule uninervis	Moreton Bay, SE Qld, Aust	0.56	0.08	15:1	Udy and Dennison 1997b
	Halodule uninervis	Green Island, N Qld, Aust	0.5	0.11	22:1	Udy *et al.* 1999
Roots	*Halodule uninervis*	Moreton Bay SE Qld, Aust	1.2	0.11	24:1	Udy and Dennison 1997b
	Zostera capricorni	Moreton Bay, SE Qld, Aust	0.99	0.08	27:1	Udy and Dennison 1997b
	Halodule uninervis	Green Island, N Qld, Aust	1.3	0.14	21:1	Udy *et al.* 1999
	Syringodium filiforme	San Salvador, Bahamas		0.27	49:1	Short *et al.* 1985

Chapter 2 General materials and methods

Summary

This chapter describes the general methodology that is common to all aspects of this thesis. It details the sampling equipment, the samples collected, the parameters derived from these samples and the techniques used to extract and determine nutrients from the sediments and plant tissues.

Each porewater sample provided data on dissolved inorganic NH_4^+, NO_2^- + NO_3^- and PO_4^{3-}. Sediment cores provided data on adsorbed NH_4^+ and adsorbed PO_4^{3-}. Information on adsorbed PO_4^{3-} was duplicated for each core because of the different techniques (Bray and bicarbonate methods) used to extract this nutrient. Supplementary sediment cores were taken to provide information on sediment grain size, particle size density and porosity, percent vegetative matter and percent carbonate matter. Eh and pH measurements were also taken to characterize the sedimentary environment. Each quadrat of excavated seagrass generated data on epiphytic algae, leaf, rhizome, root, total biomass and shoot density. These seagrass samples also produced data on the tissue nutrient contents in relation to N and P for leaves, rhizome, roots, whole plant and plant nutrient state on a per metre square basis. Replication of samples varied according to the investigation being undertaken.

2.1 Introduction

This chapter describes the general methodology that is common to all aspects of this thesis. It details the sampling equipment, the parameters sampled and techniques used to extract and determine nutrients from the sediments and plant tissue. Methods or techniques that were specific to a certain aspect of the study are described in the material and methods section of the relevant chapter (e.g. plant growth parameters–Subchapter 4.3 and mineralogy–Subchapter 5.1). Due to multiple cross-referencing of tables and figures within the text of the chapters, the tables and figures are numbered consecutively for each chapter but as previously mentioned have been placed separately (i.e. a section for figures and a section for tables) the end of the relevant Subchapter. For example Figure 4.2 is located at the end of Subchapter 4.1, while Figure 4.5 is located at the end of Subchapter 4.2. I considered that this method of placement and numbering of tables and figures would: a) facilitate reading of the text, and b) ease confusion with respect to numbering of sections within subchapters.

2.2 Sampling

My sampling was restricted to relatively homogenous seagrass-covered areas. Three elements of the seagrass environment were sampled routinely throughout this study: (1) the nutrient environment including sediment nutrients and those parameters that have an effect on the chemistry of the sediments; (2) sediment structure, those parameters that pertain to sediment grain size and (3) the seagrasses themselves, i.e. biomass, shoot density and plant tissue nutrients.

Sediments provide the primary source of nutrients for seagrass growth (Iizumi and Hattori 1982, Short 1983, Short and McRoy 1984, Brix and Lyngby 1985, Boon 1986, Short 1987, Moriarty and Boon 1989, Fourqurean *et al.* 1992, Udy and Dennsion 1996). Determination of the nutrient status of a rhizosphere (the volume of sediment seagrass rhizomes and roots reside), therefore requires sampling the porewater (the water contained within the spaces between sediment grain particles) for dissolved nutrients, and the sediments for adsorbed exchangeable nutrients. The adsorbed nutrients are held on the electrically charged surfaces of the sediment. The remainder of the nutrient pool is dissolved in the porewater and is in dynamic equilibrium with nutrients held

electrostatically. Plant uptake or water movement depletes nutrients in the porewaters. The nutrients attached to sediment particles then move into the porewaters as a result of this nutrient depletion in the porewaters. This is known as nutrient exchange (Baker and Eldershaw 1993).

Determining the chemical environment of sediments

Nutrients

As explained above, the sediment nutrient pool is comprised of porewater nutrients and adsorbed/exchangeable nutrients. Two sampling techniques were used to sample the different nutrient pools. From these samples the different forms of nutrients were chemically determined (Fig. 2.1).

Porewater

Sample collection

Sediment porewater was collected *in situ* using sediment sippers (modified from Murray *et al.* 1992, Udy and Dennison 1996). The *in situ* sipper was a two-stage vacuum filtration device. It was made of an external perforated PVC pipe with an inner 10 µm mesh screen. The top of the sipper was connected to a micro-pore filter (0.45 µm) held in place within a filter holder. The top of the filter holder was connected to a 50 mL central aperture syringe, via a 3 cm length of catheter (Fig. 2.2). The sipper was placed in the sediment and a vacuum created by pulling up the syringe plunger (Fig. 2.3). This vacuum caused the porewater to be pulled through the first stage of filtration (sipper) and then through the micropore filter into the syringe. The sample was then transferred to sterilized 10 mL vials and sealed, and placed on dry ice in the field to minimize further chemical transformation and microbial activity. Sippers were made to two different lengths (10 cm and 2.5 cm) to incorporate the dissimilar rhizosphere depths associated with the different seagrass species and locations. Sipper samples were assumed to be a depth integrated sample of the rhizosphere.

Chemical determination of dissolved inorganic nutrients

Porewater samples were analysed for dissolved inorganic nutrients, ammonium, and nitrite + nitrate and phosphate using a Skalar segmented flow auto-analyser, using standard water quality techniques (Strickland and Parsons 1972, Ryle *et al.* 1981).

Sediment

Sample collection

Hypodermic syringes (50 mL) with their ends removed, were pushed to the depth of the rhizosphere at each location and the core was removed from the sediment and the syringe stoppered. Samples to be analysed for exchangeable inorganic nutrients were placed on ice then refrigerated until they could be analysed. This collection method was also used for acquiring samples for the analyses of sediment grain size, porosity, and per cent carbonate and organic content.

Nutrient extraction and chemical determination of adsorbed exchangeable nutrients

Sediment samples were analysed for extractable inorganic ammonium, and phosphate. Cores were homogenized to provide a depth-integrated sample. Adsorbed exchangeable ammonium was extracted using KCl (Rayment and Higginson 1993) and chemically determined using methodologies outlined in Strickland and Parsons (1972).

Two techniques were used to extract phosphate: the Bray method (Bray and Kurtz 1945, Rayment and Higginson 1993) hereafter referred to as ‘Bray’ and the Olsen/Colwell/Bicarbonate method (Mengel and Kirkby 1987, Rayment and Higginson 1993), hereafter referred to as ‘bicarbonate’. The Bray technique tends to extract phosphate incompletely in an alkaline environment due to the presence of calcium carbonate (Pailles and Moody 1995). The bicarbonate method is not affected by pH and is more appropriate for alkaline soils pH>7.8 (Baker and Eldershaw 1993). Both techniques were used in an attempt to determine which is a better measure of biologically available phosphate. The chemical determination for the extracted phosphate is based on the method of Murphy and Riley (in Rayment and Higginson 1993).

Nutrient related chemical parameters

Redox potential (Eh) and pH

Redox potential (Eh) in soils is generally measured using a platinum electrode against a reference electrode and is expressed in terms of voltage. A low potential is indicative of a high reducing power or a surplus of electrons, whereas a high redox potential indicates

a lack of electrons and low reducing power. Conversely, these measures are also used to indicate the oxidation state of sediment. In the presence of O_2, rather high potentials result (Friedman 1978).

The uptake of various plant nutrients is pH dependent. Generally anions including nitrate and phosphate are taken up at a higher rate in the weak acid pH range. Phosphate availability and therefore uptake by plants is lessened between pH 7.5–8.5 and ceases at a pH 9 (Friedman 1978). Eh and pH were measured *in situ* to characterize the chemical environment of the rhizosphere by placing probes in the sediment in the general area of where the other sampling occurred. The probes were left in the sediment to equilibrate prior to each reading as Eh measurements are particularly sensitive to physical disturbance of the sediment profile.

Calcium carbonate and organic content

Sediment samples were prepared for analysis by air-drying for at least 48 hrs. They were homogenized in a Bowl Pulveriser prior to calcium carbonate and organic content determination. The calcium carbonate from any biological source (e.g. shells or diatoms) and any large plant parts were included in the analyses. The samples were then analysed for percent carbonate using a weight loss method involving hydrochloric acid (Blakemore *et al.* 1987). Percent organic content was determined using a weight loss method by ignition (Gale and Hoare 1991).

Determining the physical environment of the rhizosphere

Sediment grain size analysis

The relative proportions of particles of various sizes determine the texture of a given sediment. This sediment property is important to the physical behaviour of the sediment. In addition, it is also very closely related to nutrient status and nutrient availability since many plant nutrients such as K^+ Mg^+ and PO_4^{3-} are largely present in the clay fraction (Freidman 1978).

The particle size distribution of each sediment sample was determined by laser analysis using a Malvern Mastersizer X. The advantage of using laser diffraction is that it allows a quick analysis of a large number of samples with excellent precision. The grain size output derived by laser diffraction was then collated into particle size categories and

subcategories according to the scheme of Udden and Wentworth (Gale and Hoare 1991).

Particle size density

The density of sediment particle sizes is required for the calculation of porosity. Replicate samples (3) of saturated sediment cores were collected at each site at the time of nutrient sampling. Cores were collected in 'cut-off' 50 mL syringes and rubber stoppered, as previously described in the section on sample collection. I was careful not to compress the core. The volume of each core was measured from the syringe gradations. The intact syringe was weighed (g), dried in an oven (80°C, 48 h) and then reweighed to determine weight loss. Particle size density (p_s) was calculated using the following equation.

Equation 1:

P_s = (Dry sample wt - Syringe weight)/(Volume - ((Wet sample wt - Dry sample wt)/d_w)))
Where d_w = specific gravity of water = 1.025

Porosity

Porosity (as determined by Equation 2) results from the sediment particles not occupying all the possible space. It is therefore the measure of the volume of void space to the total volume of sediment and is dependent on grain size (Folk 1974, Freidman 1978).The void spaces or pores accommodate fluids, generally water. As explained above this fluid is known as porewater and is the site for dissolved nutrients. Whilst analyses of porewater and adsorbed nutrients in isolation of each other can be achieved using their own units (µmol L^{-1} and µmol kg^{-1} respectively), any comparison of these two nutrient pools require the units to being converted to µmol $L_{sediment}^{-1}$. This conversion is accomplished using the measure of porosity as per equations 3 and 4. With the nutrient concentrations in similar units, ratios of adsorbed-nutrients to porewater nutrients were constructed for each location and used as a descriptor for each location (see inventory of biogeochemical parameters Chapter 3).

Equation 2:

ϕ (porosity) = (H/1.025)/(H/1.025 + ((1-H)/p_s))

where H = proportion of water - (wet weight - dry weight)/ wet weight

and P_s = particle size density

Equation 3:

Porewater nutrients (µmol $L_{sediment}^{-1}$) = µmol L^{-1} x □

Equation 4:

Adsorbed nutrients (µmol $L_{sediment}^{-1}$) = µmol kg^{-1} x p_s x (1- □)

Determination of seagrass parameters

Plant production

Biomass

Seagrass samples excavated from 0.25 m^{-2} quadrats (0.5 m x 0.5 m) were rinsed initially in seawater then in tap water. In the laboratory, leaves, rhizomes and roots were separated. Epiphytic algae were physically removed from each component of the plant. Samples were oven dried at 60°C, to a constant weight.

Shoot density

While the biomass samples were still wet, a sub sample was taken and every shoot in the sub-sample was counted and then multiplied up for the entire sample so that a density measurement of the quadrat could be reported. This occurred for each investigation except during the enhancement experiment (Chapter 5) where every shoot within the quadrat was counted.

Plant tissue analysis

Dried biomass samples of leaves, rhizomes and roots were separately homogenized by milling to a fine powder. Nitrogen and phosphorus were extracted using a standardized selenium Kjeldahl digest and the concentrations determined with an automatic analyser using standard techniques (Strickland and Parsons 1972). N:P ratios were calculated using atomic weights. The nutrient state of a meadow was characterized by $gN_{seagrass}$ m^{-2} and $gP_{seagrass}$ m^{-2} as calculated by equation 5:

Equation 5:

% plant tissue nutrient x biomass (g DW m^{-2}) = g $Nutrient_{seagrass}$ m^{-2}

2.3 Experimental design

Experimental design varied for each aspect of this study. Therefore the experimental design pertinent to each investigation is described within the relevant subchapters.

2.4 Statistical methods

Statistical methods used in each investigation are described in the relevant chapter. The statistical packages used throughout this thesis were SPSS 10 (SPSS Inc.) and GenStat 5 (VSN International Ltd.). Below is a description of the 28 parameters that were collected during each sampling trip and how the variables were arranged for statistical analyses. The number of replicates for each parameter varied according to the investigation.

Data sets

Throughout this thesis unless stated otherwise N refers to nitrogen, P to phosphorus, NH_4^+ to ammonium, PO_4^{3-} to phosphate and $NO_2^- + NO_3^-$ to nitrite and nitrate.

Variables were grouped into the following data sets: chemical, physical, plant abundance and plant tissue nutrient content (Table 2.1). The sediment structure data set consisted of variables that describe the physical environment of the rhizosphere, sediment grain size classes and porosity (Table 2.1). The data set of sediment nutrients and associated chemically-derived parameters consisted of extracted nutrients, porewater nutrients and chemically derived-variables assumed to influence the chemical environment of the rhizosphere. The plant parameter data set included biomass measurements of leaves, rhizomes, roots, total (leaves, rhizomes, roots combined) and leaf density. The plant tissue data set consisted of the percent total N and total P content of each of the plant components.

Data transformation and outlying data

I examined residual plots to determine whether the data required transforming to homogenize the variance. A $\log_{10}$ transformation was used if required to satisfy the assumptions of MANOVA and ANOVA which in general are relatively robust to slight deviations from assumptions (Tabachnick and Fidell 1989).

Data points greater than two standard deviations from the mean were removed from the data sets and the analysis rerun. All outcomes from these reruns were the same as the original analyses, indicating that these divergent data points were not influencing the analyses and required no further consideration.

2.5 Study sites

Study area

The study area was within the central part of the Great Barrier Reef Lagoon between Cairns and Bowen (Figure 2.4). In this region, continental islands are common and the coast is characterized by many headlands and bays facing north and north-east. These bays are sheltered from the southeast trade winds (Coles *et al.* 1989, Morrissette 1992). Sediments in these bays are mud and sand (Maxwell 1968). Between Cairns and Ingham (the Wet Tropics), there are many continuous flowing rivers, which originate from the rainforest–covered Great Dividing Range. Between Ingham and Bowen (the Wet–Dry Tropics) rivers are less common and their flow is generally associated with monsoon rain events. The coastal plain south of Ingham is wider and drier than to the north.

Winds are predominantly south-easterly trades, strongest during winter, weaker and with a north-easterly element during the summer months (Maxwell 1968, Brandon 1973). The coast is protected against oceanic swells by the complex reefs and shoals of the Great Barrier Reef system. Tides in this region are semi-diurnal and tidal amplitude varies between a minimum of 2.7 m near Cairns and a maximum of 3.3 m near Bowen. The spring low tides occur during daylight hours in the winter months. The pattern reverses during the summer months. Rainfall is extremely seasonal, with a well-defined wet and dry season in this region and large variations between years. Along this coastline, rainfall during the wet season can vary from a minimum monthly total of 1015 mm at Bowen, to a maximum monthly total of 3813 mm at Innisfail (Bureau of Meteorology, http://www.bom.gov.au/). Cyclones are another feature of this region. At least one or sometimes as many as three cyclones typically affect this region each year, usually during January, February and March, but have been recorded in December and April (Brandon 1973, Puotinen *et al.* 1997). In addition to cyclones, there are on average, a number of tropical depressions, which are similar in type and frequencies to cyclones but less violent (Brandon 1973). Consequently, the pattern of night time low

tides and rainfall events that occur during the summer months and the pattern of day time low tides and strong south easterly winds that occur during the winter months means that seagrasses in this region are subjected and expected to be acclimatized to nutrient pulses and high turbidity.

Site selection

I conducted an aerial survey of the shoreline of the Central Section of the Great Barrier Reef Marine Park (GBRMP) between Bowen and Clump Point at a spring low tide in July 1992. The more substantive intertidal seagrass beds in this region were easily visible from a height of 150 m. The aerial survey provided insights into the position and accessibility of intertidal seagrass beds that could be examined during the broad spatial scale investigations (Chapter 3, and Subchapter 4.1, 4.3). I then selected ten locations as possible sites (Table 2.2, Figure 2 4). Another location, Ellie Point, Cairns (Figure 2.4) was added prior to sampling in July 1994. This location was included as a duplicate to Windy Point, Upstart Bay, as dense beds of *Zostera capricorni* characterize both these locations. This extended my study area into the Cairns Section of the GBRMP. In this thesis, this study area, from Cairns to Bowen will be referred to as the central region of the Great Barrier Reef World Heritge Area.

At many locations, the entire seagrass meadow was multi-specific with single species arranged in monospecific stands. I sampled within the monospecific stands of the dominant seagrass species within each location. Thus for the purposes of this study, each location was characterized by a dominant species of seagrass as summarized in Table 2.2. My study area spanned approximately 556 km of coastline, with the majority of locations in close proximity to Townsville (Figure 2.4).

Figure 2.1 Schematic diagram of the sampling equipment used for the relevant parts of the nutrient pool and the nutrients determined and extracted from the porewater nutrient pool and the adsorbed nutrient pool (modified from Udy and Dennison 1996).

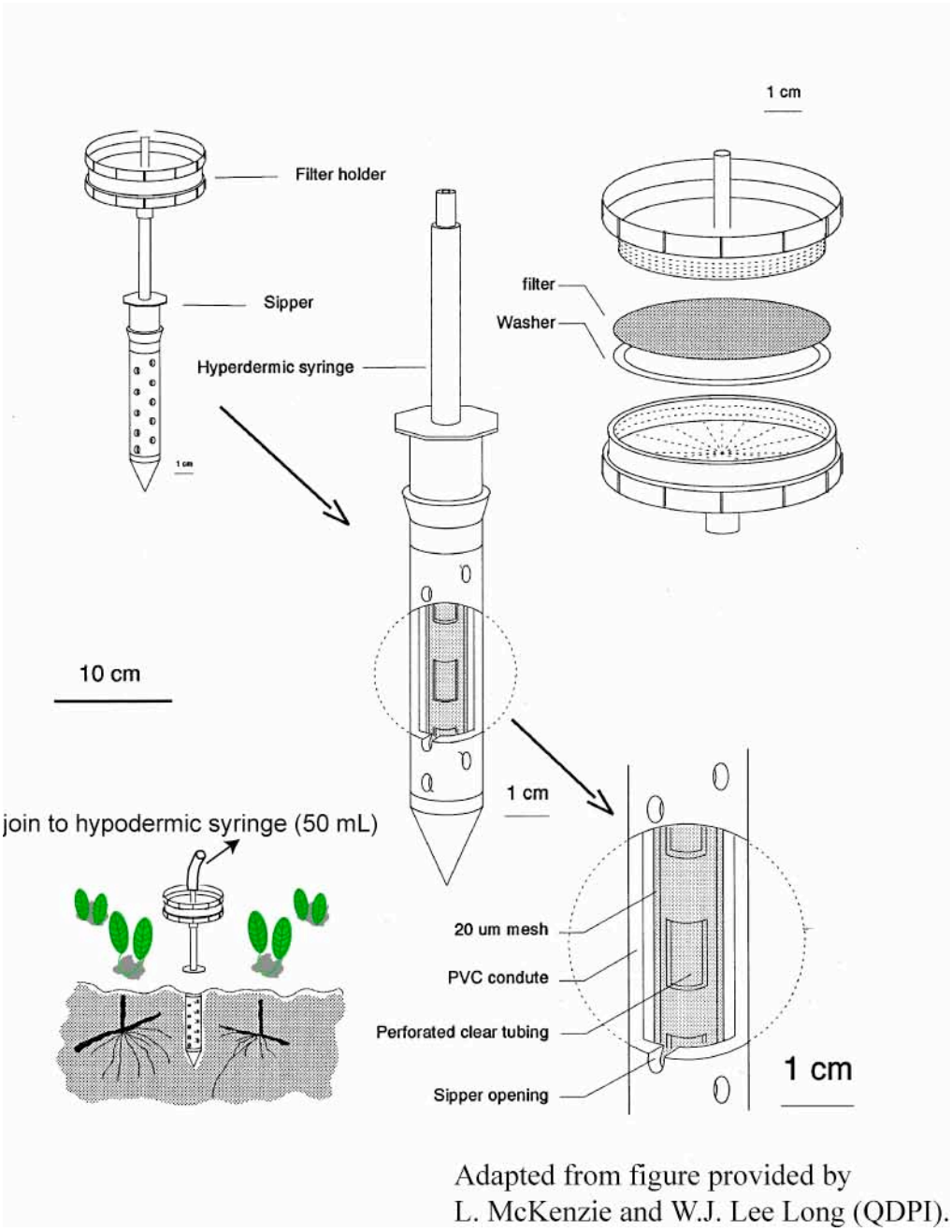


Figure 2.2 Illustration of the *in situ* sediment sipper, depicting its two stage filtration system, and placement in the rhizosphere for the collection of porewater.

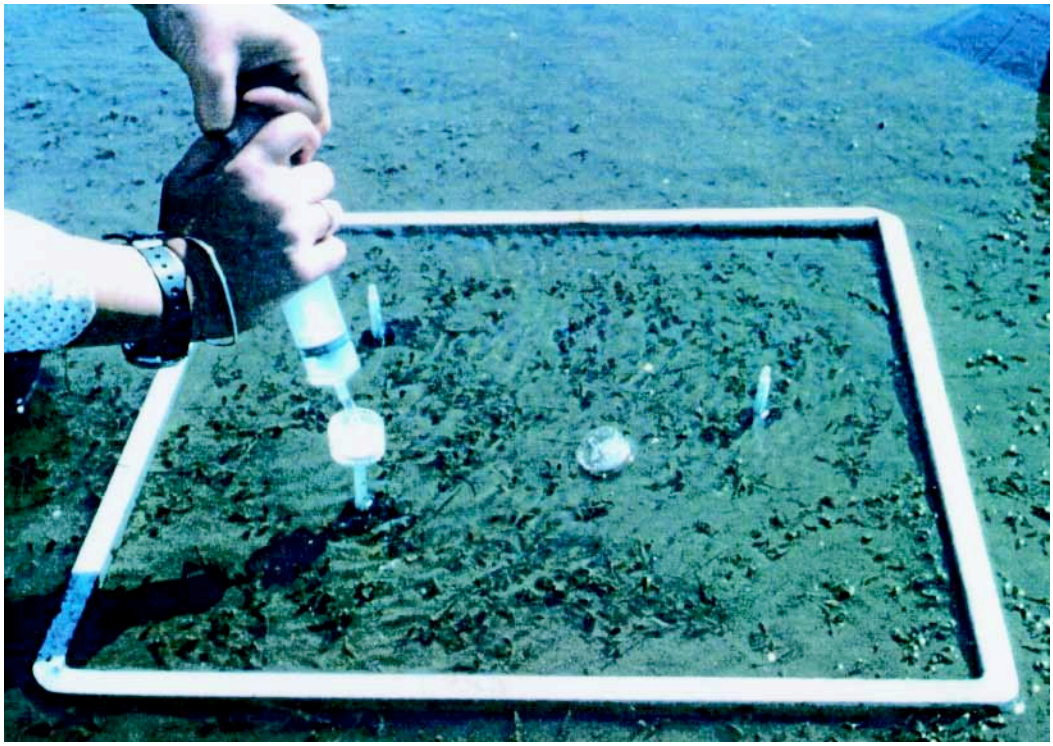


Figure 2.3 Triggering the vacuum in the field of the *in situ* sediment sipper by pulling up the plunger on the syringe.

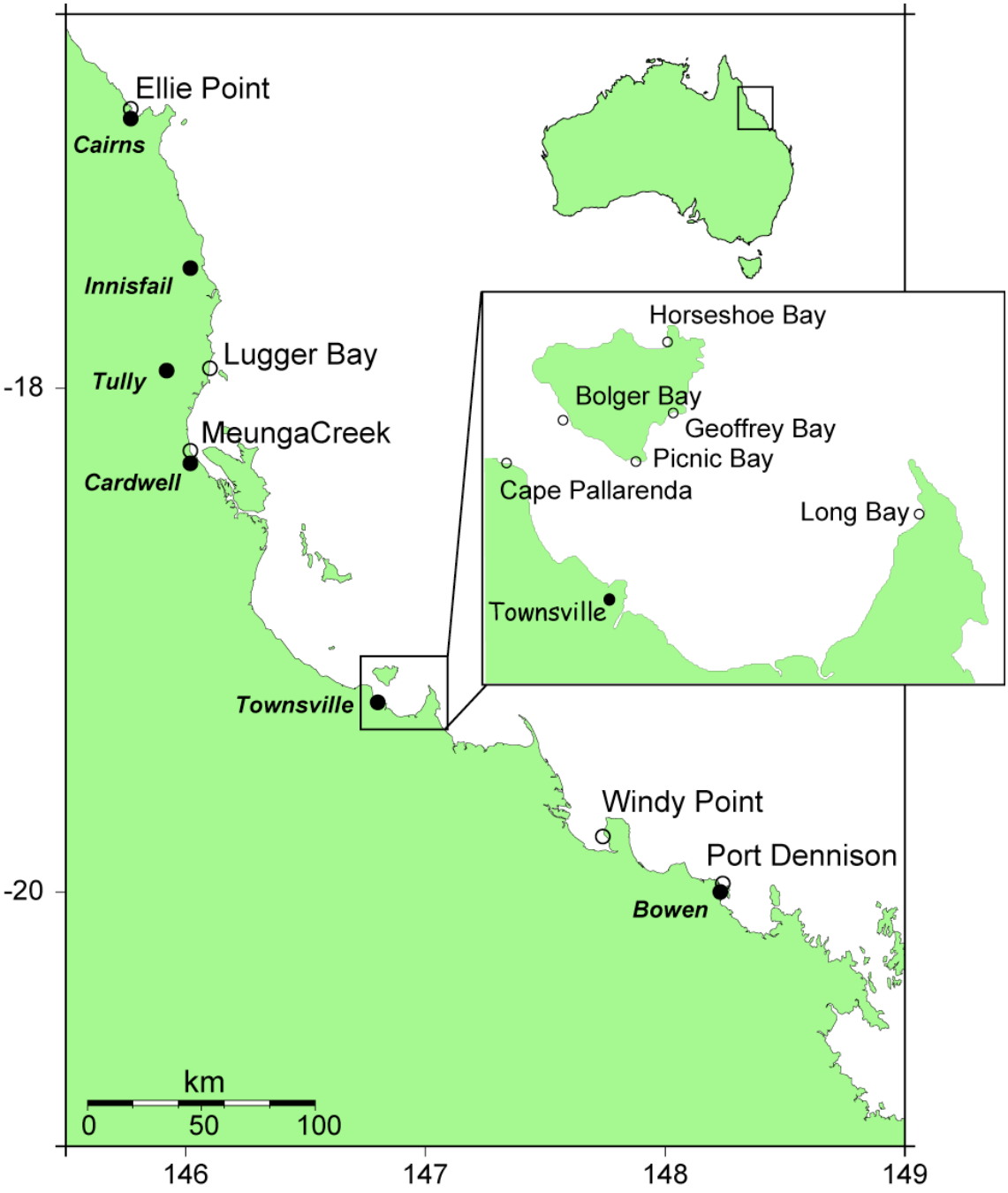


Figure 2.4 The locations of eleven intertidal seagrass meadows (open circles) investigated in this study, within the central region of the Great Barrier Reef World Heritage Area.

Table 2.1 Parameters used throughout this study grouped into data sets.

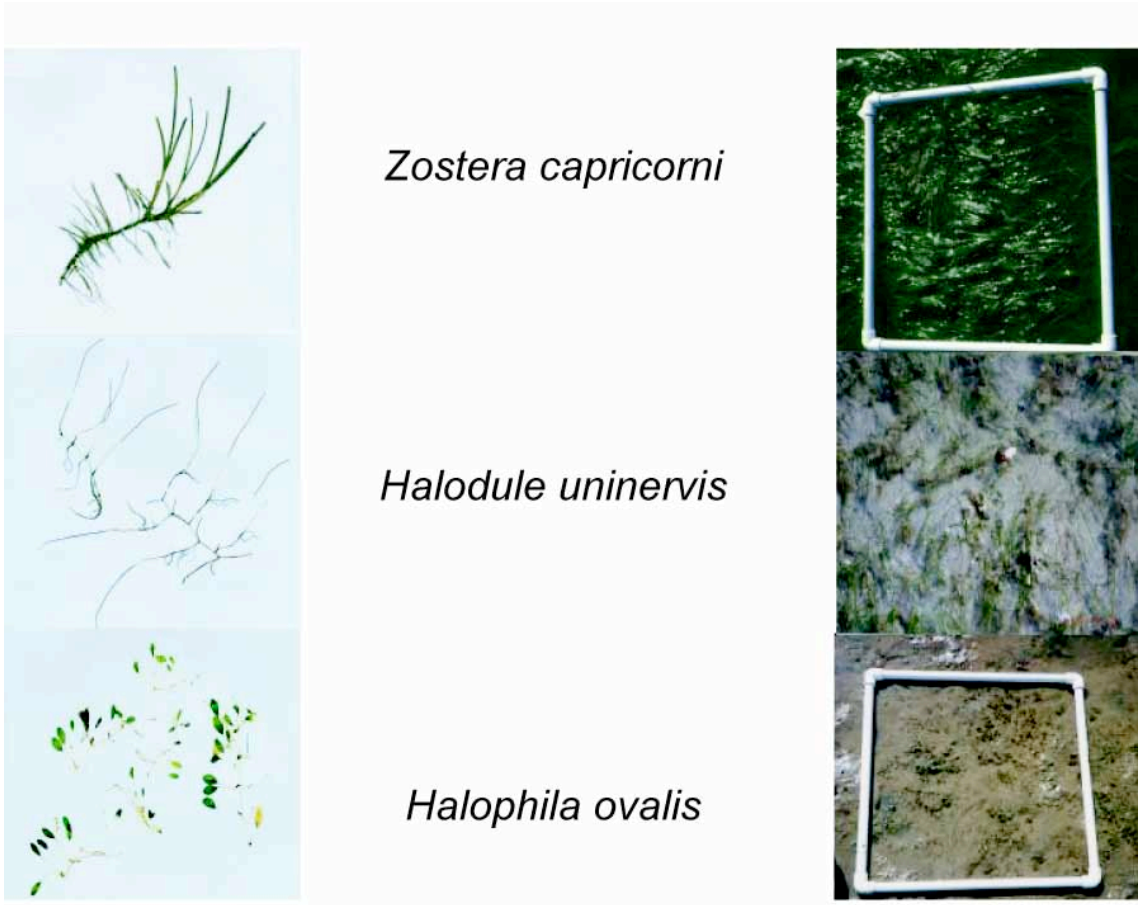
Sediment structure	Sediment nutrients and associated chemically derived parameters	Plant parameters	
		Plant abundance	Plant tissue nutrients
Clay	Bicarbonate extracted phosphate	Leaf biomass	% leaf N
Very fine silt	Bray extracted phosphate	Rhizome biomass	% leaf P
Fine silt	Extracted ammonium	Root biomass	% rhizome N
Medium silt	Dissolved inorganic ammonium	Total biomass	% rhizome P
Coarse silt	Dissolved inorganic nitrate and nitrite	Leaf density	% root N
Sand	Dissolve inorganic phosphate		% root P
Porosity	pH		
	Eh		
	Percent carbonate matter		
	Percent vegetative matter		

Table 2.2 The location of eleven intertidal seagrass meadows investigated in this study. Longitudes and latitudes (WGS 84), predominant seagrass species with average percent cover, as determined by a visual estimate within 0.25 m^{-2} quadrats at each location.

Location	Longitude[1]	Latitude[1]	Predominate species (% quadrat cover)
Ellie Point, Cairns	145.77°E	16.88°S	*Zostera capricorni* (80%)
Lugger Bay, South Mission Beach	146.10°E	17.92°S	*Halodule uninervis* (10–20%)
Meunga Creek, Cardwell	146.02°E	18.30°S	*Halodule uninervis* (40%)
Cape Pallarenda, Townsville	146.76°E	19.18°S	*Halodule uninervis* (30–40%)
Bolger Bay, Magnetic Island, Townsville	146.80°E	19.16°S	*Halophila ovalis*[2] (<5%)
Picnic Bay, Magnetic Island, Townsville	146.85°E	19.18°S	*Halophila ovalis* (50–70%)
Geoffrey Bay, Magnetic Island, Townsville	146.86°E	19.16°S	*Halodule uninervis* (20–30%)
Horseshoe Bay, Magnetic Island, Townsville	146.86°E	19.12°S	*Halodule uninervis* (10%)
Long Bay, Cape Cleveland, Townsville	147.02°E	19.22°S	*Halodule uninervis* (10–20%)
Windy Point, Cape Upstart	147.74°E	19.78°S	*Zostera capricorni* (60–70%)
Port Dennison, Bowen	148.25°E	19.94°S	*Halodule uninervis* (20–40%)

[1] longitudes and latitudes from Morrissette 1992
[2] in 1992 Bolger Bay recorded 70% 0.25 m^2 quadrat cover

Chapter 3 A biogeochemical inventory of intertidal coastal seagrass meadows in the central region of the Great Barrier Reef World Heritage Area (GBRWHA)



The variability of seagrass form and density encountered in this study.

Summary

The eleven locations surveyed for this study are representative of the intertidal beds present in the central region of the Great Barrier Reef World Heritage Area (Lee Long *et al.* 1993). Observations on the chemical environment of this region (Eh and pH) were consistent with measurements indicative of intertidal areas in general (Garrels and Christ 1965). Porosity measurements were consistent with the range of sediment types encountered in this area, where sandy sediments have low porosity, and silt-clay sediments have high porosity (Folk 1974). The majority of locations sampled were characterised by terrigenous sediments with low organic content. Sediment nutrient adsorbed:porewater ratios indicated that the majority of nutrients were bound up in the adsorbed phase. Porewater nutrient levels were within the range reported in the literature, but were generally at the lower end of the range for both NH_4^+ and PO_4^{3-} suggesting potential N and P limitation for seagrass growth. Molar ratios of porewater N:P were large, indicating low porewater PO_4^{3-} low relative to NH_4^+. Levels of adsorbed nutrients were higher than those recorded from comparative studies, particularly for adsorbed NH_4^+. However molar ratios of adsorbed N:P were small indicating that the pool of P relative to N is small.

Whilst the number of locations represented by *Zostera capricorni* and *Halodule uninervis* is indicative of their abundance in this region, *Halophila ovalis* is under represented in this study (cf. Lee Long *et al.* 1993). Standing crop measurements of all species were generally low relative to values in the literature. Roots and rhizomes typically represented the largest fraction of plant biomass, as observed by Lanyon and Marsh (1995). The ratio of N:P for plant tissue nutrients observed in this study encompass a wide range. In comparison to ratios reported for other seagrasses globally these ratios are highly variable and indicate the importance of location influencing seagrass nutrient status. All *Halodule uninervis* sites and *Halophila ovalis* sites recorded higher %N and %P than the critical values that Duarte (1990) proposed to indicate nutrient limitation. Nutrient limitation of seagrass in the central region of the Great Barrier Reef is discussed in light of critical values and molar ratios for porewater, adsorbed and plant tissue nutrients.

3.1 A biogeochemical inventory.

This section provides a general qualitative overview of conditions in intertidal seagrass meadows for the central region of the GBRWHA and provides baseline information about these locations. It also adds to the scarce knowledge of nutrient information available for Indo-Pacific seagrass meadows. A survey was conducted during the daytime low tide between 1st and 31st of July 1994. From this survey, an inventory of the sediment nutrients, chemical environment, sediment profile and the seagrass parameters of biomass, shoot density and tissue nutrient content for each of the eleven intertidal seagrass meadows along a 556 km length of coastline within the central region of the Great Barrier Reef World Heritage Area (GBRWHA) was compiled. The overall mean results for samples of seagrass biomass, plant tissue nutrients of leaves, rhizomes and roots, percent carbonate and organic content, a generalized sediment grain size profile and sediment nutrients for each seagrass meadow are plotted against a map of the region for reference (Fig. 3.1). Figure 3.1 did not allow for the presentation of standard errors, so these have been listed along with the ranges encountered at each location in Tables 3.1–4.

Nutrient related parameters

Nutrient related parameters are presented Table 3.1 and summarized in Fig. 3.1.

Sediment pH ranged from alkaline (9.0) at Geoffrey Bay (a reflection of the high carbonate content within its sediment) to slightly acidic (6.8) at Horseshoe Bay. Sediments were well oxidized with Eh values ranging from 81.33 mV at Picnic Bay to 180.33 mV at Horseshoe Bay. All paired Eh and pH readings at each location were well within the range of values that characterize marine transitional/intertidal areas (Garrels and Christ 1965). Percent carbonate matter ranged from 1.58% at Ellie Point to 75.46% at Geoffrey Bay (Fig. 3.1) Using Scoffin's (1987) description of carbonate sediments only Geoffrey Bay could be considered to have carbonate sediments (≥ 50%). However any amount of carbonate present in sediments or soil will affect the adsorption chemistry of phosphorus (Pailles and Moody 1995). Percent organic content in sediment cores ranged from 0.51% at Port Dennison to 2.48% at Windy Point. Porosity measures varied from a low of 0.29 at Picnic Bay consistent with coarse sand dominating the

sediment structure to a high of 0.62 at Meunga Creek consistent with the majority of grain sizes being in the clay size range.

Sediment nutrients

The sediment nutrient parameters discussed in this section are displayed in Table 3.2 and summarized in Fig. 3.1.

Porewater nutrient samples varied immensely between locations. Horseshoe Bay recorded the highest mean porewater NH_4^+ level (144.43 µM), while the lowest (1.84 µM) was recorded at Ellie Point. The highest $NO_2^- + NO_3^-$ value was at Long Bay (4.40 µM); the lowest at Horseshoe Bay and Cape Pallarenda (0.02 µM). Long Bay recorded the lowest porewater phosphate level (0.51 µM), while Meunga Creek recorded the highest (6.08 µM).

The different methods used for extracting adsorbed PO_4^{3-} gave varying results. Meunga Creek recorded the highest adsorbed PO_4^{3-} values (820 µmol kg^{-1} $PO_4^{3-}{}_{(Bray)}$ and 471.21 µmol kg^{-1} $PO_4^{3-}{}_{(bicarbonate)}$). Geoffrey Bay had the lowest Bray extracted PO_4^{3-} measure (11.40 µmol $kg^{-1}PO_4^{3-}{}_{(Bray)}$) reflecting the deficiencies in this extraction technique in a high carbonate environment. The lowest recording of PO_4^{3-} for the bicarbonate extraction method was at Port Dennison (66.44 µmol kg^{-1} $PO_4^{3-}{}_{(bicarbonate)}$) (Fig. 3.1).

Generally different seagrass species were associated with different sediment nutrient characteristics. *Zostera capricorni* was associated with the lowest porewater nutrients, *Halodule uninervis* with the highest nitrogen porewaters (NH_4^+ and $NO_2^- + NO_3^-$), while *Halophila ovalis* was associated with the highest PO_4^{3-} porewater levels (Table 3.2). The adsorbed nutrient data revealed a different pattern of seagrass species associations. *Zostera capricorni* was associated with the highest adsorbed NH_4^+ and $PO_4^{3-}{}_{(Bray)}$ levels. *Halophila ovalis* was associated with the highest $PO_4^{3-}{}_{(bicarbonate)}$ levels. The presence of *Halodule uninervis* was consistent with the lowest adsorbed NH_4^+ levels.

The association of a seagrass species with the lowest levels of adsorbed PO_4^{3-} (both extraction methods) varied according to the inclusion or exclusion of Geoffrey Bay, the only carbonate site (as defined according to Scoffin's definition of 1987) in this survey. I also classify Picnic Bay as a carbonate site (25% carbonate matter), but in comparison to Geoffrey Bay it had a larger component of coarser grained sediments (Fig. 3.1, Table

3.2), which is known to alter the adsorption chemistry of phosphorus onto carbonate minerals (Erftemeijer and Middelburg 1993). Consequently the importance of choosing the most appropriate methodology for the type of sediments encountered with respect to mineralogy and grain sizes is paramount. For example, when Geoffrey Bay (a location dominated by *Halodule uninervis*) was included, *Zostera capricorni* was coincident with low levels of $PO_4^{3-}{}_{(bicarbonate)}$, while *Halodule uninervis* corresponded with low levels of $PO_4^{3-}{}_{(Bray)}$. However when Geoffrey Bay was excluded from this examination, low $PO_4^{3-}{}_{(bicarbonate)}$ levels were associated with the presence of *Halodule uninervis,* and *Halophila ovalis* was associated with low levels of $PO_4^{3-}{}_{(Bray)}$ (Table 3.2). This comparison highlights the differences between locations and seagrass – nutrient relationships based on the differences in methodology for extracting adsorbed PO_4^{3-}.

The ratio of adsorbed:porewater nutrients are often used to denote the size and contribution of each nutrient pool. To do this, porewater nutrients and adsorbed nutrients were converted to the same units (μmol $L_{sediment}^{-1}$ Chapter 2). The adsorbed phase made the largest contribution to the NH_4^+ pool, with all NH_4^+ ratios greater than one (Table 3.2). Phosphate like NH_4^+ is also largely present in the adsorbed phase but at much greater ratios than those for NH_4^+ (Table 3.2)

Nutrient limitation may be inferred from the ratio of N:P in sediments as used by Udy and Dennsion (1997a). If the ratio is small, the phosphorus pool is larger than the nitrogen pool) and N limitation is inferred. Large ratios (i.e. the nitrogen pool is larger than the phosphorus pool) imply P limitation. N:P ratios were calculated for porewaters and for adsorbed nutrients using both methods of PO_4^{3-} extraction. The porewater ratios ranged from 2:1 (Ellie Point) indicating N limitation to 295:1 (Horseshoe Bay), indicating P limitation (Table 3.2). This range of ratios suggests that nutrient limitation is location dependent. For both methods of extraction, adsorbed N:P ratios ranged from 0.2:1 to around 6:1, implying N limitation. The exception to this was Geoffrey Bay , using $PO_4^{3-}{}_{(Bray)}$ measurements (30:1) implying N limitation. However this ratio was 0.7:1 using $PO_4^{3-}{}_{(bicarbonate)}$ measurements once again underlining the importance of extraction technique and amount of carbonate present when assessing bioavailability of PO_4^{3-}.

Small ratios of N:P nutrients represent equivalent size pools of PO_4^{3-} relative to NH_4^+, while large ratios represent small pools of PO_4^{3-} relative to NH_4^+. However, the actual

value of the ratio is very location dependent. The regional averaged porewater N:P (36:1) indicated porewater PO_4^{3-} was low relative to porewater NH_4^+ and may be P limiting. The mean adsorbed N:P ($N:P_{(Bray)}$—3:1 and $N:P_{(bicarbonate)}$—1:1) shows that the adsorbed PO_4^{3-} pool was relatively similar in size to the adsorbed NH_4^+ pool. The higher ratio for $N:P_{(Bray)}$ was overly influenced by values calculated for Geoffrey Bay. When this mean was recalculated without the Geoffrey Bay site, the ratio becomes 1.4:1, equivalent to the ratio calculated using $PO_4^{3-}{}_{(bicarbonate)}$ values. With the exception of Geoffrey Bay (Bray measure) all N:P ratios were small indicating equivalent pools of NH_4^+ and PO_4^{3-} therefore depending on the actual levels of these nutrients these ratios may indicate no limitation, limitation of both nutrients or limitation of N (nutrient pool in favour of PO_4^{3-}as generally plants have a greater need for N than P). Hence, location and the amount of carbonate matter present within the sediment are important factors for determining the bio-availability of nutrients and their limitation to seagrass growth.

Seagrass

Biomass

The parameters discussed in this section are displayed in Table 3.3 and summarized in Fig. 3.1).

Halodule uninervis was the predominant species at seven locations; two locations were dominated by *Zostera capricorni*, and two locations were dominated by *Halophila ovalis*. *Halodule uninervis* has two leaf morphologies, a broad leaf (>1 mm) and a narrow leaf (<1 mm). The meadows of *Halodule uninervis* investigated in this study were typically of the narrow leaved morphology; consequent reference to *Halodule uninervis* through out this thesis will mean *Halodule uninervis* (narrow).

Ellie Point, Cairns, a meadow dominated by *Zostera capricorni*, recorded the highest seagrass biomass (252.16 g DW m^{-2}), whilst, Bolger Bay, a location dominated by *Halophila ovalis*, recorded the lowest (0.2 g DW m^{-2}). Cape Pallarenda recorded the highest biomass of *Halodule uninervis* (55.02 g DW m^{-2}) and had the third highest biomass of the locations surveyed. With the exception of *Zostera capricorni* at Ellie Point, Cairns, the below ground components contributed more biomass than the above ground component, as shown by the small (<1) above-ground:below-ground ratios. Rhizomes provided a larger component of the below ground biomass than the root

biomass. The seagrass was patchy at four of the 11 beds surveyed as evidenced by the large standard errors in relation to their mean biomass: Lugger Bay, Cape Pallarenda, Bolger Bay and Long Bay (see Table 3.3).

Plant tissue nutrients

The parameters discussed in this section are displayed in Table 3.4 and summarized in Fig. 3.1).

Seagrasses from Meunga Creek had the highest nutrient content (%N and %P) for all plant components for this region. Seagrasses from Ellie Point had the lowest nutrient content (%N and %P) for both leaves and roots. Seagrasses from Cape Pallarenda had the lowest %N for rhizomes and Horseshoe Bay had the lowest %P for rhizomes. These values were not as variable as the biomass data within locations (Table 3.4 cf. size of the standard error).

Halodule uninervis recorded the highest nutrient content (%N and %P) for all plant components, with the exception of % leaf P, which was highest in *Halophila ovalis*. *Zostera capricorni* recorded the lowest nutrient content (%N and %P) for leaves and roots, while the lowest rhizome %N and %P occurred in *Halophila ovalis* (see Fig. 3.1, Table 3.4). Most nutrients were stored in the leaves. The pattern across species in relation to nutrient content (i.e. highest % leaf N for *Halodule uninervis*, highest leaf %P for *Halophila ovalis* and the lowest nutrient content (%N and %P) in *Zostera capricorni*) followed patterns in porewater levels in the rhizosphere of each species.

Using atomic weights, N:P ratios were also calculated for plant tissue nutrients. Leaf N:P ranged from 14:1 (Picnic Bay–*Halophila ovalis*) to 44:1 (Horseshoe Bay–*Halodule uninervis*). Rhizome N:P was lowest (7:1) at Cape Pallarenda (*Halodule uninervis*) and was highest for *Halodule uninervis* at Geoffrey Bay and Horseshoe Bay (18:1). Root N:P varied from 9:1 at Ellie Point (*Zostera capricorni*) to 18:1 at Long Bay (*Halodule uninervis*). The average N:P for all species across locations was 30:1 for leaves, for rhizomes 13:1, and for roots, 12:1.

3.2 Overview of the study region

The intertidal beds studied within the central region of the GBRWHA were characterized by low biomass with the below ground component contributing more to total biomass measurements than the above ground components. Within this region, *Zostera capricorni* tended to occur in areas low in porewater nutrients while *Halodule uninervis* was associated with high porewater nutrients (Table 3.2). This variation in nutrient levels was also reflected in the leaf %N and %P of these two species (Table 3.4). This supports the notion that tissue nutrient content may be a good indicator of nutrient availability in porewaters for intertidal seagrass beds within this region.

Porewater nutrient levels were within the range reported in the literature, but were generally at the lower end of the range (Table 3.5). Adsorbed NH_4^+ levels, overall were higher than those recorded by Udy and Dennison (1996, 1997a), and Udy *et al. (*1999). A comparison of carbonate sites between the two studies (Geoffrey Bay–this study vs. Green Island–Udy and Dennison 1996) revealed that levels of PO_4^{3-} were similar. Porewater levels of NH_4^+ and PO_4^{3-} were, in general, lower than the proposed 'critical values' required for growth in the literature (100 □M NH_4^+ (Dennison *et al.* 1987 and 10 □M of PO_4^{3-} (Erftemeijer 1994)). Adsorbed NH_4^+ levels were higher and adsorbed PO_4^{3-} levels (using the same extractive techniques) were lower than values recorded from comparative studies (Udy and Dennison 1996).

The regional leaf N:P ratio, from this study, for the Central Region of the GBRWHA is 30:1. This ratio is greater than the global ratio of 24:1 calculated by Duarte (1990) and suggests that seagrasses of North Queensland have a large pool of available N relative to P. Birch (1975) measured nutrient content of seagrass at Magnetic Island, Townsville and calculated a N:P ratio of 14:1. This is often cited as being representative of N:P ratios for seagrasses of North Queensland. It is equivalent to the ratio that I calculated for Picnic Bay, Magnetic Island, a location in close proximity to Birch's sampling site. However, considering the small sample size on which Birch's ratio is based, it is inappropriate to continue to use this ratio as an indicator of North Queensland seagrass plant nutrients. It is better to use the ratio I have calculated from a variety of locations within this region. Based on Duarte (1990, 1.8%N and 0.2%P) critical levels in seagrass tissue that infer nutrient limitation, the results for all *Halodule uninervis* sites and the *Halophila ovalis* sites would indicate no nutrient limitation. Based on the size of the

N:P values for leaf nutrient content from my study (30:1), P limitation could be inferred from the large amount of N present in the leaves relative to P (cf. Perez *et al.* 1991, Fourqurean *et al.* 1992). However the %P values from this study are not low in absolute terms, but rather low in comparison to the %N values, which are also high relative to other values in the literature (Table 3.6).

Are seagrasses of this region, N or P limited?

A limiting factor to biological activity is defined as material in an amount approaching the critical minimum required to sustain that activity (Odum 1971). Evidence for nutrient limitation of nitrogen of phosphorus in plants has often been inferred from critical levels of a particular nutrient within the sediment (Sposito 1989) or plant or the molar ratios of the sediments that plants inhabit (Smith 1984) or the plants themselves (Duarte 1990).

Levels of porewater NH_4^+ for this region are generally lower (Table 3.2) than the critical level of 100 µM that has been proposed as limiting to seagrass growth (Dennison *et al.* 1987). Levels of porewater PO_4^{3-} were comparable to values recorded from seagrass meadows that were considered to be potentially P limited (Bahamas: Short *et al.* 1985, Florida: Forqurean *et al.* 1992). Porewater nutrient levels in this study were generally even lower than porewater levels (60 µM NH_4^+ and 10 µM PO_4^{3-}) recorded from carbonate and terrigenous sediments from the Indo-Pacific that showed no nutrient limitation (Erftemeijer *et al.* 1994). Based on these porewater critical values from the literature, seagrasses in this region could be both N and P limited. Critical values indicating limitation for adsorbed nutrients have not been stated for seagrass meadows. A comparison of adsorbed nutrients for this study with ambient values from seagrass meadows just outside this study region (Udy and Dennison 1997a, b, Udy *et al.* 1999) showed that levels of adsorbed NH_4^+ were higher whilst levels of adsorbed PO_4^{3-} (either the Bray or Bicarbonate extraction method) were lower. Udy and Dennison (1997a,b) and Udy *et al.* (1999) concluded from their enhancement studies that the meadows they investigated showed N limitation. Hence it could be inferred via comparison of adsorbed nutrient levels between these studies that the meadows within this study region may be P limited. Nonetheless, a comparison of levels of plant tissue nutrients for this region and the critical levels suggested by Duarte (1990: 1.8%N and 0.2%P)

suggests that nutrient limitation of seagrasses such as *Halodule uninervis* and *Halophila ovalis* does not exist.

In contrast, examination of both porewater and adsorbed N:P ratios suggests N limitation because the ratios are small, symptomatic of a large pool of P compared to the N pool. Whereas leaf N:P ratios are large suggesting that N is more readily taken up from the available nitrogen pool relative to the phosphorus pool and therefore P is limiting due to its non-availability (Table 3.7). I consider that molar ratios of sediment nutrients are poor indicators of nutrient limitation. Low N:P ratios are indicative of N and P pools of the same size, but gives no indication of whether these pools are small and thereby limiting or large and satiating. Plant N:P ratios are an indicator of nutrient availability and are therefore indicative of nutrient limitation. However nutrient limitation is also dependent on which nutrient phase is a better indicator of nutrient availability: porewater (intensity) or adsorbed (quantity). For some terrestrial crops, neither of these phases is relevant. It is the rate at which adsorbed nutrients are made available to the porewater (buffering) that is the critical parameter (Moody *et al.* 1990, Holford and Moody, 1991). Additionally it may be the mechanism by which the nutrient is taken up that is the limiting step (Touchette and Burkholder 2000).

This section provided a general overview of conditions and nutrient limitation in intertidal seagrass beds for the central region of the GBRWHA (Fig. 3.1, Table 3.7). A comparison of the nutrient levels collected during this study and published literature values, shows that levels from this study were relatively low for sediment nutrients (Table 3.5) but high for plant nutrient levels (Table 3.6). The information presented here adds to the scarce information on nutrients available for Indo-Pacific seagrass beds. These measurements were a snapshot of nutrient status for a subset of seagrass beds in this region, taken at a time that I now know seagrasses are not actively growing (see Subchapter 4.3). As such, the measurements represent a static measurement, which may give only a small indication of the nutrient dynamics occurring within this section of the GBRWHA. Caution is also required when comparing critical values and molar ratios from other areas. Experience from terrestrial examples indicates that there is no universal critical value for any nutrient (Moody 1985). The validity of a critical value is dependent on its being tested against a plant response as in a nutrient enhancement experiment (see Subchapter 5.3).

Figure 3.1 (facing) A graphical summary of the biogeochemical inventory of 11 intertidal seagrass meadows across the central region of the Great Barrier Reef World Heritage Area. The mean results for seagrass biomass, plant tissue nutrients, percent carbonate and organic content, a generalized sediment grain size profile and sediment nutrients (adsorbed and porewater) are plotted in reference to the location of the meadow studied. Each seagrass species is represented by a different colour.

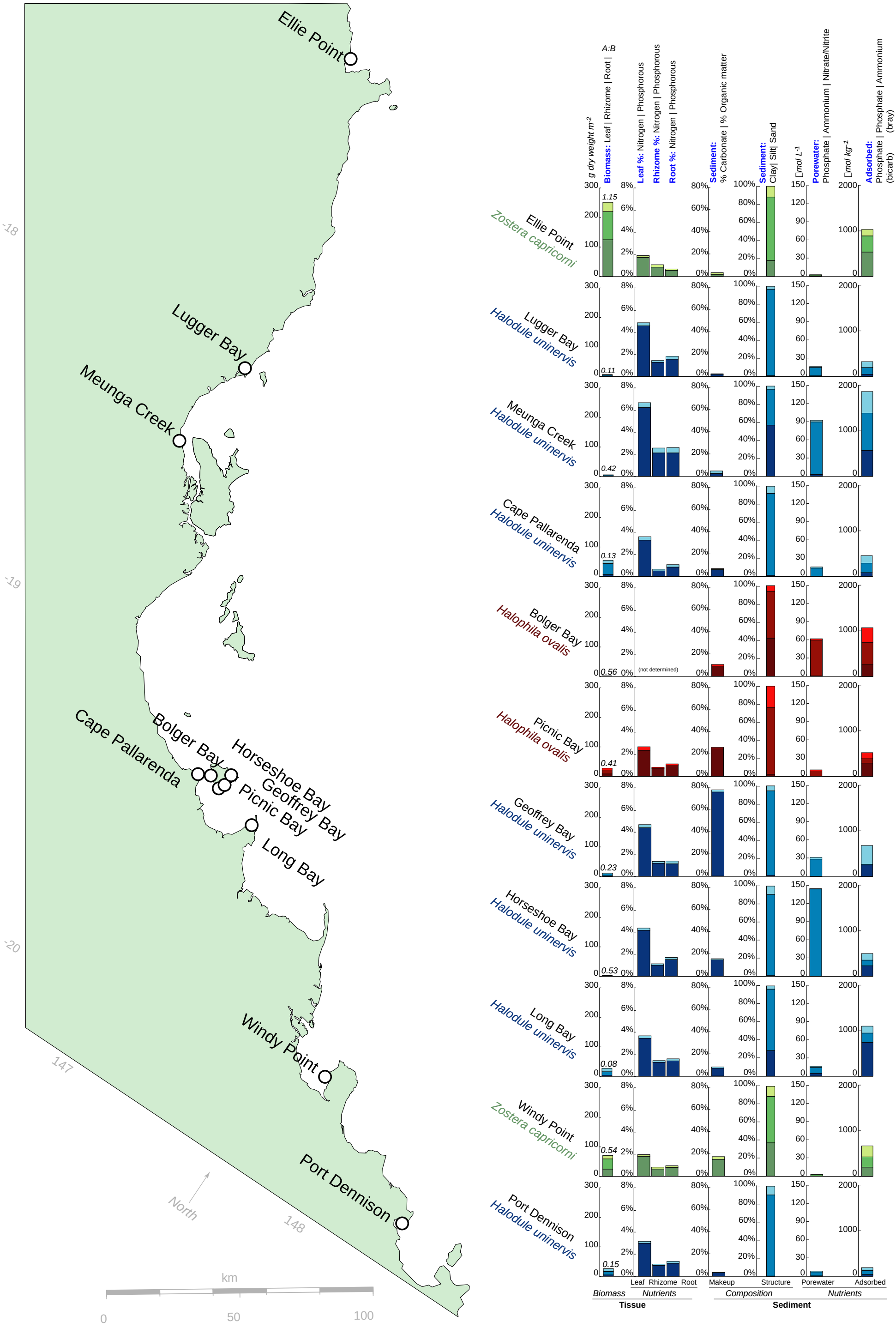

Ellie Point
Lugger Bay
Meunga Creek
Cape Pallarenda
Bolger Bay
Horseshoe Bay
Geoffrey Bay
Picnic Bay
Long Bay
Windy Point
Port Dennison
-18
-19
-20
147
148
North
km
0
50
100
A:B
g dry weight m-2
Biomass: Leaf | Rhizome | Root |
Leaf %: Nitrogen | Phosphorous
Rhizome %: Nitrogen | Phosphorous
Root %: Nitrogen | Phosphorous
Sediment: % Carbonate | % Organic matter
Sediment: Clay| Silt| Sand
mol L-1
Porewater: Phosphate | Ammonium | Nitrate/Nitrite
mol kg-1
Adsorbed: Phosphate | Phosphate | Ammonium (bicarb) (bray)
Ellie Point
Zostera capricorni
1.15
Lugger Bay
Halodule uninervis
0.11
Meunga Creek
Halodule uninervis
0.42
Cape Pallarenda
Halodule uninervis
0.13
Bolger Bay
Halophila ovalis
0.56
(not determined)
Picnic Bay
Halophila ovalis
0.41
Geoffrey Bay
Halodule uninervis
0.23
Horseshoe Bay
Halodule uninervis
0.53
Long Bay
Halodule uninervis
0.08
Windy Point
Zostera capricorni
0.54
Port Dennison
Halodule uninervis
0.15
Leaf Rhizome Root
Makeup Structure
Porewater Adsorbed
Biomass Nutrients
Composition Nutrients
Tissue
Sediment

Table 3.1 A comparison of the chemical environment of the eleven intertidal seagrass meadows surveyed within the central region of the Great Barrier Reef World Heritage Area. (Seagrass species and total biomass are also presented as a reference to the type of seagrass meadow at each location; means ± s.e.)

Location	Species biomass g dw m^{-2}	pH	Eh	% carbonate	% organic content	porosity
Ellie Point, Cairns	*Zostera capricorni* 252.16 ±24.52	7.76 ± 0.12	82.33± 13.92	1.58 ± 0.38	1.83 ± 0.53	0.51 ± 0.05
Lugger Bay, South Mission Beach	*Halodule uninervis* 5.38 ± 2.32	8.77 ± 0.09	117.67 ± 6.76	1.49 ± 0.15	0.59 ± 0.05	0.39 ± 0.03
Meunga Creek, Cardwell	*Halodule uninervis* 5.01 ± 0.31	8.13 ± 0.15	91.33 ± 7.26	2.39± 0.94	2.36 ± 0.12	0.62 ± 0.02
Cape Pallarenda, Townsville	*Halodule uninervis* 55.02 ± 23.80	7.07 ± 0.03	114.67 ± 15.84	6.05 ± 1.67	0.84 ± 0.14	0.33 ± 0.02
Bolger Bay, Magnetic Island	*Halophila ovalis*. 0.20 ± 0.12	7.10 ± 0.00	157.33 ± 12.33	9.22 ± 0.66	1.43 ± 0.05	0.39 ± 0.02
Picnic Bay, Magnetic Island	*Halophila ovalis* 28.34 ± 4.78	8.93 ± 0.17	81.33 ± 18.22	24.95 ± 1.63	1.15 ± 0.007	0.29 ± 0.05
Geoffrey Bay, Magnetic Island	*Halodule uninervis* 11.89 ± 0.73	9.00 ± 0.36	147.00 ± 4.58	75.46 ± 0.81	2.00 ± 0.07	0.35 ± 0.03
Horseshoe Bay, Magnetic Island	*Halodule uninervis* 2.92 ± 0.87	6.80 ± 0.09	152.67 ± 11.29	14.66 ± 0.28	0.98 ± 0.09	0.32 ± 0.04
Long Bay, Cape Cleveland	*Halodule uninervis* 26.86 ± 14.57	8.10 *	182.00 *	7.03 ± 0.60	1.13 ± 0.17	0.46 ± 0.02
Windy Point, Cape Upstart	*Zostera capricorni* 72.34 ± 3.96	8.03 ± 0.06	92.00 ± 6.66	15.14 ± 1.38	2.48 ± 0.25	0.51 ± 0.007
Port Dennison, Bowen	*Halodule uninervis* 25.10 ± 5.56	8.80 ± 5.77	161.00 ± 9.17	2.89 ± 0.46	0.51 ± 0.04	0.38 ± 0.03

*one measurement taken

Table 3.2 Biomass, porewater and adsorbed nutrients levels at locations in the central region of the Great Barrier Reef World Heritage Area (means, ±s.e. and ranges (in parentheses) are presented)[1]

Location	Species Biomass g DW m^{-2}	Porewater $NO_2^-+NO_3^-$ µmol L^{-1} n = 15 (range)	Porewater NH_4^+ µmol L^{-1} n = 15 (range)	Porewater PO_4^{3-} µmol L^{-1} n = 15 (range)	Adsorbed NH_4^+ µmol kg^{-1} n = 5 (range)	Adsorbed PO_4^{3-} (Bray) µmol kg^{-1} n = 5 (range)	Adsorbed PO_4^{3-} (bicarbonate) µmol kg^{-1} n = 5 (range)	Adsorbed: Porewater[1] NH_4^+ n = 5 (porewater N:P)	Adsorbed: Porewater[1] PO_4^{3-} (Bray) n =5 ($N:P_{(Bray)}$)	Adsorbed: Porewater[1] PO_4^{3-} (bicarbonate) n= 5 ($N:P_{(bicarboante)}$)
Ellie Point, Cairns *Zostera capricorni*	252.16±24.52	0.41±0.13 (bd[2]–1.26)	1.84±0.09 (1.34±2.42)	0.84±0.06 (0.45–1.19)	532.47±152.66 (123.38–937.24)	353.19±47.81 (268.60–526.93)	142.57±12.10 (103.78–163.73)	1004.11 (1.8)	1112.474 (1.8)	374.150 (3.9)
Lugger Bay, Mission Beach *Halodule uninervis*	5.38±2.32	0.67±0.23 (0.06–3.07)	13.75±2.58 (2.67–36.05)	1.57±0.14 (0.83–3.17)	43.10±12.51 (12.003–85.61)	147.3±12.30 (117.61–179.61)	130.37±11.85 (87.23–150.30)	5.66 (19)	374.150 0.3)	350.688 (0.3)
Meunga Creek, Cardwell *Halodule uninervis*	5.01±.31	3.12±1.08 (0.03–15.31)	86.85±7.15 (37.34±127.37)	2.65±0.46 (0.41–6.63)	563.11±40.67 (483.89–709.32)	820.08±61.85 (638.39–1026.04)	471.21±64.92 (329.69–712.19)	6.97 (41.5)	416.707 (0.7)	199.981 (1.4)
Cape Pallarenda, Townsville *Halodule uninervis*	55.02±23.80	0.04±0.02 (bd-.25.00)	13.54±4.52 (1.44–52.89)	1.92±.29 (0.59–4.86)	77.55±29.53 (30.06–193.45)	209.41±44.54 (119.04–328.08)	165.07±7.14 (149.81–188.51)	73.06 (2.1)	629.524 (0.2)	438.650 (0.3)
Bolger Bay, Magnetic Is. *Halophila ovals*	0.20±0.12	0.32±0.13 (bd–1.63)	59.35±6.34 (23.51–98.51)	2.20±.47 (0.56–7.70)	257.72±24.71 (178.64–314.75)	482.83±75.81 (339.93–784.47)	328.36±42.40 (207.32–426.28)	15.44 (26.54)	599.644 (0.7)	465.499 (0.9)
Picnic Bay, Magnetic Is *Halophila ovalis*	28.34±4.78	0.15±.06 (0.02–1.00)	8.67±1.62 (2.25–26.95)	1.78±0.18 (0.71–3.18)	285.67±92.40 (45.60–585.14)	94.95±5.95 (82.37–113.48)	134.47±27.20 (92.35–239.48)	70.51 (21.2)	374.712 (3.9)	425.235 (3.7)
Geoffrey Bay, Magnetic Is *Halodule uninervis*	11.89±0.73	0.09±0.02 (0.02–0.21)	28.68±4.01 (7.88–48.66)	3.15±0.45 (1.77–9.07)	252.49±34.65 (149.74–312.34)	17.59±3.78 (5.23–26.59)	408.30±32.51 (317.57–506.75)	46.34 (11.9)	22.89 (29.7)	700.651 (0.7)
Horseshoe Bay, Magnetic Is *Halodule uninervis*	2.92±.87	0.03±0.007 (bd–0.09)	144.43±25.12 (2.60–298.00)	0.69±0.10 (0.34–1.54)	229.96±10.27 (212.14–263.55)	124.41±13.22 (90.63–164.70)	144.72–8.32 (122.42–167.96)	6.46 (294.6)	1292.92 (1.7)	1418.44 (1.6)
Long Bay, Cape Cleveland *Halodule uninervis*	26.86±14.57	4.40±1.41 (0.04–19.41)	9.47±1.65 (2.87–28.44)	2.20±0.88 (0.53–13.78)	736.68±145.53 (300.47–1181.74)	206.05±19.13 (142.90–252.60)	152.60±14.68 (105.41–182.79)	314.13 (9.6)	691.77 (3.7)	430.12 (6.1)
Windy Point, Cape Upstart *Zostera capricorni*	72.34±3.96	0.17±0.09 (bd–1.27)	2.47±.25 (0.15–4.17)	0.85±0.16 (0.15–2.16)	203.11±59.16 (69.86–383.08)	225.34±21.78 (186.12–307.34)	240.36±34.10 (145.95–357.00)	279.70 (3.5)	696.675 (1.1)	800.296 (1)
Port Dennison, Bowen *Halodule uninervis*	25.10±5.56	0.76±0.29 (bd–3.55)	6.31±.87 (1.33–14.27)	1.60±0.16 (0.79–3.01)	38.64±14.66 (4.85–81.84)	85.57±4.46 (74.80–96.79)	66.44±12.39 (32.90±93.07)	20.68 (6.4)	274.64 (0.5)	165.11 (1.1)

[1] both porewater and adsorbed units converted to µmol $L^{-1}_{sediment}$

[2] bd—below detection

Table 3.3 Biomass data (mean and s.e.) for dominant species within the monospecific stands of the seagrass beds surveyed for the central region of the GBRWHA.

Location (n=3)	Dominant species	Total biomass	Leaf biomass	Rhizome biomass	Root biomass	Above:below ground ratio
Ellie Point, Cairns	*Zostera capricorni*	252.16±24.52	124.49±13.56	95.17±25.96	31.51±6.09	1.15:1
Lugger Bay, Mission Beach	*Halodule uninervis*	5.38±2.32	0.56±0.35	4.01±1.70	0.77±0.28	0.11:1
Meunga Creek., Cardwell	*Halodule uninervis*	5.01±0.31	1.43±0.41	2.53±0.24	1.02±0.15	0.42:1
Cape Pallarenda, Townsville	*Halodule uninervis*	55.02±23.8	6.37±2.96	37.3416.70	11.21±4.31	0.13:1
Bolger Bay, Magnetic Island	*Halophila ovalis*	0.20±0.12	0.06±0.03	0.05±0.04	0.04±.02	0.66:1
Picnic Bay, Magnetic Island	*Halophila ovalis*	28.34±4.78	8.35±2.71	13.48±1.95	6.34±.60	0.41:1
Geoffrey Bay, Magnetic Island	*Halodule uninervis*	11.89±.0.73	2.14±0.89	7.02±0.77	2.69±.29	0.23:1
Horseshoe Bay, Magnetic Island	*Halodule uninervis*	2.92±0.87	1.17±0.43	1.23±.38	0.45±0.08	0.63:1
Long Bay, Cape Cleveland	*Halodule uninervis*	26.86±14.57	3.18±2.56	11.77±8.71	11.86±3.64	0.09:1
Windy Point, Cape Upstart	*Zostera capricorni*	72.34±3.96	24.77±4.39	34.72±2.68	11.58±2.09	0.54:1
Port Dennison, Bowen	*Halodule uninervis*	25.10±5.56	3.52±1.51	11.95±2.53	9.55±2.46	0.15:1

Table 3.4 Means and standard errors of plant tissue nutrients and their molar ratios for each of the seagrass species sampled from intertidal meadows within the central region of the Great Barrier Reef World Heritage Area.

Location Species	Biomass g dw m^{-2} (n=3)	% leaf N	% leaf P	% rhizome N	% rhizome P	% root N	% root P	leaf N:P	rhizome N:P	root N:P
Ellie Point, Cairns *Zostera capricorni*	252.16±24.52	1.73±0.23	0.18±0.02	0.85±0.17	0.23±0.03	0.55±0.10	0.13±0.03	22:1	8:1	10:1
Lugger Bay, Sth Mission Beach *Halodule uninervis*	5.38±2.32	4.64±0.27	0.28±0.01	1.3±0.19	0.17±0.03	1.57±0.33	0.28±0.03	37:1	16:1	12:1
Meunga Creek, Cardwell *Halodule uninervis*	5.01±0.31	6.30±0.25	0.45±0.07	2.16±0.17	0.46±0.03	2.14±0.14	0.50±0.07	32:1	11:1	10:1
Cape Pallarenda, Townsville *Halodule uninervis*	55.02±23.80	3.32±0.08	0.32±0.01	0.51±0.04	0.16±0.03	0.85±0.04	0.23±0.09	23:1	7:1	8:1
Picnic Bay, Magnetic Island *Halophila ovalis*	28.34±4.78	2.36±0.20	0.36±0.19	0.71±0.05	0.14±0.02	0.98±0.13	0.17±0.03	14:1	12:1	13:1
Geoffrey Bay, Magnetic Is *Halodule uninervis*	11.89±0.73	4.45±0.18	0.28±0.02	1.2±0.14	0.17±0.03	1.13±0.08	0.26±0.03	35:1	18:1	10:1
Horseshoe Bay, Magnetic Island *Halodule uninervis*	2.92±0.87	4.19±0.14	0.21±0.05	1.01±0.14	0.13±0.09	1.51±0.11	0.20±0.03	44:1	18:1	17:1
Long Bay, Cape Cleveland *Halodule uninervis*	26.86±14.57	3.47	0.23	1.28±0.09	0.16±0.01	1.40±0.09	0.19±0.01	33:1	17:1	18:1
Windy Point, Cape Upstart *Zostera capricorni*	72.34±3.96	1.80±0.17	0.18±0.03	0.66±0.06	0.18±0.02	0.80±0.11	0.16±0.01	24:1	8:1	11:1
Port Dennison, Bowen *Halodule uninervis*	25.10±5.56	3.02±0.46	0.18±0.04	0.99±0.05	0.14±0.01	1.18±0.21	0.19±0.03	38:1	16:1	14:1

(Bolger Bay is not represented in this table as there was insufficient plant material to do the plant tissue analysis)

Table 3.5 A comparison between porewater nutrient levels from this study and literature values for porewater nutrients in seagrass beds around the world characterized by location and sediment type.

Location	Sediment type	Seagrass species	Porewater nutrients		Source
			NH_4^+ (µM)	PO_4^{3-} (µM)	
Tropical/subtropical					
Alfacs Bay, Spain	terrigenous	*Cymodocea nodosa*	200-400	4-30	Perez *et al.* 1994
Green Island, FNQld, Aust	carbonate	*Halodule uninervis (w)* *Cymodocea serrulata*	5.6	1.3	Udy and Dennison 1996
Moreton Bay, SEQld, Aust	terrigenous	*Halodule uninervis (w)*	7.1	4.7	Udy and Dennison 1996
S. Sulawesi, Indonesia	carbonate	*Thalassia hemprichii* *Enhalus acoroides*	38.8 –117.6	4.1 – 13.1	Erftemeijer1994
S. Sulawesi, Indonesia	terrigenous	*Thalassia hemprichi* *Syringodium isoetifolium* *Cymodocea serrulata*	19.2–27.l	7.7 – 10.1	Erftemeijer 1994
S. Sulawesi, Indonesia	terrigenous	*Enhalus acoroides*	44.8-88.4	2.9 – 8.7	Erftemeijer 1994
San Salvador Is, Bahamas	carbonate	*Syringodium filiforme*	100	2	Short *et al.* 1985
Moreton Bay, SEQld, Aust.	terrigenous	*Zostera capricorni* *Cymodocea serrulata*	15-60		Boon 1986
Florida, USA	carbonate	*Halodule wrightii* *Thalassia testudinum*	98-160	0.5-3	Fourqurean *et al.* 1992
Florida, USA	carbonate	*Thalssia testudinum* *Halodule wrightii*	191	0.8	Powell *et al.* 1989
Ellie Point, Cairns FNQld, Aust.	terrigenous	*Zostera capriconi*,	1.84	0.84	this study
Windy Point, Cape Upstart NQld, Aust.	terrigenous	*Zostera capricorni*	2.47	0.85	this study
Lugger Bay, Mission Beach, FNQld, Aust	terrigenous	*Halodule uninervis*	13.75	1.57	this study
Meunga Ck, Cardwell, NQld, Aust.	terrigenous	*Halodule uninervis*	86.85	2.65	this study
Cape Pallarenda, Townsville, NQld, Aust.	terrigenous	*Halodule uninervis*	13.54	1.92	this study
Geoffrey Bay, Magnetic Is., NQld, Aust.	carbonate	*Halodule uninervis*	28.68	3.15	this study
Horseshoe Bay, Magnetic Is., NQld, Aust.	terrigenous	*Halodule uninervis*	144.43	0.69	this study
Long Bay, Cape Cleveland, NQld., Aust	terrigenous	*Halodule uninervis*	9.47	2.20	this study
Port Dennison, Bowen, NQld, Aust	terrigenous	*Halodule uninervis*	6.31	1.60	this study
Bolger Bay, Magnetic Island, NQld, Aust.	terrigenous	*Halophila spp*	59.35	2.20	this study
Picnic Bay, Magnetic Island, NQld, Aust	terrigenous	*Halophila spp*	8.67	1.78	this study
Texas, USA	terrigenous	*Halodule wrightii*	100-350	10-20	Pulich 1985
Temperate					
Western Port Bay, no response to enrichment	terrigenous	*Heterozostera tasmanica*	200-1700	3-60	Bulthius & Woelkerling 1981
Port Phillip Bay responded to enrichment	terrigenous	*Heterozostera tasmanica*	11-19	6-8	Bulthius *et al.* 1984
Massachchusetts, USA	terrigenous	*Zostera marina*		75	McRoy *et al.* 1972
Alaska, USA	terrigenous	*Zostera marina*	30-130	6-25	Short 1983
Massachusetts, USA	terrigenous	*Zostera marina*	180-300		Dennison *et al.* 1987
NE Japan	terrigenous	*Zostera marina*	300		Iizumi and Hattori 1982

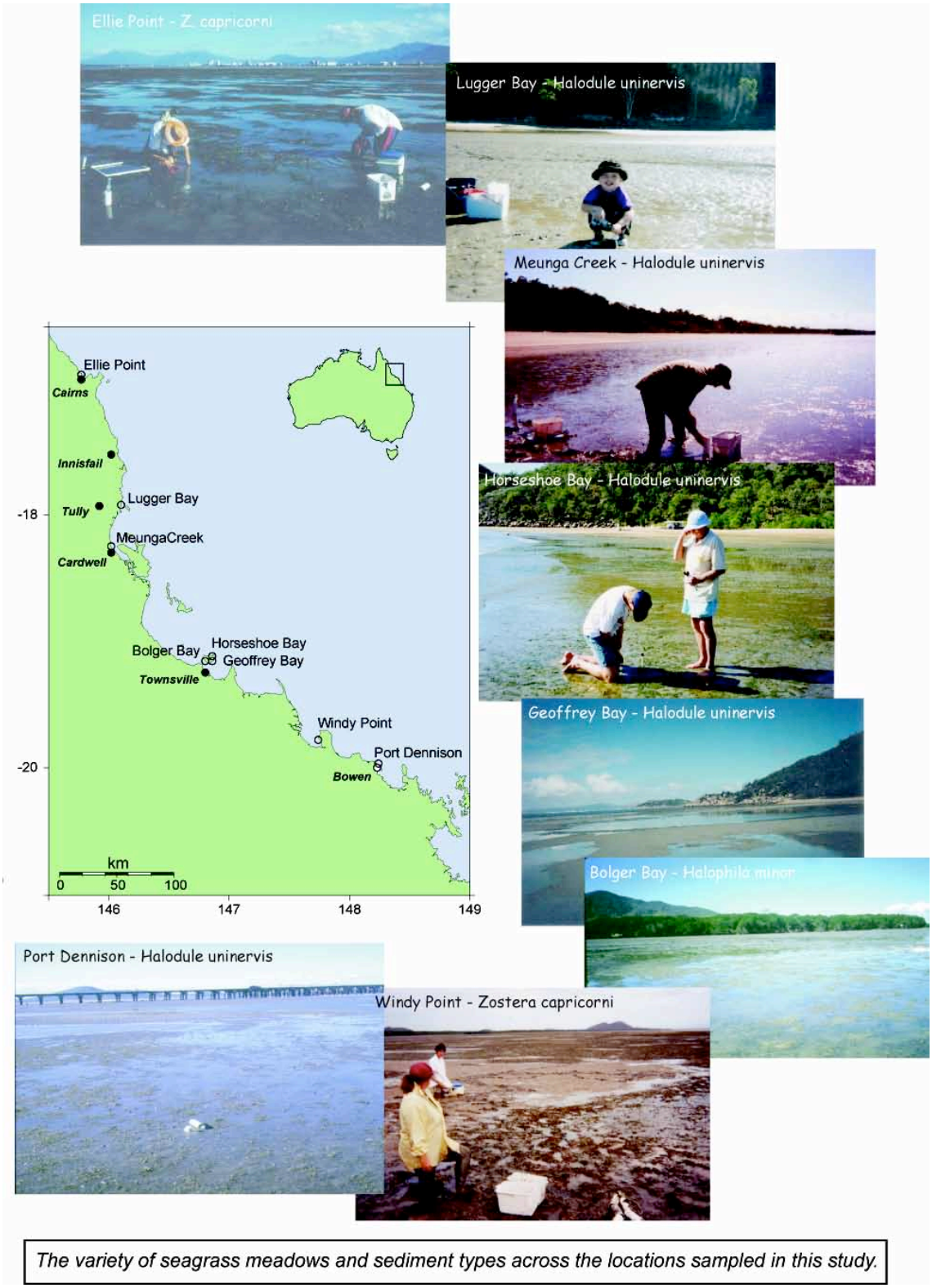
Table 3.6 A comparison of plant tissue nutrients and their molar ratios for seagrass species investigated in this study with literature values characterized by plant component. Where values have been included from fertilization experiments, ambient values only are displayed. - = no value quoted in the literature.

Species	Location	%N	%P	$N:P_{atomic}$	Source
Leaf					
Halophila ovalis	Cockle Bay, MI, NQld, Aust	0.72	0.16	10:1	Birch 1975 (combined data)
Halophila ovalis	Shelley Beach,, NQld, Aust	1.57	-	-	Lanyon 1991
Halophila ovalis	Picnic Bay, MI, NQld, Aust	2.36	0.36	14:1	This study
Halophila ovalis	global average N = 2	0.7	0.18	9:1	from Duarte 1990
Halohila ovalis	Swan-Canning Est, W.A., Aust	-	-	8:1	Connell and Walker 2001
Zostera marina	various USA	1.8–4.5	0.33–0.45	12–30	Thayer *et al.* 1984
Syringodium filiforme	San Salvador, Bahamas	1.29	0.061	47:1	Short *et al.* 1985
Syringodium isoetifolium	Green Island, FNQld, Aust	1.6	0.21	17:1	Udy *et al.* 1999
Zostera capricorni	global average N= 7	1.5	0.26	13:1	from Duarte 1990
Zostera capricorni	Moreton Bay, SEQld, Aust	1.6	0.2	18:1	Udy and Dennison 1997b
Zostera capricorni	Cairns, FNQld, Aust	1.73	0.18	22:1	This study
Zostera capricorni	Cape Upstart, NQd, Aust	1.8	0.18	24:1	This study
Halodule uninervis	Green Island, FNQld, Aust	2.4	0.26	20:1	Udy *et al.* 1999
Halodule uninervis	Moreton Bay, SEQld, Aust	2.4	0.24	22:1	Udy and Dennison 1997b
Halodule uninervis	Magnetic Island, NQld, Aust	0.92	0.15	14:1	Birch 1975
Halodule uninervis	Townsville, NQld, Aust	1.91	-	-	Lanyon, 1991
Halodule uninervis	global average N = 15	2.4	0.19	27:1	from Duarte 1990
Halodule uninervis	Sth Mission Beach, FNQld, Aust	4.64	0.28	37:1	This study
Halodule uninervis	Cardwell, NQld, Aust	6.30	0.45	32:1	This study
Halodule uninervis	Townsville, NQld, Aust	3.32	0.32	23:1	This study
Halodule uninervis	Geoffrey Bay, MI, NQld, Aust	4.45	0.28	35:1	This study
Halodule uninervis	Horseshoe Bay, MI NQld, Aust	4.19	0.21	44:1	This study
Halodule uninervis	Cape Cleveland, NQld, Aust	3.47	0.23	33:1	This study
Halodule uninervis	Bowen, NQld, Aust	3.02	0.18	38:1	This study
Cymodcea nodosa	Spain	1.9–2.3	0.11–0.14	38–39:1	Perez *et al.* 1991
Rhizome					
Halopila ovalis	Picnic Bay MI, Nqld, Aust	071	014	12:1	This study
Halophila ovalis (belowground)	Swan-Canning Est., W.A. Aust.	-	-	3:1	Connell and Walker 2001
Zostera capricorni	Moreton Bay, SEQ	0.43	0.07	14:1	Udy and Dennison 1997b
Zostera capricorni	Cairns, FNQld, Aust	0.85	0.23	8	This study
Zostera capricorni	Cape Upstart, NQd, Aust	0.66	0.18	8	This study
Syringodium isoetifolium	Green Island, FNQld, Aust	0.9	0.23		Udy *et al.* 1999
Syringodium filiforme	San Salvador, Bahamas	0.59	0.27	49:1	Short *et al.* 1985
Halodule uninervis	Magnetic Island NQ	1.14	0.18	14:1	Birch 1975
Halodule uninervis	Moreton Bay, SEQ	0.56	0.08	15:1	Udy and Dennison 1997b
Halodule uninervis	Green Island, FNQld, Aust	0.5	0.11	22:1	Udy *et al.* 1999
Halodule uninervis	Sth Mission Beach, FNQld, Aust	1.3	0.17	16:1	This study
Halodule uninervis	Cardwell, NQld, Aust	2.16	0.46	11:1	This study
Halodule uninervis	Townsville, NQld, Aust	0.51	0.16	7:1	This study
Halodule uninervis	Geoffrey Bay, MI, NQld, Aust	1.2	0.17	18:1	This study
Halodule uninervis	Horseshoe Bay, MI NQld, Aust	1.01	0.13	18:1	This study
Halodule uninervis	Cape Cleveland, NQld, Aust	1.28	0.16	17:1	This study
Halodule uninervis	Bowen, NQld, Aust	0.99	0.14	16:1	This study
Roots					
Halophila ovalsi	Picnic Bay, Magnetic Island				
Halodule uninervis roots	Moreton Bay SEQ	1.2	0.11	24:1	Udy and Dennison 1997b
Zostera capricorni roots	Moreton Bay, SEQ	0.99	0.08	27:1	Udy and Dennison 1997b
Zostera capricorni	Cairns, FNQld, Aust	0.55	0.13	10:1	This study
Zostera capricorni	Cape Upstart, NQd, Aust	0.80	0.16	11:1	This study
Halodule uninervis	Green Island, FNQld, Aust	1.3	0.14	21:1	Udy *et al.* 1999
Syringodium filiforme	San Salvador, Bahamas		0.27	49:1	Short *et al.* 1985
Halodule uninervis	Sth Mission Beach, FNQld, Aust	1.57	0.28	12:1	This study
Halodule uninervis	Cardwell, NQld, Aust	2.14	0.50	10:1	This study
Halodule uninervis	Townsville, NQld, Aust	0.85	0.23	8:1	This study
Halodule uninervis	Geoffrey Bay, MI, NQld, Aust	1.13	0.26	10:1	This study
Halodule uninervis	Horseshoe Bay, MI NQld, Aust	1.51	0.20	17:1	This study
Halodule uninervis	Cape Cleveland, NQld, Aust	1.40	0.19	18:1	This study
Halodule uninervis	Bowen, NQld, Aust	1.18	0.19	14:1	This study

Table 3.7 A presentation of the evidence that suggests which nutrient may be causing limitation of seagrass growth on a regional scale based on the sediment and plant nutrient critical levels and molar ratios I recorded for the intertidal seagrass meadows of the central region of the Great Barrier Reef World Heritage Area

Nutrient limitation	Evidence
'For' N limitation	Porewater NH_4^+ below critical level
'Against' N limitation	% leaf N above critical level
'For' P limitation	Porewater PO_4^{3-} below critical level Low levels of adsorbed PO_4^{3-}
'Against' P limitation	% leaf P above critical level
No limitation	Plant tissue nutrients %N and %P above critical levels

Chapter 4.0 An evaluation of the accepted concepts of ecological processes in seagrass environments with respect to coastal intertidal seagrass communities in north-east Australia.



The variety of seagrass meadows and sediment types across the locations sampled in this study.

Summary

In this chapter, I investigate the differences between seagrass vegetated and adjacent unvegetated areas to determine if structurally small seagrasses within low biomass meadows trap sediment and nutrients within the central region of the Great Barrier Reef World Heritage Area. I examine this concept further by assessing sediment structure, nutrient status, plant abundance and plant tissue nutrients between meadows of different species and abundances and at different times of the year.

I found that seagrass meadows in this region could be differentiated by sediment type (muddy versus sandy), but that within these groupings no difference existed between meadows, particularly of *Halodule uninervis*, and adjacent unvegetated sites. In contrast, sediment and nutrient state within meadows of *Zostera capricorni*, though not significantly different from their surroundings, displayed a tendency to have larger quantities of finer sediments and higher levels of adsorbed NH_4^+ than adjacent unvegetated areas. I attributed this to *Zostera capricorni* (the species and meadow) being more similar in structure and form to the high biomass meadows of structurally large species on which the sediment trapping role of seagrass is based. Species specific interactions between sediment structure, the geochemical environment and nutrient state of the sediment and plants also occurred. I also discovered significant temporal differences within meadows with respect to the nutrient state of both the sediments and the plants, which were linked to temporal changes in the seagrass's growth parameters. These temporal changes were evident across locations despite differences in sediment structure and nutrient state between locations.

4.0.1 Introduction

As explained in the previous chapter, seagrass meadows of *Halophila ovalis* and *Halodule uninervis* (narrow) predominate along the coastline of the central region of Great Barrier Reef World Heritage Area (Lee Long *et al.* 1993). Isolated meadows of *Zostera capricorni* are also present. Relative to all seagrass species, these particular species are structurally small, opportunistic and pioneering with rapid rhizome turnover and large seed banks (Walker *et al*. 1999). However in comparison with *Halodule uninervis* (narrow morphology) and *Halophila ovalis, Zostera capricorni* is larger structurally and forms persistent meadows of high biomass, in this study region

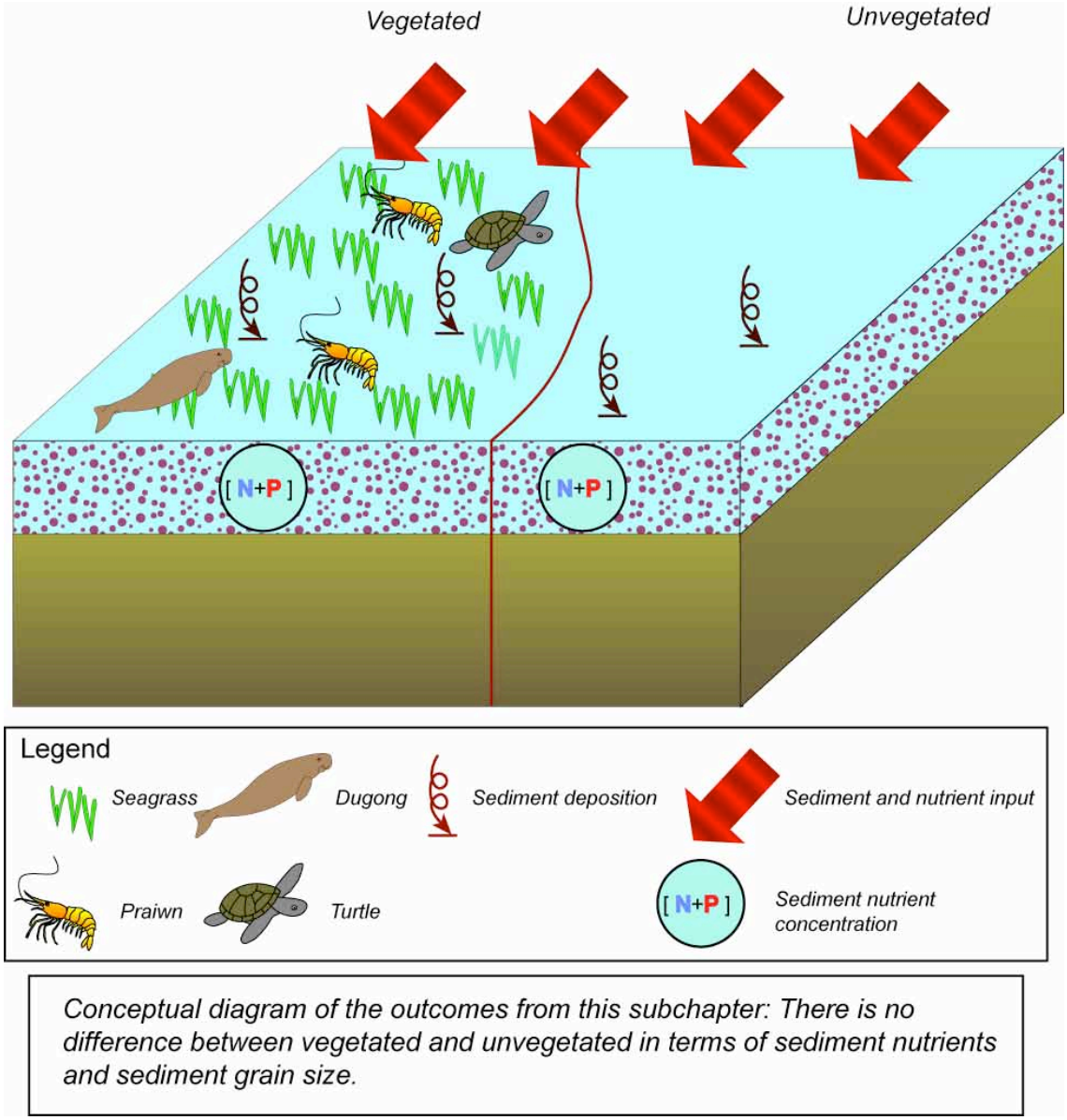
The seagrass beds of the central region of the Great Barrier Reef World Heritage Area are functionally important for food and shelter of other organisms. They provide food for the macro-herbivores, the dugong (*Dugong dugon*) and the green turtle (*Chelonia mydas*) (Heinsohn and Birch 1972, Marsh *et al.* 1982, Lanyon *et al.* 1989). Their function as nursery areas for commercially important juvenile tiger prawns is also well documented (Coles and Lee Long 1985, Coles *et al.* 1987, Lee Long *et al.* 1993). However, little is known about the functions of these meadows with respect to habitat stabilization and as a source or sink of nutrients. These functions are related to the capacity of seagrasses to trap and retain sediment, organic matter and nutrients. The aim of this component of my study is to evaluate the significance of the coastal intertidal areas in this region as traps for nutrients and sediments.

This study developed from the information gathered on sediment structure and chemistry of seagrass meadows in this region (Chapter 3). As that study progressed, I started to doubt the trapping function of seagrass beds in this region. I asked the following questions: Do seagrass meadows of these species in this region differ from adjacent unvegetated areas with respect to sediment structure and nutrient status (Subchapter 4.1). I found that these seagrass meadows could be differentiated by sediment type (muddy versus sandy), but that within these groups no difference existed between vegetated and unvegetated sites in relation to sediment structure or sediment nutrient status, particularly with regard to meadows of *Halodule uninervis* and *Halophila ovalis*. In contrast, meadows of *Zostera capricorni* (high biomass) are similar in functional form to the meadows and species of seagrass that have been documented to trap sediment, organic matter and nutrients (Subchapter 4.1). This result led me to

question species-specific relations with the sedimentary environment, and whether sediment structure and sediment nutrient status could be related to the abundance of seagrass and whether the nutrient environment is reflected in the plant tissue nutrients of the different seagrass species (Subchapter 4.2). My results indicated species-specific responses to sediment structure, geochemical environment and nutrient status (Subchapter 4.2). I recognized that these measurements taken in July (winter), when it was suspected that seagrass meadows are senescent, may differ from measurements taken when seagrasses are actively growing. Consequently, I also investigated whether variables associated with seagrass meadows varied at different times of the year (Subchapter 4.3). In Subchapter 4.3, I concentrated my sampling on the two *Halophila ovalis* meadows. My results showed that locational differences with respect to sediment structure and nutrient status of sediments and plants were maintained at different times of the year. However, there were also significant temporal differences at each location in both sediment and plant nutrients. This was probably related to temporal changes in seagrass growth parameters.

These studies did not specifically test the concepts of sediment trapping and the relationships between seagrass abundance, sediment structure, nutrient status, tissue plant nutrients and seasonality. They did show that seagrasses are a product of their local environment and that tropical seagrass biomass changes intra-annually. The concept of sediment trapping and its associated flow-on interactions with the sedimentary environment such as nutrients and fine sediment accumulation, may not be as obvious for these structurally small species of seagrass as it is for larger species. Further examination of this function in meadows of structurally small seagrasses is warranted.

Subchapter 4.1 Testing the sediment-trapping paradigm of seagrass: Do seagrasses influence nutrient status and sediment structure in tropical intertidal environments in the central region of the Great Barrier Reef World Heritage Area?



Conceptual diagram of the outcomes from this subchapter: There is no difference between vegetated and unvegetated in terms of sediment nutrients and sediment grain size.

Note: Most of this subchapter has been published as: Mellors, J. Marsh, H., Carruthers, T. and Waycott, M. (2002). *Testing the sediment-trapping paradigm of seagrass: Do seagrasses influence nutrient status and sediment structure in tropical intertidal environments?* Bulletin of Marine Science **71(3):** 1215–1226 (see Appendix A).

Summary

Seagrass meadows are considered important for trapping and stabilising meadows. Deposition of fine sediments and associated adsorbed nutrients is considered an important part of the chemical and biological functions attributed to seagrass communities. These ideas were based on work in temperate regions on *Zostera marina* and in tropical regions on *Thalassia testudinum,* two species that maintain stable meadows of relatively high biomass. I investigated this concept for three species of intertidal tropical seagrass meadows in north eastern Australia. Sediment structure and nutrient status did not differ between vegetated and unvegetated habitats in intertidal areas within the central region of the Great Barrier Reef World Heritage Area. The 'trapping' functions that have been attributed to seagrasses need to be re-assessed for a variety of locations and species before they can be accepted as dogma. In tropical Australia, intertidal meadows fluctuate in time and space and are comprised of structurally small species of low biomass. Consequently, sediment trapping within these meadows is largely insignificant. A comparison between total nutrient pools, which for vegetated sites includes a plant contribution, shows obvious differences exist between vegetated and unvegetated sites. This implies that within this region seagrass meadows are a significant sink. However, in meadows of low biomass, it is still the sediment nutrients that contribute the most to the total nutrient pool.

4.1.1 Introduction

Seagrass meadows have been considered important for sediment trapping, sediment stabilisation and as nutrient sinks (Hemminga and Duarte 2000). The concept of seagrass meadows acting as a sink for particles (sediments and adsorbed nutrients) is due to a reduction of flow velocities by the plant canopy (Gacia *et al.* 1999). As the flow velocity drops, the capacity of the water to hold particles decreases, resulting in the deposition of fine sediments and their adsorbed nutrients. This paradigm is based on historical accounts of differences in sedimentation patterns, sediment structure and nutrient content between seagrass areas and bare sand (Wilson 1949, Odum 1971, McRoy and McMillan 1977, Christiansen *et al.* 1981). The sediment-trapping paradigm has been an important component of our understanding of how seagrass meadows function, as many chemical and biological processes are related to the sedimentary environment in which seagrasses grow.

Nitrogen cycling (Iizumi and Hattori 1982, Howarth 1988, Blackburn 1990, Caffrey and Kemp 1990), nutrient parameters (McRoy *et al.* 1972, Orth 1977, Kenworthy *et al.* 1982, Thayer *et al.* 1984, Pulich 1985, Boon 1986, Moriarity and Boon 1989) and sediment structure (Scoffin 1970, Almasi *et al.* 1987, McGlathery *et al.* 1994) are all related to fine scale sediment movement and have been measured as being different between seagrass and associated unvegetated substrates. Seagrass species and meadows come in a variety of functional forms ranging from small leafed species that form ephemeral, low biomass beds to large leafed species forming stable, high biomass beds (Walker *et al.* 1999). Historically, much of the research on the 'trapping' paradigm was undertaken at locations characterized by *Zostera marina* (Scoffin 1970, McRoy *et al.* 1972, Orth 1977). Thus, the dogma relating to sediment trapping and nutrient status of seagrass meadows is based on the results of a single Northern Hemisphere temperate species, usually studied at one location (small spatial scale). In more recent years, the scope of seagrass research has expanded, as outlined in Chapter 1, but the literature is still dominated by studies devoted to *Thalassia testudinum*, *Posidonia oceanica* and *Zostera marina*, and research effort concentrated in the Caribbean, Mediterranean and North Atlantic (Duarte 1999). Studies on these species perpetuate the dogma, as they are all structurally large species that tend to form stable meadows of high biomass (see Walker *et al.* 1999).

The diversity of seagrass form coupled with the requirement to examine processes on larger spatial scales for management, necessitates a re-assessment of the attributes that have become universally ascribed to seagrasses. This study aimed to investigate the nutrient status and sediment trapping paradigm for tropical intertidal seagrass meadows on the north-eastern coast of Australia (145°46'E 16°53'S–148°25'E 19°56'S). Nutrient status and sediment structures were compared between seagrass-vegetated areas that were low in biomass, and comprised of structurally small species and adjacent non-vegetated intertidal areas.

4.1.2 Material and methods

Study Area

The intertidal locations selected for this study are on the mainland coast within the central region of the Great Barrier Reef Lagoon between Cairns and Bowen, spanning approximately 556 km of coastline (Chapter 2–Fig. 2.1). Sediments along this coastline are comprised of terrigenous–derived mud and sand (Maxwell 1968). For a location to be included in this study, which aimed to test the influence of established seagrass meadows, seagrass presence had to have been recorded at that location for three years (see Table 4.1).

Sampling within the vegetated sites was restricted to areas of monospecific, homogenous seagrass-cover. Disturbed areas and bare patches within the meadows were avoided. Unvegetated sites were identified within the same geographical confines as the vegetated site for each location, generally separated by around 100 m and were sampled at approximately the same distance from the shoreline to ensure that each site was subjected to the same light, tidal and wave regimes. Fifteen porewater samples, five random sediment cores (nutrient analysis), and an additional three random sediment cores (grain size analysis) were collected concurrently from a vegetated and parallel non-vegetated site at each location. Sediment pH (15 replicates) was also measured and averaged to characterize locations.

The exception to this was at Long Bay, Cape Cleveland where the only unvegetated tract of sediment at this bay was found inshore of the vegetated area. I considered that the absence of seagrass from this area was more likely to be related to longer periods of exposure/desiccation rather than differences in nutrient levels, consequently

unvegetated sites were bare patches (devoid of even below-ground biomass) within the vegetated sites. Nutrient related parameters also measured during this study included sediment Eh and pH, percent carbonate content, and percent organic content.

Sediment structure

Grain size analysis

Patterns in sediment structure between vegetated and unvegetated sites were similar across all grain size classes within a location. Only the results from the fine silt fraction (classified as 15.625 μm to 7.813 μm) for sandy locations and the results from the very fine silt fraction (classified as 7.182 μm to 3.906 μm) for muddy locations are presented.

Chemical analyses

Porewater nutrients

As explained in Chapter 2, porewater samples were taken from the rhizosphere using sediment sippers of appropriate length (i.e. that corresponded to the depth of the meadows' rhizosphere, 2.5 cm deep *Halophila ovalis*, 10 cm deep *Halodule uninervis* and *Zostera capricorni*). The same depth range was used in the adjacent unvegetated sites. The samples were analysed for dissolved inorganic nutrients, ammonium (NH_4^+), nitrite + nitrate (NO_2^- + NO_3^-), and phosphate (PO_4^{3-}) (Strickland and Parsons 1972, Ryle *et al.* 1981, Chapter 2).

Adsorbed nutrients

Sediment samples were collected to the depth of the rhizosphere at each location (2.5 cm *Halophila ovalis*, 10 cm *Halodule uninervis* and *Zostera capricorni*). The same core depth was used at the corresponding unvegetated site. Sediment core samples to be analysed for exchangeable inorganic nutrients were placed on ice then refrigerated until they could be analysed the following day. These samples were analysed for extractable inorganic NH_4^+ and PO_4^{3-} as described in Chapter 2.

Calcium carbonate and organic content

Sediment samples were prepared for analyses of percent calcium carbonate and organic content as described in Chapter 2.

Calculation of nutrient pools

I calculated the total nutrient pool based on a litre of sediment, as all nutrient measures were required to be in similar units as previously explained in Chapter 2. In vegetated areas this total nutrient pool included seagrass + sediment nutrients. To convert to a volume (g Nutrient $L_{sediment}^{-}1$), the seagrass measure of nutrient (g Nutrient $_{seagrass}$ m $^{-2}$) was multiplied by the depth of the rhizosphere (*Zostera capricorni* 10 cm, *Halodule uninervis* 10 cm and *Halophila ovalis* 2.5 cm). Grams of each tissue nutrient were converted using the elemental molecular weight of the nutrient (N—14 and P—31). This resulting value was directly comparable to the other nutrient pool measures of µmol $L_{sediment}^{-1}$ as per Equations 3 and 4, Chapter 2.

Statistical methods

Principal Components Analysis (PCA) was used as an exploratory tool to identify the existence of relationships within the data set using SPSS. After grouping the data according to the PCA, sediment grain size and nutrient data were analysed using analysis of variance. Locations were considered as blocks. Measurements taken within a site were considered as samples rather than true replicates. Thus the location by site interaction term was considered the appropriate error for testing the site term. Distributional assumptions for the analyses were assessed by inspection of residual and normal probability plots. Data were log transformed where appropriate.

4.1.3 Results

Location characterization

All vegetated sites were monospecific stands of seagrass. *Halodule uninervis* (narrow) was the predominant species found at five locations, two locations were dominated by *Zostera capricorni,* and one location, *Halophila ovalis* (Table 4.1). Biomass measurements were extremely variable between locations. The highest biomass was recorded at Ellie Point, a meadow dominated by *Zostera capricorni,* (252.16 g DW m^{-2}), the lowest biomass was recorded at Bolger Bay, a location dominated by *Halophila ovalis* (0.2 g DW m^{-2}). Sediment pH measurements were indicative of marine influences (over pH 8.0) with the exception of Bolger Bay and Horseshoe Bay with recordings of pH 7.1 and pH 6.8 respectively (Table 4.1). These measurements are characteristic of a freshwater influence, possibly from ground water intrusion.

Carbonate content ranged from 1.44% at Ellie Point to 75.97% at Geoffrey Bay (Table 4.1). Of these sites, only Geoffrey Bay could be considered to have carbonate sediments (carbonate content ≥ 50%, Scoffin 1987). Organic content ranged from 0.51% at Port Dennison to 2.14% at Windy Point (Table 4.1).

Locations within the central region of the Great Barrier Reef World Heritage Area where seagrass beds occurred were categorised by sediment type as either muddy or sandy (PCA, Fig. 4.1, Table 4.1). The muddy sites were more variable in grain size and nutrients than the sandy sites (Fig. 4.2). This variability may be related to the more complex mineralogy associated with clay minerals found in muddy sediments compared with the more uniform mineralogy at sandy sites. Sandy sites were inhabited predominantly by the narrow morph of *Halodule uninervis*. The muddy sites were inhabited by a variety of species, including *Halodule uninervis*, *Halophila ovalis* and both locations dominated by *Zostera capricorni* (Table 4.1). Analyses were conducted separately on each sediment type, because of the potential influences of sediment grain size on sediment geochemistry (see Short 1987, Erftemeijer and Middelburg 1993).

Sandy locations

Sediment structure

Analysis of the fine silt fraction of the sediment (as a representative of all sediment analyses) showed that there was no significant difference in percent fine silt between vegetated and unvegetated sites ($F_{(1,3)} = 0.24$, $p = 0.656$, Fig. 4 2a). There were, however, large differences between locations (Fig. 4.2a). Lugger Bay and Geoffrey Bay had proportionately higher percentages of fine silt present than the other two sandy locations, Horseshoe Bay and Port Dennison (Fig. 4.2a).

Sediment nutrients

Mean porewater $NO_2^- + NO_3^-$ ranged from 0.02 µM (Horseshoe Bay) to 1.27 µM (Port Dennison) (Table 4.2). Conversely, Port Dennison recorded the lowest mean porewater NH_4^+ (6.31 µM), while Horseshoe Bay recorded the highest mean concentration (144.43 µM).

Measurements of mean porewater PO_4^{3-} ranged from 0.69 µM (Horseshoe Bay) to 3.15 µM (Geoffrey Bay). Geoffrey Bay recorded the highest mean concentration of adsorbed

NH_4^+. The lowest concentration of adsorbed NH_4^+ was recorded from Lugger Bay (Table 4.2). The highest and lowest concentrations (a 30 fold difference) of adsorbed PO_4^{3-} were recorded from Geoffrey Bay and depended on the method of extraction used (Table 4.2). The Bray technique tends to extract phosphate incompletely in an alkaline environment due to the presence of calcium carbonate (Pailles and Moody, 1995). The bicarbonate method is not affected by pH and is more appropriate for alkaline soils pH > 7.8 (Baker and Eldershaw 1993). This large difference in adsorbed PO_4^{3-} concentrations from the same site using different extractive techniques demonstrates the need to consider sediment type and to choose appropriate analytical methods for adsorbed PO_4^{3-}.

No significant differences were detected between vegetated and unvegetated sites for any of the nutrient parameters (Table 4.3). Comparison of the Location sums of squares in relation to the Site sums of squares indicated that the majority of the variance within these data sets was the result of differences between locations (Table 4.3).

Muddy locations

Sediment structure

The amount of very fine silt (as a representative of sediment grain size analyses) was not significantly different between vegetated and unvegetated sites ($F_{(1,3)} = 0.13$, $p = 0.738$, Fig. 4.2b). However at locations dominated by *Zostera capricorni* (Windy Point and Ellie Point) there was an apparent species effect with a higher percentage of very fine silt (Fig. 4.2b). Although the two vegetated sites both had a higher proportion of very fine silt than the unvegetated sites, the effect was significant only at Windy Point ($F_{(1,4)} = 181.43$, $p = 0.001$).

Sediment nutrients

Windy Point (*Zostera capricorni*) recorded the lowest porewater $NO_2^- + NO_3^-$, adsorbed NH_4^+ and adsorbed $PO_4^{3-}{}_{(Bray)}$ (Table 4.2). The lowest concentrations of porewater NH_4^+, PO_4^{3-} and adsorbed $PO_4^{3-}{}_{(bicarbonate)}$ were reported from Ellie Point, (also *Zostera capricorni*, Table 4.2). The highest concentrations of all nutrients were recorded from Meunga Creek (Table 4.2).

No significant differences were detected between vegetated and unvegetated sites for any of the nutrient parameters (Table 4.3). Comparison of the Location sums of squares and the Site sums of squares showed that, with the exception of adsorbed NH_4^+, most of the data variance was allocated to differences between locations (Table 4.3). For adsorbed NH_4^+ the variance was due to both Location (meadow) and Site (vegetated vs unvegetated (Table 4.3) and a trend was obvious, with concentrations of adsorbed NH_4^+ being greater in vegetated sites (Fig. 4.2c), although the difference was not significant (Table 4.3, $p = 0.096$).

Total nutrient pools

Whilst there was no difference between vegetated and unvegetated areas in their sediment nutrient pools, there were noticeable differences in the total nutient pools between vegetated (plant + sediment nutrient pool) and unvegetated (sediment nutrient pool) areas (Table 4.4). Locations that supported a relatively larger biomass of seagrass had a greater total nutrient pool than adjacent unvegetated areas (e.g. Ellie Point, Biomass: 252.16 ± 24.52 g DW m^{-2} ; Vegetated nutrient pool : Unvegated nutrient pool (veg:unveg for N, 71.4:1; veg:unveg for $P_{(bray),}$ 10.3:1, veg:unveg for $P_{(bicarb)}$, 15.3) and Windy Point, Biomass: 72.34 ± 3.96 g DW m^{-2} ; veg:unveg for N, 29.3:1, veg:unveg for $P_{(bray),}$ 6.4:1, veg:unveg for $P_{(bicarb)}$, 4.0:1, Table 4.4). Even those meadows that support lower seagrass biomass (e.g. Bolger Bay , 0.2 ± 0.12 g DW m^{-2} ; veg:unveg for N,1.7:1; veg:unveg for $P_{(bray),}$ 1.0:1, veg:unveg for $P_{(bicarb)}$, 1.1:1;, Horseshoe Bay, 2.92 ± 0.87 g DW m^{-2} ; veg:unveg for N, 2.0:1; veg:unveg for $P_{(bray),}$ 1.5:1, veg:unveg for $P_{(bicarb)}$, 1.0:1, Table 4.4) recorded more total nutrients in the vegetated sites compared with adjacent unvegetated areas. However, when comparing the amount of nutrient bound up in the plant pool compared to that in the sediment pool, Plant nutrients:Sediment nutrients (Pl nut:Sed nut), it is only those meadows that support large biomasses where the biome comprises the majority of the total nutrient pool (e.g. Ellie Point (Plant N:Sediment N, 14.2:1, Plant P:Sediment $P_{(bray)}$, 10.1:1 and Plant P:Sediment $P_{(bicarb)}$ 21.8:1 cf Bolger Bay (Plant N:Sediment N, 0.2:1; Plant P:Sediment $P_{(bray)}$, 0.01:1, Plant P:Sediment $P_{(bicarb)}$, 0.1:1), Table 4.4). This result is intuitive but it serves to highlight the differences between locations and species that support and produce meadows of high biomass with those locations and species that do not and once again emphasizes the uniqueness of location and species-specific interactions with the local environment.

4.1.4 Discussion

Across a range of mud and sand localities in a tropical intertidal habitat, the paradigm of seagrass meadows trapping sediments and nutrients did not hold. Porewater and adsorbed nutrient concentrations and sediment grain size distributions were not significantly different between seagrass meadows and adjacent unvegetated sites. I considered seagrass functional form and biomass were important in determining sedimentation processes. The relatively high biomass and stable *Zostera capricorni* meadows showed trends towards an increase in sedimentation and a decrease in nutrient concentration (increases in nutrient utilisation) in vegetated compared with unvegetated areas (Fig. 4.2b, Fig. 4.2c). In contrast, no trends were evident in the low biomass meadows of *Halodule uninervis* and *Halophila ovalis* (Fig. 4.2a, b and c).

The seagrass biomass values reported here are comparable to those reported elsewhere in tropical Queensland (Lee Long *et al.* 1993). These values are less than the values quoted for temperate Australian waters (see Hillman *et al.* 1989), and do not approach the recorded maxima for Caribbean seagrass beds (Bauersfield *et al.* 1969), North American beds (McRoy *et al.* 1972) or Mediterranean seagrass beds (Gacia *et al.* 1999). Most seagrass species in the central region of the Great Barrier Reef World Heritage Area are structurally small and their meadows are ephemeral compared with temperate seagrass communities and some other tropical regions. Regardless of their diminutive state, these seagrasses play a central role in supporting grazing by large populations of macro-herbivores (dugongs and green turtles) (Aragones and Marsh 2000).

Differences between vegetated and unvegetated sites were evident, with some of the nutrient parameters, but these differences were not significant once the influence of location was removed. The two *Zostera capricorni* meadows had the highest biomass (1200 times that of *Halophila ovalis*) and occurred in areas low in porewater nutrients while *Halodule uninervis* was associated with high porewater nutrients suggesting a difference in nutritional requirements of these species or their ability to modify their nutrient environment.

This study shows that seagrass meadows of structurally small species do not act in accordance with the paradigm that seagrasses trap sediments and nutrients. Within these beds, none of the measured nutrient parameters demonstrated evidence for detrital

cycling in sediments. All measurements showed low organic content and no difference in sediment structure or nutrient state between vegetated and unvegetated sites. However, the paradigm was partially supported in the meadows of *Zostera capricorni* (high biomass) that are similar in functional form to the meadows and species that have contributed to the 'trapping' paradigm.

The combination of low water column nutrients (Furnas 2003) and the comparison between the total nutrient pools of vegetated and unvegetated areas suggests that the nutrients in the coastal shallow environments of this region are bound up in the sediments and biome rather than free in the water column. However, a dichotomy exists between meadows of high biomass and those of low biomass. In low biomass meadows most nutrients are bound up in the sediment suggesting that the sediments in this region act as nutrient sinks and that the seagrasses are nutrient sponges (Richardson *et al.* 1978), as shown by the high plant tissue nutrient contents observed from meadows in this region (Chapter 3, Table 3.6).

4.1.5 Conclusions

Within the central region of the Great Barrier Reef World Heritage Area, *Zostera capricorni* maintains beds of relatively high biomass that have persisted for decades (Coles *et al.* 1985). Seagrass meadows of this species are more comparable to structurally larger seagrass species that have been shown to alter the sediment. This is in contrast to the more empheral species that dominate this region which have no effect on sediment structure. There is a considerable amount of the total nutrient pool bound up in these 'high' biomass meadows of *Zostera capricorni*. In contrast, *Halodule uninervis* and *Halophila ovalis* meadows do not trap sediments or nutrients. However, the total nutrient pool of these low biomass meadows is still greater than that of adjacent unvegetated areas indicating that these meadows contribute to the nutrient budget for this region. A within meadow comparison of nutrient pools for these low biomass meadows showed that most of the nutrient pool was bound up in the sediments rather than in the plants. I suggest that, this once again highlights the differences in the functioning of high biomass meadows of structurally large seagrass with that of the low biomass meadows of the structurally small species. The functional form model of Walker *et al.* (1999) conceptualizes the manner in which different seagrass species form functionally different meadows and should be tested over a variety of seagrass habitats.

In tropical Australia, the ‘trapping’ paradigm is largely insignificant as this region is typified by species that create low biomass ephemeral seagrass meadows in the intertidal coastal regions of the central region of the Great Barrier Reef World Heritage Area.

This examination of the trapping concept in relation to these structurally small seagrasses raises the question of whether other processes that flow on from this trapping function such as the relationship between sediment-structure–seagrass-abundance, nutrient-environment–seagrass-abundance and seagrass-tissue-nutrients–nutrient-environment also apply to these types of seagrasses and the differently structured meadows they form. These questions are evaluated in Subchapter 4.2

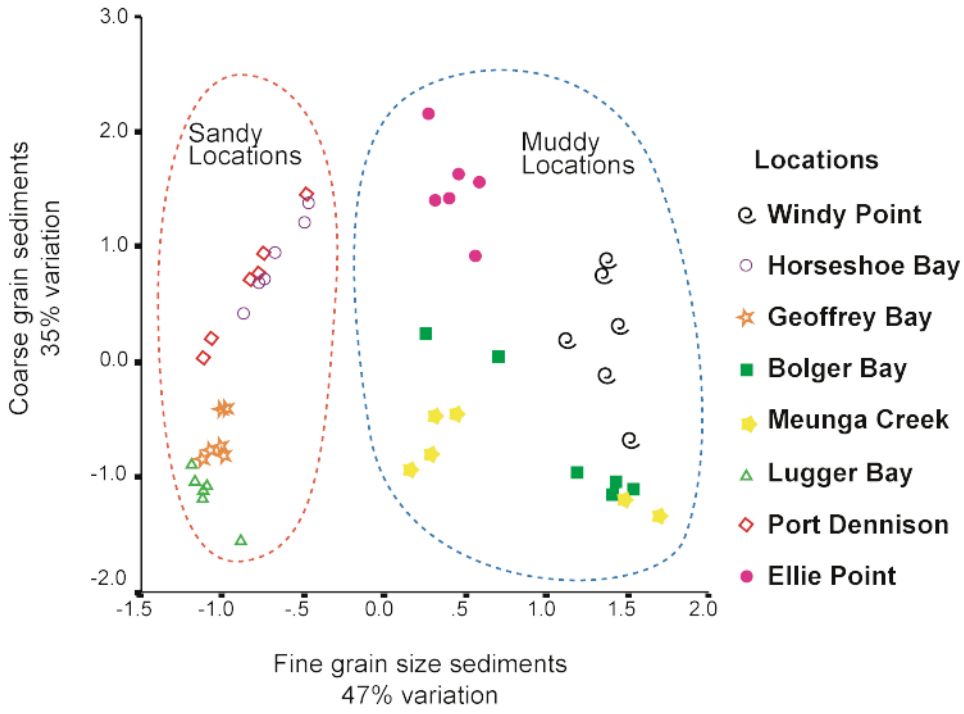


Figure 4.1 Plot of the first two axes based on Principle Component Analysis of intertidal areas (locations) categorised by sediment types (muddy or sandy). Axis 1 reflects sediment grain size, while Axis 2 is based on sediment nutrient levels.

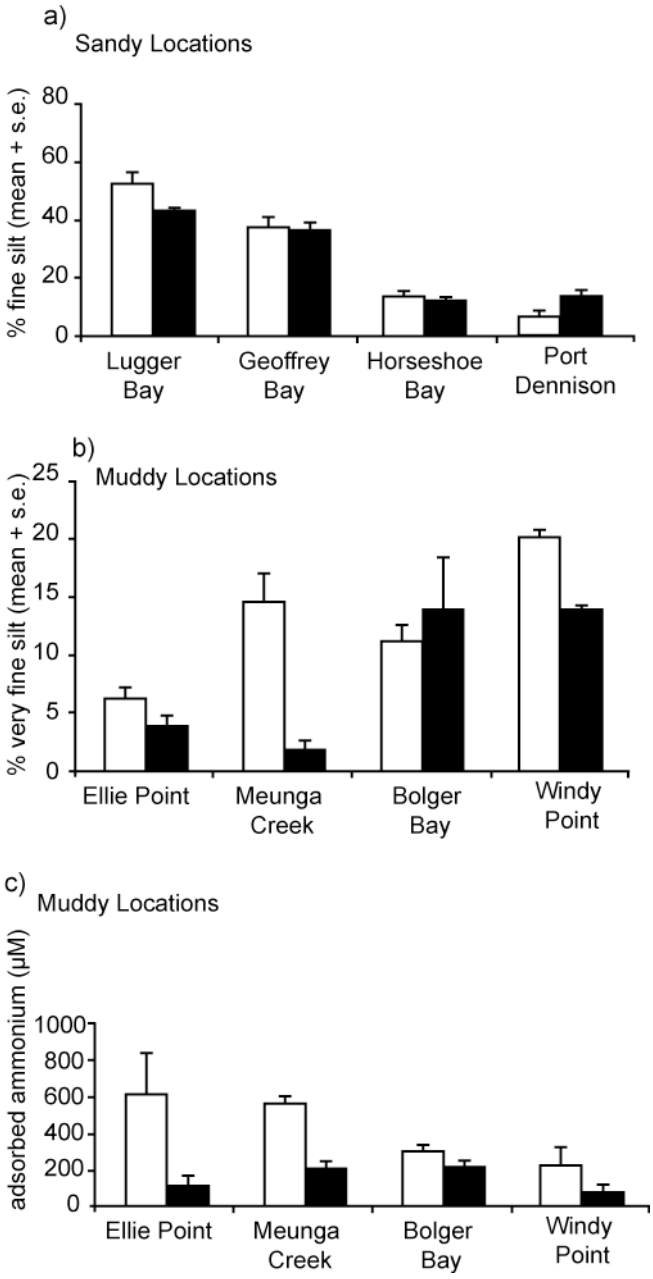


Figure 4.2: a) Fine silt at sand locations for vegetated and unvegetated sites, **b)** very fine silt at muddy locations for vegetated and unvegetated sites, **c)** adsorbed NH_4^+ at muddy locations for vegetated and unvegetated sites. Means and standard errors presented. Vegetated = open; unvegetated = closed. The patterns observed here are representative of the patterns observed for all grain size and nutrient analyses.

Table 4.1 Categorization of intertidal seagrass beds within the central region of the Great Barrier Reef World Heritage Area (values are mean ± s.e.).

Location (n=3)	Sediment type	Dominant species	Total biomass (g DW m^{-2})	pH	% carbonate	% organic content
Ellie Point, Cairns	Mud	*Zostera capricorni*	252.16 ± 24.52	8.0± 0.16	1.44 ± 0.24	1.30 ± 0.35
Meunga Creek, Cardwell	Mud	*Halodule uninervis*	5.01 ± 0.31	8.2 ± 0.07	1.85 ± 0.51	2.05 ± 0.23
Bolger Bay, Magnetic Island	Mud	*Halophila ovalis*	0.20 ± 0.12	7.1 ± 0.00	12.66 ± 1.62	1.82 ± 0.20
Windy Point, Cape Upstart	Mud	*Zostera capricorni*	72.34 ± 3.96	8.1 ± 0.05	14.4 ± 0.98	2.14 ± 0.20
Lugger Bay, Mission Beach	Sand	*Halodule uninervis*	5.38 ± 2.32	8.8 ± 0.05	1.94 ± 0.22	0.55 ± 0.04
Geoffrey Bay, Magnetic Island	Sand	*Halodule uninervis*	11.89 ± 0.73	8.9 ± 0.17	75.97 ± 0.46	2.00 ± 0 04
Horseshoe Bay, Magnetic Island	Sand	*Halodule uninervis*	2.92 ± 0.87	6.8 ± 0.05	14.39 ± 0.19	0.96 ± 0.05
Port Dennison, Bowen	Sand	*Halodule uninervis*	25.10 ± 5.56	8.7 ± 0.03	4.45 ± 0.78	0.51 ± 0.02

Table 4.2 Concentrations of sediment nutrients (means ± s.e.) recorded for each location at unvegetated (unveg) and vegetated (veg) sites at each of eight locations in the central regions of the Great Barrier Reef World Heritage Area.

Location	Site	Porewater $NO_2^-+NO_3^-$ µmol L^{-1} n = 15	Porewater NH_4^+ µmol L^{-1} n = 15	Porewater PO_4^{3-} µmol L^{-1} n = 15	Adsorbed NH_4^+ µmol kg^{-1} n = 5	Adsorbed PO_4^{3-} (Bray) µmol kg^{-1} n = 5	Adsorbed PO_4^{3-} (bicarbonate) µmol kg^{-1} n = 5
Sandy locations							
Lugger Bay	unveg	0.56 ± 0.14	27.36 ± 6.76	1.40 ± 0.07	27.90 ± 9.76	123.31 ± 3.36	126.55 ± 3.07
	veg	0.67 ± 0.23	13.75 ± 2.58	1.57 ±0.14	43.10 ± 12.51	147.3 ± 12.30	130.37 ± 11.85
Port Dennison	unveg	1.27 ± 0.70	47.57 ± 5.69	2.92 ± 0.51	115.23 ± 36.75	133.20 ± 15.19	135.66 ± 11.10
	veg	0.76 ± 0.29	6.31 ± 0.87	1.60 ± 0.16	38.64 ± 14.66	85.57 ± 4.46	66.44 ± 12.39
Geoffrey Bay	unveg	0.04 ± 0.01	31.73± 5.81	2.63 ± 0.18	183.30 ± 43.49	11.40 ± 3.61	394.22 ± 25.17
	veg	0.09 ± 0.02	28.68 ± 4.01	3.15 ± 0.45	252.49 ± 34.65	17.59 ± 3.78	408.30 ± 32.51
Horseshoe Bay	unveg	0.02 ± 0.003	73.47 ± 18.74	0.95 ± 0.09	191.02 ± 13.16	96.48 ± 5.08	153.13 ± 5.53
	veg	0.03 ± 0.007	144.43 ± 25.12	0.69 ± 0.10	229.96 ± 10.27	124.41 ± 13.22	144.72 ± 8.32
Muddy locations							
Ellie Point	unveg	0.44 ± 0.15	45.27 ± 6.94	2.82 ± 0.48	88.00 ± 31.65	312.80 ± 28.75	228.66.± 22.03
	veg	0.41 ± 0.13	1.84 ± 0.09	0.84 ± 0.06	532.47 ± 152.66	353.19 ± 47.81	142.57 ± 12.10
Meunga Creek	unveg	2.28 ± 0.78	66.75 ± 9.39	6.08 ± 1.04	299.66 ± 60.58	459.04 ± 21.89	286.47 ± 22.68
	veg	3.12 ± 1.08	86.85 ± 7.15	2.65 ± 0.46	563.11 ± 40.67	820.08 ± 61.85	471.21 ± 64.92
Bolger Bay	unveg	0.66 ± 0.16	70.04 ± 6.52	1.32 ± 0.22	210.55 ± 15.08	439.98 ± 45.65	341.94 ± 29.27
	veg	0.32 ± 0.13	59.35 ± 6.34	2.20 ± 0.47	257.72 ± 24.71	482.83 ± 75.81	328.36 ± 42.40
Windy Point	unveg	0.43 ± 0.16	18.99 ± 3.04	0.99 ± 0.13	91.77 ± 21.63	167.72 ± 12.21	251.11 ± 16.88
	veg	0.17 ± 0.09	2.47 ± 0.25	0.85 ± 0.16	203.11 ± 59.16	225.34 ± 21.78	240.36 ± 34.10

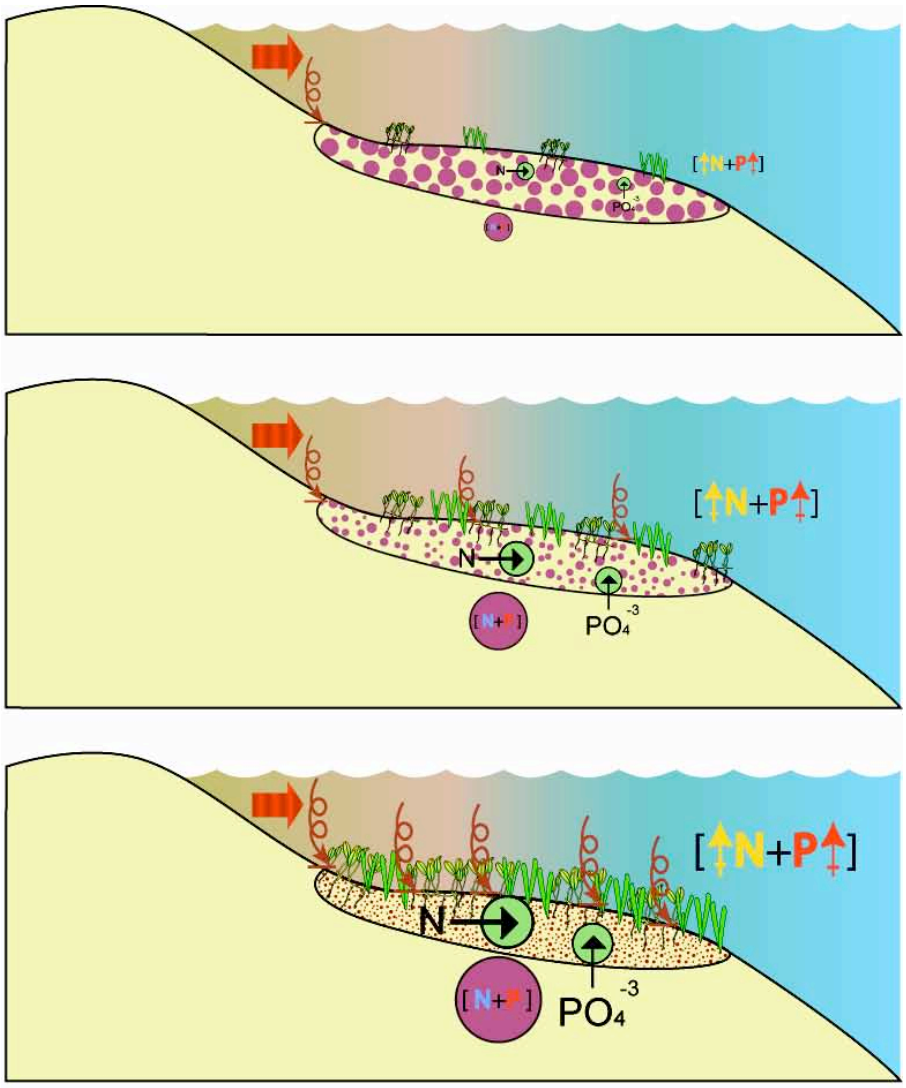
Table 4.3 The results of two series of ANOVAs (one for locations with sandy substrates and for one locations with muddy substrates) for comparing the differences between the vegetated and unvegetated sites at these locations.

Variable	Location SS	Site SS	$F_{(df)}$	*p*
Sandy locations				
adsorbed PO_4^{3-} (bicarbonate)	307206.9	1399.00	$0.30_{(1,4)}$	0.620
adsorbed PO_4^{3-} (Bray)	51089.8	12.00	$0.001_{(1,4)}$	0.934
adsorbed NH_4^+	132664.0	2678.00	$0.20_{(1,4)}$	0.686
porewater PO_4^{3-}	0.77	0.014	$2.05_{(1,14)}$	0.284
porewater NH_4^+	1.782	0.0018	$0.02_{(1,14)}$	0.908
porewater $NO_2^- + NO_3^-$	4.148	0.2346	$0.14_{(1,14)}$	0.736
Muddy locations				
adsorbed PO_4^{3-} (bicarbonate)	0.58	0.002	$0.03_{(1,4)}$	0.879
adsorbed PO_4^{3-} (Bray)	1.38	0.13	$5.04_{(1,4)}$	0.111
adsorbed NH_4^+	1.60	1.58	$5.76_{(1,4)}$	0.096
porewater PO_4^{3-}	5.83	1.21	$1.84_{(1,14)}$	0.268
porewater NH_4^+	28.41	8.50	$2.35_{(1,14)}$	0.223
porewater $NO_2^- + NO_3^-$	1.94	0.019	$0.47_{(1,14)}$	0.540

Table 4.4 A comparison of N and P nutrient pool ratios between vegetated and adjacent unvegetated areas, with a within bed comparison of plant nutrients and sediment nutrient ratios.

Location species	**Total biomass (g DW m^{-2})**	**Total nutrient N pool veg:unveg**	**Plant N: sediment N**	**Total nutrient $P_{(Bray)}$ pool veg:unveg**	**Plant P: sediment $P_{(Bray)}$**	**Total nutrient $P_{(bicarb)}$ pool veg:unveg**	**Plant P: sediment $P_{(bicarb)}$**
Ellie Point, Cairns Zostera capricorni	252.16 ± 24.52	71.4	14.2	10.3	8.7	15.3	21.8
Meunga Creek, Cardwell *Halodule uninervis*	5.01 ± 0.31	4.3	1.5	1.7	0.3	1.5	0.7
Bolger Bay, Magnetic Island *Halophila ovalis*	0.20 ± 0.12	1.7	0.2	1.0	0.0	1.1	0.1
Windy Point, Cape Upstart *Zostera capricorni*	72.34 ± 3.96	29.3	13.1	6.4	5.0	4.0	4.3
Lugger Bay, Mission Beach *Halodule uninervis*	5.38 ± 2.32	8.3	8.2	1.7	0.7	1.6	0.7
Geoffrey Bay, Magnetic Island *Halodule uninervis*	11.89 ± 0.73	7.3	3.0	12.8	12.9	1.5	0.5
Horseshoe Bay, Magnetic Island *Halodule uninervis*	2.92 ± 0.87	2.0	0.7	1.5	0.2	1.0	0.2
Port Dennison, Bowen *Halodule uninervis*	25.10 ± 5.56	10.1	28.6	3.2	3.3	2.6	5.3

Subchapter 4.2 Putting ecological processes in seagrass communities into context: Do north-east Australian intertidal seagrass communities conform?



Conceptual diagram of the current generally accepted view of sediment trapping concept within seagrass meadows.

Summary

I assessed current understanding of the ecological processes associated with the sediment trapping function and nutrient interactions within intertidal seagrass meadows of the central region of the Great Barrier Reef World Heritage Area. My evaluation indicated that the accepted relationships between: (1) seagrass abundance and sediment structure, (2) the geochemical environment and seagrass abundance, and (3) plant tissue nutrients and the geochemical environment were not appropriate for the species and locations I examined. I concluded that the accepted views were appropriate only for structurally large seagrasses, which form high biomass meadows with closed canopies. In contrast, I studied low biomass meadows of structurally small species, with open leaf canopies. I attributed this divergence from the commonly accepted views on seagrass sediment trapping and its associated nutrient relationships to be a function of the differences in seagrass architecture and meadow development which are in turn influenced by each meadows' local environment, climate and geography, that is, location.

4.2.1 Introduction

Several independent studies have shown that the presence of seagrasses can reduce the mean particle size of the sediment by trapping and accumulating a large proportion of the silt-clay fraction (Fonseca *et al.* 1982, Kenworthy *et al.* 1982, Hemminga and Duarte 2000). The leaf canopy reduces the water flow velocity and turbulence increasing the amount of sediment trapped within the meadow (Fonseca *et al.* 1982, Harlin *et al.* 1982, Fonseca and Fisher 1986, Fonseca 1989, Walker 1989). The settlement and retention of organic matter are also enhanced (Orth 1977, Kenworthy *et al.* 1982, Kemp *et al.* 1984, Hemminga and Duarte 2000). This new sediment and organic matter are bound by the network of roots and rhizomes. This increases stabilization of the existing sediment and minimizes the potential for erosion and sediment re-suspension (Phillips and Meñez 1988, Hemminga and Duarte 2000).

Sediment accretion is thought to vary between species of differing morphologies and the associated differences in abundances (Phillips and Meñez 1988, Zieman and Zieman 1989). Seagrass meadows vary in size from small, isolated patches, less than one metre in diameter, to a continuous distribution many square kilometres in area. Within a meadow, the plants often display a large variation in density and morphology (Phillips *et al.* 1983, Short 1983, Short *et al.* 1985, Short 1987, Thayer *et al.* 1984, Perez *et al.* 1994). These differences between and within meadows have been explained by differences in the supply of nutrients in the sediments, where a greater supply of nutrients corresponds to a greater biomass of seagrass (Patriquin 1972, Thayer *et al.* 1984, Hillman *et al.* 1989, Erftemeijer 1990). In light of this, sediment geochemistry of seagrass beds is important in determining the nutrients limiting seagrass abundance (biomass, shoot density) (Short 1987).

Hence, it has been presumed that meadows with more seagrass should have higher rates of accretion than meadows of lower seagrass abundance. With higher rates of sediment accretion there should be higher retention rates of organic matter. Since organic matter contains nitrogen and phosphorus, it follows that elevated concentrations of organic matter may also result in quantitative and qualitative changes in the sedimentary nutrient pool (e.g. *Zostera marina* meadows Phillips and Meñez 1988; *Posidonia oceanica* meadows Terrados and Duarte 1999, Gacia and Duarte 2001). Increased

availability of nutrients for uptake should lead to increased productivity and growth and therefore greater abundances of seagrasses (e.g. Short 1983 *viz.*, *Zostera marina* abundance and nitrogen pools). Uptake rates of nutrients are generally related to seagrass tissue nutrient content (Mengel and Kirkby 1987). Hence, the nutrient content of the seagrass will reflect its nutrient environment (Fourqurean *et al.* 1992, Udy and Dennison 1996, 1997a). Thus, there is a link between increases in sediment nutrient levels as a by-product of sediment accretion and the delivery and uptake of nutrients by seagrass.

In Subchapter 4.1, I established that the paradigm that seagrass meadows trap more sediments and nutrients than bare sediments, did not hold across a range of mud and sand localities in the Central region of the Great Barrier Reef World Heritage Area. Differences in location rather than the presence of seagrass *per se* explained sediment structure and associated nutrient levels, suggesting that location, the surrogate for many biophysical factors, plays the greatest role in structuring seagrass populations in the regions. However, I also found that meadows of *Zostera capricorni,* which have higher biomass and more complex plant architecture than meadows of the low biomass, structurally small, *Halodule uninervis* and *Halophila ovalis,* trapped more finer sediments than other species. Consequently, I decided to assess these sediments relationships further.

I assessed the following three concepts:

i. *Seagrass abundance affects sediment structure (physical environment).* As seagrass abundance increases, mean sediment structure will change by retaining a larger proportion of the silt-clay fraction (Fonseca *et al.* 1982, Kenworthy *et al*. 1982, Phillips and Meñez 1988, Zieman and Zieman 1989, Hemminga and Duarte 2000).

ii. *Sediment nutrients and related parameters (chemical environment) affect seagrass abundance.* Differences in the supply of nutrients in the sediments explain differences in seagrass abundance between and within meadows (Patriquin 1972, Thayer *et al.* 1984, Short 1987, Hillman *et al.* 1989, Erftemeijer 1990).

iii. *Sediment nutrients are reflected in seagrass plant tissue nutrients.* Seagrass tissue nutrient content reflects the nutrient environment inhabited by seagrass (Phillips and Meñez 1988, Fourqurean *et al.* 1992, Udy and Dennison 1996, 1997b).

Each of these concepts was evaluated for each of the different species encountered in the seagrass meadows that were examined in this region of the Great Barrier Reef Lagoon. Only seagrass meadows that were known to have persisted over the previous three years were studied.

4.2.2 Materials and methods

Only those methodologies relevant to this chapter (e.g. number of locations represented, the number of nutrient and seagrass samples collected and the parameterization of these samples) are described below. All general methodologies (e.g. the extraction and analysis of inorganic nutrients, the digest and consequent nutrient analysis of plant tissue nutrients and the collection and analysis of sediment structure) have been described in Chapter 2.

Study sites

Eleven locations were studied, all located within the central region of Great Barrier Reef Lagoon (GBRL) (see Fig. 2.4). The seagrass species and percent seagrass cover at each location is detailed in Table 4.5.

Experimental design

Three randomly selected 0.25m^2 quadrats of seagrass (above and below ground biomass) were collected from the landward edge of each seagrass meadow (location). Prior to seagrass removal, two porewater samples and two sediment cores (one for nutrient analyses, the other for sediment grain size and analyses of percent organic and carbonate matter) were collected. This design meant that the biomass and nutrient content of the seagrass samples could be directly related to the samples of porewater and adsorbed nutrients taken from within the quadrat from which the seagrass biomass was sampled.

Sampling

Nutrients

Porewater-dissolved inorganic nutrients

Two porewater samples per seagrass quadrat were collected *in situ* at each location using sediment sippers (modified from Murray *et al.* 1992, Udy and Dennison 1996). The treatment and chemical determinations of the porewater PO_4^{3-}, NH_4^+ and NO_2^- + NO_3^- are described in Chapter 2. As I was primarily interested in differences between locations and not between quadrats within location, the results from the porewater samples within each quadrat were averaged.

Adsorbed–extractable inorganic nutrients

One sediment core was taken per seagrass quadrat and treated as a depth integrated sample of the rhizosphere. Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$, $PO_4^{3-}{}_{(Bray)}$ and NH_4^+ were extracted from this depth integrated core. The methodologies of the extractions and consequent chemical determination of the nutrients are outlined in Chapter 2.

Physico chemical environment of the sediments

One sediment core per seagrass quadrat (i.e. three per location) was collected for the analysis of porosity, grain size, and percent organic and carbonate content. Eh and pH were measured in each quadrat (three times) and averaged for location. Methodologies and equipment used in the determination of porosity, sediment grain size, percent organic and carbonate matter, Eh and pH are described in Chapter 2.

Seagrass

At each location three, 50 x 50 cm (0.25 m^{-2}) quadrats were excavated. Seagrass shoots were counted from each quadrat. The seagrass was then separated into leaves, rhizomes, and roots. Each component was dried and weighed then prepared for plant tissue digest and analyses as described in Chapter 2.

Statistical methods

Three different concepts were assessed. The variables for each concept are outlined in Table 4.6–Concept 1, Table 4.10–Concept 2 and Table 4.13–Concept 3. Pearson Rank

Correlations were performed for each species on the suite of variables that related to each concept, to determine if any gross relationships existed for all locations combined. In addition MANOVA or ANOVA analyses were performed in SPSS to examine the relationships between locations, dependent variables and covariates for each species. Location was always defined as the independent categorical variable.

Within a data set (each species), the group of variables defined as the dependent variables (response parameter) or the covariates (influential variables) depended on the concept being tested. MANOVAs were performed when there was more than one dependent variable. If there was only one dependent variable, an ANOVA was used. Because of the small sample size of the data sets of *Zostera capricorni* and *Halophila ovalis*, the full compliment of the dependent variables and the covariates could not be tested together. Consequently, models using univariate analyses (ANOVA) and/or a single covariate were performed where appropriate. Because of a lack of sufficient plant material at Bolger Bay, analysis of plant tissue nutrients and sediment nutrient interactions for *Halophila ovalis* could not be performed. Also because of the weak power of the MANOVA, the results of the analyses for *Zostera capricorni* and *Halophila ovalis* must be viewed with caution. In particular the probability of a Type II error is high.

For assessing Concepts 1 and 2 several MANOVA models were run. Three models were used to assess Concept 1 based on the three covariate groupings: 1) total biomass, 2) leaf, rhizome and root biomass and 3) leaf density (Table 4.6). The three models used to test Concept 2 were based on the three dependent variable groupings: 1) total biomass, 2) leaf, rhizome and root biomass and 3) leaf density (Table 4.10). A single model was used to assess Concept 3 (Table 4.13).

These analyses were repeated for each of the three species *Halodule uninervis, Zostera capricorni,* and *Halophila ovalis.* A significant result was identified in a MANOVA when the Pillai's trace had a $p < 0.05$. If the MANOVA was not significant, the covariates were removed from the model to examine the relationship of location on the dependent variables. If a MANOVA was significant, the tables for the 'between subjects test' were examined to determine which dependent variable and covariate were influencing the outcome. As a result of the large number of samples collected and their subsequent parameterization (957 variables) and statistical analyses, only the significant

results are displayed and discussed in this subchapter. Full tables of the significant analyses and correlations are found in Appendix B.

4.2.3 Results

Concept 1: Seagrass abundance affects sediment structure

To evaluate this concept a MANOVA, which included the sediment structure characteristics as the dependent variable and seagrass abundance measures as covariates, was performed on each species of seagrass (Table 4.6). Location (independent categorical variable) was effectively treated as a blocking factor.

Halodule uninervis

Differences in sediment structure were primarily different between locations. Very fine silt varied significantly with total biomass and rhizome biomass (Table 4.7). The proportion of very fine silt was negatively related to below ground biomass (Fig. 4.3)

Zostera capricorni

Multivariate analysis revealed that sediment structure did not differ between the two *Zostera capricorni* meadows regardless of plant abundance measures being different between the locations (Table 4.8). These analyses included only two locations, (hence the power of the test is weak) which were separated by 400 km. However, this result suggests that a certain type of sediment or area is preferentially suited to *Zostera capricorni* colonization, as both these locations are extremely muddy (Chapter 4.1, Fig. 4.1).

Halophila ovalis

Sediment structure in *Halophila ovalis* meadows was not moderated by any measure of plant abundance (Table 4.9). There were large differences in sediment structure between the two locations. The meadow at Bolger Bay had a higher proportion of finer sediments (clay and very fine silt) than Picnic Bay, while Picnic Bay recorded higher percentages of sand sized sediment than Bolger Bay (Fig. 4.4). However, as the replication was low, this result should be treated cautiously.

Concept 2: Sediment nutrients (chemical parameters) affect seagrass abundance

To evaluate this concept, a series of ANOVAs and a MANOVA, which included the seagrass abundance parameters of total biomass (Model 1), leaf, rhizome and root biomass (Model 2) and shoot density (Model 3) as the dependent variables, and the sediment nutrients and related parameters of Eh, Ph, percent carbonate and percent organic content as covariates, was performed on each species of seagrass (Table 4.10). Location was treated as a categorical independent variable or blocking factor.

Halodule uninervis

There were strong negative correlations between below ground biomass and porewater NH_4^+ (Fig. 4.5). However, the differences between locations were greater than the relationship between sediment nutrients and seagrass abundance and no significant relations were observed, possibly because the geochemical parameters were extremely variable between locations (Chapter 3, Fig. 3.1). As there were no significant findings, no table has been included.

Zostera capricorni

There were differences in leaf, rhizome and root biomass and leaf density between locations (Table 4.11). Plant abundance appeared to be moderated by components of the geochemical environment within each location studied. The percent organic content in the sediments was positively correlated with biomass measures and increases in leaf densities were associated with increasing porewater NH_4^+. These results must be interpreted cautiously due to the small number of replicates (6) for this species.

Halophila ovalis

Plant abundance was significantly different between locations because of the very low biomasses at Bolger Bay. Plant abundance measures of leaf, rhizome, and root biomass and leaf density, were related to nitrogen concentrations (both adsorbed NH_4^+ and porewater $NO_2^- + NO_3^-$) (Table 4.12). The observed relationships were complex and not consistent between locations. At Picnic Bay, seagrass biomass was positively related to adsorbed NH_4^+ while at Bolger Bay, biomass was negatively related to adsorbed NH_4^+ even though levels of adsorbed NH_4^+ were lower at Bolger Bay (Fig. 4.6). This

relationship at Bolger Bay may not have been caused by concentrations of adsorbed NH_4^+ but to an extrinsic factor that caused the decline of seagrass at this site (see Chapter 2, cf. Table 2.1 with Table 4.5).

Concept 3 Sediment nutrients are reflected in seagrass plant tissue nutrients

To evaluate this concept a series of MANOVAs were run (Model 1–3), which included the seagrass plant tissue parameters of % leaf N and P, % rhizome N and P, % root N and P as the dependent variables and sediment nutrients and related parameters of Eh, pH, percent carbonate and percent organic content as covariates. These were performed on each species of seagrass (Table 4.13). Location was again treated as an independent categorical variable or blocking factor.

Halodule uninervis

Correlations revealed that plant tissue nutrients increased with increasing sediment porewater, adsorbed nutrients, and organic content. The MANOVA that included the full suite of plant tissue nutrients showed that none of the geochemical covariates were significant. However, examination of the 'between subjects table' revealed significant positive relationships between % leaf P with adsorbed phosphorous and porewater nitrogen within locations (Table 4.14).

Zostera capricorni

Overall, the multivariate analyses revealed no significant differences between locations or any relevant relationships between plant tissue nutrients of *Zostera capricorni* (Fig. 4.7) and the geochemical parameters, despite the observed geochemical differences between locations (Chapter 3, Fig. 3.1).

Halophila ovalis

As a result of the low biomass at Bolger Bay, there was insufficient plant material for any plant tissue nutrient analyses. Consequently, I could not conduct statistical analyses to examine the effect of differences between locations and whether plant tissue nutrients of *Halophila ovalis* reflect the chemical environment it inhabits. However this concept is explored further for *Halophila ovalis* at Picnic Bay in Subchapter 5.3.

4.2.4 Discussion

In general the location of the seagrass meadow explained the major differences observed between sediment structure, seagrass abundance and plant tissue nutrients. This result is not surprising, as it has been documented that regional and local differences exist within seagrass systems based on the adaptive tolerances of the seagrass species in question (Phillips and Meñez 1988). Despite the local environment dictating seagrass responses, there were also species specific responses observed (Table 4.15). The seagrass function and form model (Walker *et al. 1*999) is a first step in identifying that different seagrass species have different ecological functions such as those assessed in my study.

In my reporting and interpretation of the significant responses (Table 4.15), I acknowledge the low numbers of locations sampled for *Zostera capricorni* and *Halophila ovalis.* These results are observational rather than formal experimental tests of the commonly accepted concepts of seagrass functional ecology.

Concept 1: Is sediment structure affected by seagrass abundance?

The literature suggests that sediments of seagrass meadows are richer in fine-grained silt and clay fractions than bare areas (e.g. Kenworthy *et al*. 1982). It is generally assumed that this results from the trapping of fine-grained particles by the seagrass canopy. Seagrass canopies change the hydrodynamic conditions of the benthic environment by dissipating the current energy and dampening vertical wave energy (Gacia *et al*. 1999, Verduin and Backhaus 2000). It has also been documented that current flux decreases with shoot density (Gambi *et al*. 1990). The reduced water motion inside the canopy lowers the particle carrying capacity of the water and consequently may lead to enhanced particle deposition. In addition seagrass canopies are expected to reduce re-suspension of sediment particles. This effect will be enhanced by sediment-binding actions of the dense three dimensional web formed by seagrass roots and rhizomes (Burrell and Schubel 1977, Hemminga and Duarte 2000). Therefore it follows that increases in plant abundance should lead to differences in the sediment's fine-grained fraction. Interestingly these previous studies have been based on structurally large seagrass species with high biomass meadows and a long term standing stock (e.g. *Posidonia oceanica:* Gacia *et al.* 1999, *Zostera marina*: Kenworthy *et al.*

1982, Thayer *et al.* 1984, Phillips and Meñez 1988, Zieman and Zieman 1989, Gambi *et al.* 1990; *Thalassia hemprichii:* Burrell and Schubel 1977, Phillips and Meñez 1988, Koch and Gust 1999). Consequently aspects of the species architecture, the age and stage of development of the particular meadow, rather than plant abundance *per se* may modify sediment structure.

Sediment structure differed significantly between locations characterized by *Halodule uninervis* and *Halophila ovalis*. *Halophila ovalis* showed no relationship between biotic parameters and sediment structure. Geographical differences between the two meadows of *Halophila ovalis* that I studied were probably sufficient to explain the different sedimentary regimes. Bolger Bay faces west and is subjected to the northward movement of turbid water from Cleveland Bay. The intertidal zone of this bay is also extensive. In comparison, Picnic Bay has a narrow intertidal zone and is bound by granitic headlands that when weathered supply the bay with coarse-grained sediment. Both these bays have stands of *Cymodocea serrulata/Thalassia hemprichii* on their seaward edge. These stands maybe the depositional zone for sediments borne in the water rather than the intertidal meadows on landward edge where *Halophila ovalis* is found. This accords with other studies where the strongest flow reduction has been observed to occur in the first 50 cm of a seagrass meadow's edge, with little change thereafter (Gambi *et al.* 1990).

The meadows of *Halodule uninervis* had different sediment structures, and appeared to be related to below ground seagrass biomass. However, the usual depositional properties associated with the seagrass meadow canopy did not occur, a negative relationship between below ground biomass and very fine silt was evident. In the central region of the Great Barrier Reef World Heritage Area, at this time of year, the proportion of plant material above ground was low (see Chapter 3, Fig. 3.1). I assume that the narrow leaved (<1 mm) morphology of this species will limited current baffling capacity and hence diminished depositional capabilities. The combination of low above ground biomass and fine-leaved form presumably account for the negative relationship between above ground biomass and sediment structure.

Nonetheless, the significant relationship between rhizome biomass and very fine silt suggests that below ground biomass influences sediment structures at each location (Fig. 4.3). In general, once sediment has been transported and settled in a location, it

typically becomes trapped by the seagrass meadow, with an observable increase in fine grain-sized particles with increasing below ground biomass (McRoy 1970, Burrell and Schubel 1977, Thayer *et al.* 1984, Fourqurean *et al.* 1992). In contrast, the percentage of very fine silt increased as rhizome biomass decreased. I suggest this is due to the relative placement of sampling with the meadow relative to the depositional zone.

Despite differences in plant abundance, no significant difference in sediment structure was detected between the two locations of meadows of *Zostera capricorni*, separated by c. 400 km. This suggests that *Zostera capricorni* in this region (almost at the northern extreme of its distribution) may be more competitive in sediments that are high in clay-silt fractions. Both the locations I studied are in close proximity to large rivers (Ellie Point–Barron River; Windy Point–Burdekin River). Differences in individual grain sizes between locations were apparent, perhaps reflecting the distance of these meadows from river mouths and the mobility of small and large sediment particles in the water column. Small grain sediments tend to be transported further away from a source than larger grain sediments (Folk 1974). The Ellie Point meadow (higher percentage of large sized particles) is located very close (c. 4 km) to the mouth of the Barron River, while Windy Point (higher percentage of smaller grained particles) is further from the mouth of the Burdekin River (c. 18.3 km). In addition, the gross morphology of *Zostera capricorni*, is architecturally and/or structurally more complex and larger than *Halodule uninervis* (narrow) and *Halophila ovalis.* As a result this species may have a greater influence on sediment structure (McRoy *et al.* 1972, Harlin *et al.* 1982, Boon 1986).

While the effect of plant canopies on water flow explains the capacity of seagrass meadows to act as a particle sink, there is a paucity of direct measurements to confirm or deny this. Gacia *et al*. (1999) using direct measurements of sedimentation and current flux also found that the presence of *Posidonia oceanica* did not effectively increase sediment deposition. Rather, *Posidonia oceanica* enhanced the retention of sediments by decreasing re-suspension within the meadow when compared with bare substrates. They also found that canopy particle trapping was not enhanced by increasing shoot density or above ground biomass. Rather, the leaf area index of the plants was significantly and strongly correlated with the total deposition within the bed (Gacia *et al*. 1999), a measure that I did not analyse. They also suggested that the capacity of *Posidonia oceanica*, a structurally large seagrass, to increase particle deposition is more significant at low particle concentrations in the water and in the absence of re-

suspension. In the region I studied, high particle concentration/suspended solids are the norm either from cyclonic action or high run-off during the summer months or re-suspension events caused by strong south easterly winds during the winter months. Thus, plant abundance measures do not appear to modify sediment structure in the central region of the Great Barrier Reef World Heritage Area, possibly because of differing architecture of these structurally small species (cf. structurally large species) on which the concept is based, or because the wind regime (disturbance) dominates any process that would lead to enhanced trapping within seagrass meadows along this coastline.

Concept 2: Is plant abundance affected by sediment geochemistry?

Plant abundance measures were significantly different between locations for all three species of seagrass. For *Zostera capricorni*, abundance differences appeared to be moderated by percent organic content observed in the sediments. Changes in the nitrogen pool were reflected in the plant abundance measures for both *Zostera capricorni* and *Halophila ovalis.* No significant relationships between plant abundance measures and nutrients within locations were observed for *Halodule uninervis*, though significant correlations on a regional scale were observed between below ground biomass and total biomass and porewater NH_4^+. This relationship was negative (i.e. as porewater NH_4^+ decreased, biomass increased) and may represent an increase in adsorptive areas (i.e. rhizomes and roots) in areas of low nutrient sediment (Short 1983). When location was included in the statistical analyses, no geochemical variables were significant. The abundance of *Halodule uninervis* was dependent on the local environment, geography and the nutrient concentrations in each meadow.

Whilst differences between locations accounted for the majority of differences in plant abundance measures for *Zostera capricorni*, leaf, rhizome and root biomass together appeared to be moderated by changes in organic content while leaf density seemed to be regulated within location by levels of porewater NH_4^+ (Table 4.11). None of the individual parameters of leaf, rhizome or root biomass could be linked to changes in percent organic content. Rather the three variables as a whole were moderated by changes in organic content. Similar patterns were evident within each location. Within each location, quadrats with the lowest percentages of organic content were represented by low leaf biomass but high rhizome biomass. As percent organic content increased the

relative proportions of leaf to rhizome biomass changed in favour of leaf biomass. An explanation of this relationship could be two-fold. Organic matter increases the sediment nutrient pool, as a result of digestion and mineralization processes by bacteria in the seagrass rhizosphere. Increases in the nutrient pool promote leaf growth. With increasing sediment nutrients, less rhizome and root material is required for nutrient uptake, hence the decrease in below ground biomass (Short 1983).

Although organic matter within sediments can be viewed as a source of nutrients, its deposition within the sediment from external sources is theoretically subjected to the same influences that determine the physical characteristics of the sediment. Hence as vegetation increases, inputs of organic matter should also increase (Kenworthy *et al.* 1982, Thayer *et al.* 1984, Phillips and Meñez 1988, Zieman and Zieman 1989, Hemminga and Duarte 2000). It is likely that both these influences act in concert as *Zostera capricorni* leaf density increased with increasing levels of porewater NH_4^+ within each location, a relationship that is well documented for this genus (Kenworthy *et al.* 1982, Short 1983, Thayer *et al.* 1984, Zieman and Zieman 1989). However as leaf abundance measures had no effect on sediment structure within location (previous section), and given my small sample size, the differences in plant abundances I observed are likely to be dependent on local micro-scale environmental and geographical conditions, not sediment conditions.

The leaf, rhizome and root biomass of *Halophila ovalis* co-varied with adsorbed NH_4^+, while rhizome biomass and leaf density varied with $NO_2^- + NO_3^-$. These observations were extremely variable between locations and the trends observed between locations were conflicting (e.g. at Picnic Bay increases in adsorbed NH_4^+ were reflected in increases in plant biomass while the converse was observed at Bolger Bay). These trends may be an artefact of the declining meadow observed at Bolger Bay. Seagrass cover (within a 0.25 m^{-2} quadrat) at this bay a year prior to this sampling was at 70–80% while during this sampling period percent cover had decreased to <5% (see Table 4.5). Whilst porewater nutrients in general were high at Bolger Bay in comparison to Picnic Bay, they were still at levels considered to be limiting (Dennison *et al*. 1987 and Erftemeijer and Middelburg 1993). Consequently, some other factor(s), of which I am unaware, may have been responsible for the decline in this meadow and I conclude that it would be in appropriate to draw any conclusions with respect to the relationship between plant abundance measures and geochemical parameters within this

disturbed bed. Adsorbed NH_4^+ levels were higher at Picnic Bay than at Bolger Bay and plant abundance increased with increasing levels of adsorbed NH_4^+. This observation concurs with the literature. The density and biomass of seagrasses often vary in space and time reflecting the nitrogen pool, as nitrogen levels are often considered the most limiting nutrient to growth and increases in biomass (McRoy and McMillan 1977, Short 1983).

Consequently, the geochemical environment did not appear to influence plant abundance measures in this correlative study. However seagrass meadows are dynamic environments and I did not investigate processes that may alter the availability of nutrients to seagrasses. The rates of microbial mineralization processes show pronounced local and regional variation and hence, these explain in part the variability of nutrient levels by location (Moriarty and Boon 1989). Another element of the system that alters the availability of nutrients for seagrass uptake is the mineralogy of the rhizosphere. Adsorption and desorption of sediment nutrients are strongly dependent on the type and quantity of minerals present in the sediment (Erftemeijer and Koch 2001). Seagrass meadows are dynamic systems, therefore measurements taken during a time of year when seagrasses were not actively growing and not interacting as much with their environment may not be indicative of the geochemical environment influencing plant abundances at other times.

Concept 3: Do plant nutrient tissues reflect their chemical environment?

An overview of the relationship between plant tissue nutrients and sediment geochemistry revealed species specific responses especially for *Halodule uninervis* and *Zostera capricorni* to their geochemical environment, suggesting species-specific nutrient requirements and uptake processes.

For *Halodule uninervis* (the largest data set, number of sites = 7), sediment nutrients were positively correlated with the nutrient content of the seagrass tissue. This suggests an increase in sediment nutrient levels is accompanied by an increase in plant nutrients. These results also suggest for this species, that the %N content of the seagrasses is determined by N availability and the %P content by P availability. This supports the premise that plant tissue nutrients are indicative of the bioavailability of sediment nutrients (Atkinson and Smith 1983, Fourqurean *et al.* 1992, Udy and Dennison 1997b).

The correlations between all plant parts and porewater nutrients of the same chemical form suggests that plant tissue content may be a good indicator of available porewater nutrients. Correlations with adsorbed nutrients indicate a positive feedback mechanism between *Halodule uninervis* and the sediment nutrient pool. As plants absorb the porewater nutrients, the concentration of the nutrient in the porewater is lowered and then the rhizosphere sediments desorb their adsorbed nutrients to the porewaters.

These relationships were obvious at a regional scale, but were not usually evident within locations. However, a few measures of % leaf P actually increased with increases in adsorbed PO_4^{3-}, % carbonate matter and porewater nitrogen related to the geochemical environment at Geoffrey Bay, a meadow with a high percentage of carbonate matter (see Chapter 3, Fig, 3.1). This implies that the percentage of P present in *Halodule uninervis* leaves is linked to the geochemical relationship between carbonate sediments and PO_4^{3-} (Short *et al.* 1985, McGlathery *et al.* 1994). The relationship between %P and porewater NH_4^+ suggests a synergistic relationship between N and P whereby uptake of sediment nitrogen facilitates the accumulation of tissue phosphorus (Udy and Dennison 1997b).

For *Zostera capricorni* plants, tissue nutrients generally did not differ between locations even though the sedimentary nutrient state differed between meadows (see Fig. 3.1). Thus plant tissue nutrients were not indicative of the nutrient state within these meadows. This result was surprising as *Zostera capricorni* is similar in structural form and congeneric to one of the species on which this concept is based. Alternatively, *Zostera capricorni* plant tissue nutrients may be reflecting water column nutrients within the meadows, a relationship not examined in this study, as water column nutrients may be the preferred nutrient reservoir for this species (see Hemminga *et al.* 1991). However, the similarities between the two *Zostera capricorni* meadows, with respect to sediment structure suggests that this species may out compete other species of seagrass in these extremely muddy environments (see Chapter 3, Fig. 3.1).

This study has indicated that seagrass tissue nutrients are not a particularly good indicator of the geochemical environment they inhabit. This result maybe indicative of the species investigated (*Halodule uninervis*), fast growing, high nutrient turnover (Walker *et al.* 1999) and the small sample size analysed (*Zostera capricorni* data set). However, as discussed previously there are several phenomena that affect the

availability of sediment nutrients for uptake and as well as species-specific nutrient requirements. The result discussed here suggests species-specific responses and warrants further investigation.

Seagrass-environment interactions

Over the range of seagrass abundance I studied, seagrass does not appear to modify sediment structure, nor does the geochemical environment influence plant abundance. In addition, plant tissue nutrients are poor indicators of the geochemical environment for the species studied in this region. Several reasons have been put forward to explain these vagaries.

The traditional views of seagrass functional ecology have been based on structurally large species, which develop large stable meadows of high biomass and closed leaf canopies. In contrast, I studied structurally small seagrasses with meadows of relatively low biomass and open leaf canopies (cf. Walker *et al.* 1999). It has been suggested that the abilities of seagrass to modify sediment structure and hence the geochemical environment through enhanced trapping of sediment particles is relevant only under conditions of low suspended sediments (Gacia *et al.* 1999) and high standing biomass. The region I studied is characterized by high levels of suspended sediment within the water column due to metrological regimes that change throughout the year. Consequently local abiotic conditions may greatly influence the ability of the seagrass to trap sediment. Whilst it is accepted that seagrass species may differ in responses, individual seagrass plants may differ in adaptational tolerances and in growth patterns, hence seagrasses produce local populations that can also show the selective influence of local habitat conditions (McMillan and Phillips 1979), which further explains the importance of location, in determining the condition of the sediment and seagrass growing there.

Seasonality in seagrass growth has been well documented for temperate species and meadows (Thayer *et al.* 1984, Phillips and Meñez 1988, Zieman and Zieman 1989, Hemminga and Duarte 2000). Traditionally, seasonality has been thought to have relatively little influence on tropical seagrasses (Hillman *et al.* 1989, Duarte 1989). However, it has been established for seagrasses in this region that there is a seasonal component to biomass increases throughout the year (Mellors *et al.* 1993, Lanyon and

Marsh 1995, McKenzie 1994, see Subchapter 4.3). Therefore it follows that seagrass functionality may also vary seasonally. This study examined these concepts at a single time in the year (during winter), when seagrass meadows are thought to be less active metabolically and hence less interactive with their surrounding environment. Consequently the results from this study may be biased by the time of year. Many of the concepts on seagrass functionality were derived during the northern hemisphere summer when seagrasses are most actively growing. Those studies that sampled throughout the year often confirmed seasonal differences with respect to plant tissue nutrients (i.e. %N, %P), sediment nutrient pool dynamics (changes in µM concentrations of nutrients) and seagrass abundance (both biomass and number of shoots) (Phillips and Meñez 1988, Hemminga and Duarte 2000). Whilst seasonality in seagrass abundance has been established for seagrasses in this region, virtually no work has been done on establishing seasonal growth rates or seasonal changes in the sediment nutrient pool. I assess this in the next chapter.

4.2.5 Conclusions

Our understanding of seagrass meadow structure and function in relation to sediment structure and geochemical environment has been changed by the results of this study in the central region of the Great Barrier Reef World Heritage Area. This result may be attributed to the species being investigated being structurally small with open leaf canopies compared to the structurally large species with closed leaf canopies on which these concepts are based. Whilst individual species displayed specific responses to the three different concepts being assessed, generally, differences in sediment structure, plant abundance and plant tissue nutrient content were all explained by differences in location. Differences in meadows were related to local environmental, climatic and geographical conditions. By comparing a greater number of similar communities (characterized on environmental, climatic and geographical conditions), over several seasons, an abstract model should be able to be developed in which all local features can be are eliminated and temporal differences incorporated. Whether this model will conform to traditional views or lead to the development of new paradigms, warrants further investigation, in light of the importance of the temporally dynamic seagrass meadows of structurally small species that predominate along the coastline of the central region of the Great Barrier Reef World Heritage Area.

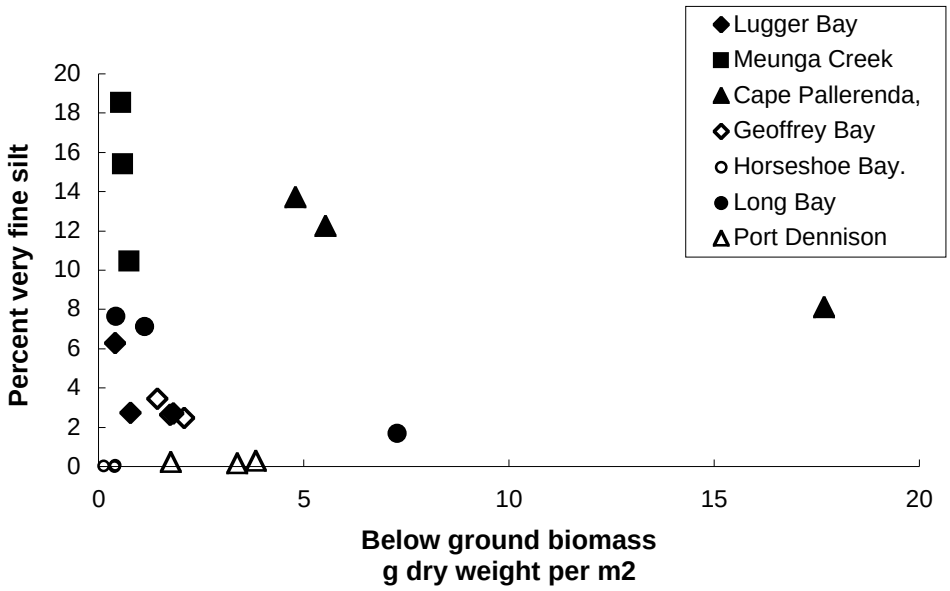


Figure 4.3 The relationship between very fine silt and below ground biomass across the locations characterized by *Halodule uninervis* in the central region of the Great Barrier Reef World Heritage Area.

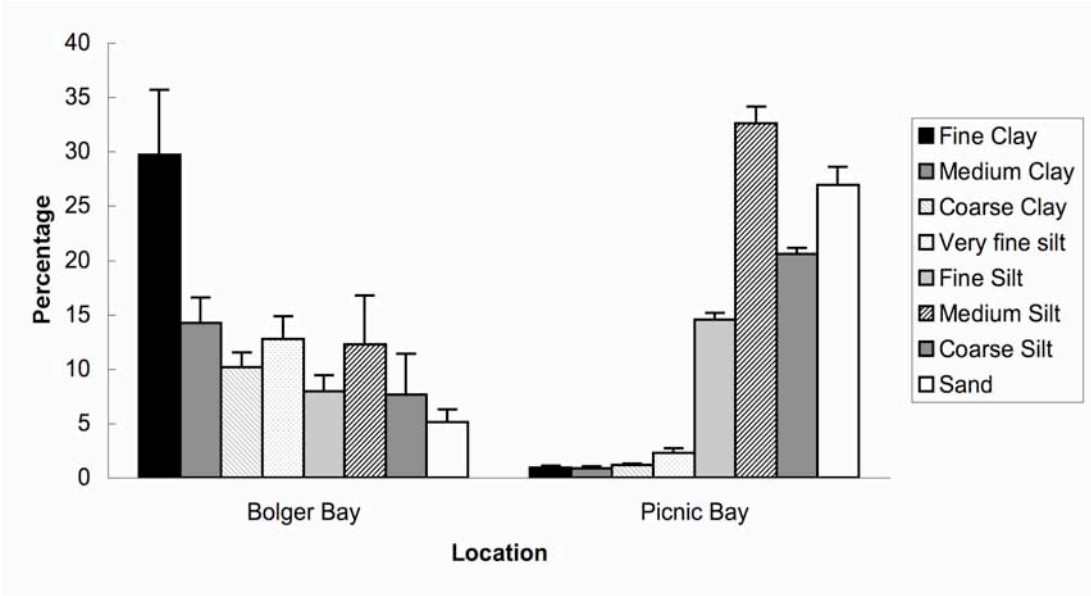


Figure 4.4 The different sediment structures measured of the two locations characterized by *Halophila ovalis*; Bolger Bay and Picnic Bay, Magnetic Island, central region of the Great Barrier Reef World Heritage Area (means and s.e. displayed).

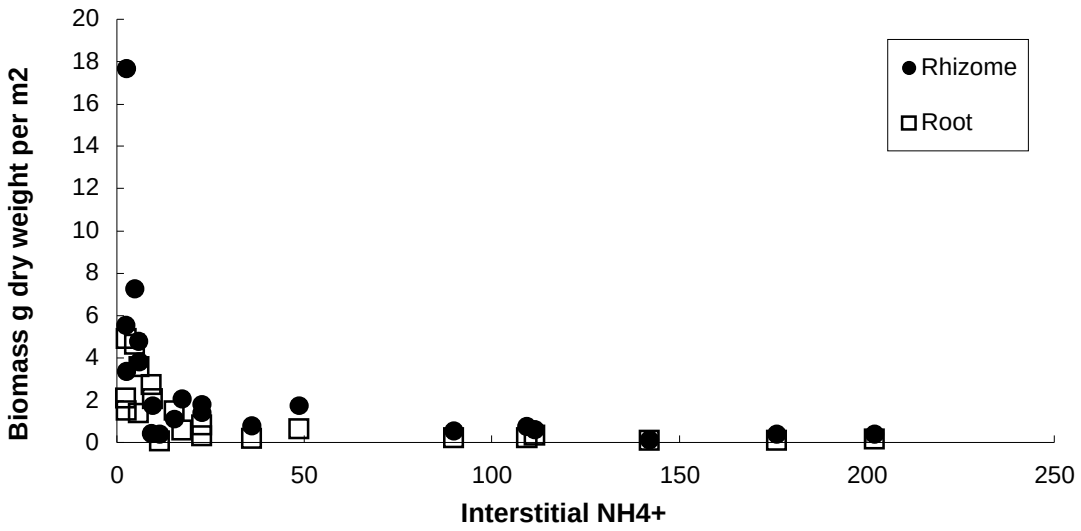


Figure 4.5 The negative relationship between below ground biomass of *Halodule uninervis* and porewater NH_4^+ for the different meadows characterized by *Halodule uninervis* within the central region of the Great Barrier Reef World Heritage Area.

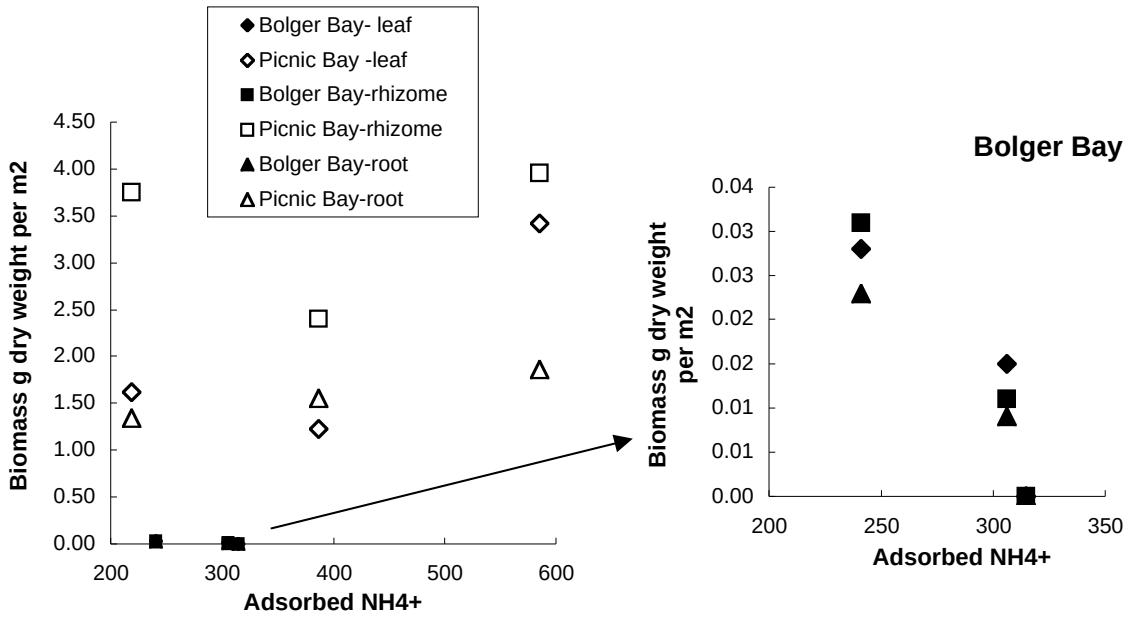


Figure 4.6 The relationship between the three biomass components (leaf, rhizome and root) of *Halophila ovalis* and adsorbed NH_4^+, demonstrating the different responses to increasing adsorbed NH_4^+ at the two sites, Picnic Bay and Bolger Bay, Magnetic Island, central region of the Great Barrier Reef World Heritage Area.

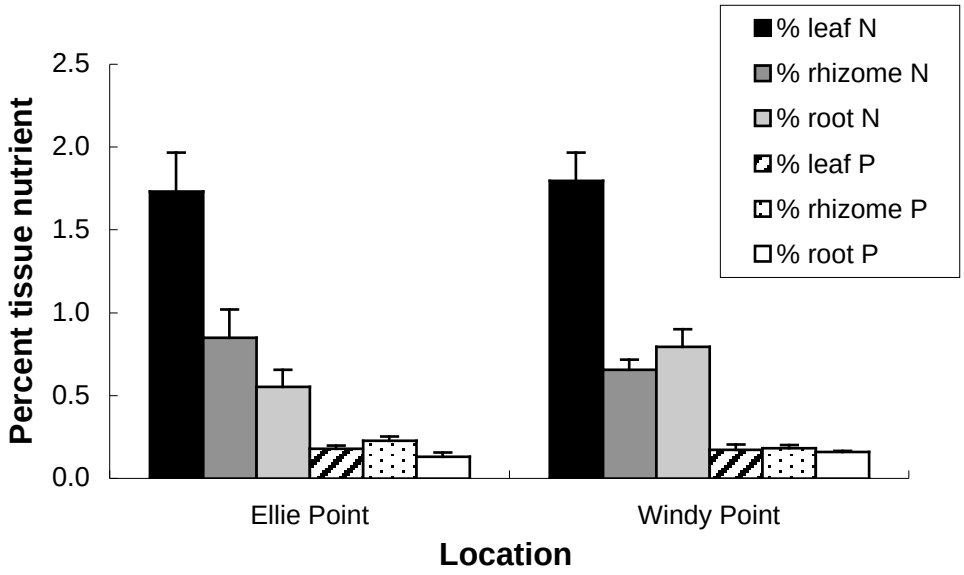


Figure 4.7 A graph of the plant tissue nutrients of the different seagrass components of *Zostera capricorni* from two locations, Ellie Point and Windy Point, characterized by *Zostera capricorni* within the central region of the Great Barrier Reef World Heritage Area, demonstrating similar trends in plant nutrient levels (means and s.e. displayed).

Table 4.5 The locality of each of the eleven intertidal seagrass meadows within the Central region of the Great Barrier Reef World Heritage Area that were assessed with respect to the ecological functioning, July 1994. Locations are grouped by seagrass species and an indication of seagrass density (percent cover per 0.25m^{-2} quadrat) at each location is displayed.

Location	Longitude[1]	Latitude[1]	Percent quadrat cover/Biomass
Halodule uninervis			
Lugger Bay, South Mission Beach	146.10°E	17.92°S	(10–20%)
Meunga Creek, Cardwell	146.02°E	18.30°S	(40%)
Cape Pallarenda, Townsville	146.76°E	19.18°S	(30–40%)
Geoffrey Bay, Magnetic Island, Townsville	146.86°E	19.16°S	(20–30%)
Horseshoe Bay, Magnetic Island, Townsville	146.86°E	19.12°S	(10%)
Long Bay, Cape Cleveland, Townsville	147.02°E	19.22°S	(10–20%)
Port Dennison, Bowen	148.25°E	19.94°S	(20–40%)
Zostera capricorni			
Ellie Point, Cairns	145.77°E	16.88°S	(80%)
Windy Point, Cape Upstart	147.74°E	19.78°S	(60–70%)
Halophila ovalis			
Bolger Bay, Magnetic Island, Townsville	146.80°E	19.16°S	(<5%)[2]
Picnic Bay, Magnetic Island, Townsville	146.85°E	19.18°S	(50–70%)

[1] longitudes and latitudes from Morrissette 1992.
[2] the year prior (1993) to this Bolger Bay recorded 70% quadrat cover

Table 4.6 The model structure of the MANOVA analyses that evaluated the concept of seagrass abundance affecting sediment structure within the rhizosphere of each seagrass species.

Analysis	Dependent variables	Independent variable	Covariates
Concept 1: Sediment structure-seagrass abundance interaction			
	very fine silt	location	total biomass (Model 1)
	fine silt		leaf, rhizome and root biomass (Model 2)
	medium silt		leaf density (Model 3)
	coarse silt		
	sand		
	porosity		

Table 4.7 Summary of the outcomes of the MANOVA analysis investigating the relationship between location and *Halodule uninervis* abundance (biomass and shoot density on sediment structure, highlighting the significant ANOVA result (bold) for the dependent variable 'very fine silt' for those meadows characterized by *Halodule uninervis* within the central region of the Great Barrier Reef World Heritage Area.

Dependent variables	**Indep. variable[1]**	**Covariate(s)**	***p* of covariate**	**Main effect**	
				$F_{(df)}$	*p*
Sediment structure	location	total biomass	0.279	$3.882_{(36,78)}$	<0.001
Very fine silt	location	total biomass	0.010	84.209	<0.001
	location	leaf biomass	0.416	$3.406_{(36,66)}$	<0.001
		rhizome biomass	0.158		
		root biomass	**0.018**		
	location	**rhizome biomass**	**0.023**	**$3.556_{(36,72)}$**	**<0.001**
		root biomass	**0.006**		
	location	leaf density	0.535	$4.381_{(36,78)}$	<0.001
	location	none		$4.905_{(36,84)}$	<0.001

[1]analysis was performed on $\log_{10}$ transformed data

Table 4.8 Summaries of the outcomes of the MANOVA analysis investigating the influence of location and *Zostera capricorni* abundance (biomass and shoot density on sediment grain sizes (sediment structure) for those intertidal seagrass meadows characterized by *Zostera capricorni* within the central region of the Great Barrier Reef World Heritage Area.

Dependent variable	**Indep variable[1]**	**Covariate(s)**	***p* of covariate**	**Main effect**	
				$F_{(d.f)}$	*p*
Sediment structure	location	total biomass	0.534	$2.366_{(3,1)}$	0.438
	location	leaf biomass	0.575	$0.050_{(1,1)}$	0.860
		rhizome biomass	0.735		
		root biomass	0.548		
	location	leaf density	0.524	$1.750_{(3,1)}$	0.495
	location	none		$44.824_{(4,1)}$	0.112

[1]analysis was performed on $\log_{10}$ transformed data

Table 4.9 Summaries of the outcomes of the MANOVA analysis investigating the relationship between location and *Halophila ovalis* abundance (biomass and shoot density) and sediment grain sizes (sediment structure) in the central region of the Great Barrier Reef World Heritage Area (significant outcomes in bold).

Indep variable[1]	Covariate(s)	*p* of covariate	Main effect	
			$F_{(df)}$	*p*
location	total biomass	0.923	$4.529_{(3,1)}$	0.330
	leaf biomass	0.804	$1.098_{(1.1)}$	0.485
	rhizome biomass	0.984		
	root biomass	0.813		
	leaf density	0.621	$49.889_{(3,1)}$	0.104
	none		**$623.426_{(4,1)}$**	**0.030**

[1]analysis was performed on $\log_{10}$ transformed data

Table 4.10 The model structure of the analyses that evaluated the concept of sediment nutrient and nutrient related parameters (chemical environment) of the meadow rhizosphere influencing the abundance of the seagrass present.

Analysis	Dependent variables	Independent variable	Covariates
Concept 2: Seagrass abundance-sediment geochemistry interaction			
1 ANOVA	total biomass	location	Adsorbed $PO_4^{3-}{}_{(Bray)}$
2 MANOVA	leaf biomass		Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$
	rhizome biomass		Adsorbed NH_4^+
	root biomass		porewater PO_4^{3-}
3 ANOVA	leaf density		porewater NH_4^+
			porewater $NO_2^- + NO_3^-$
			PH
			Eh
			% carbonate
			% organic content

Table 4.11 The significant outcomes of the MANOVA and ANOVA analyses that investigated the influence of location and the significant chemical parameters (% organic content and porewater NH_4^+) on the seagrass abundance parameters (of biomass and leaf density respectively) of *Zostera capricorni* within the rhizospheres of seagrass meadows characterized by *Zostera capricorni* within the central region of the Great Barrier Reef World Heritage Area.

Dependent variables	Independent variable	Covariate(s)	*p* of covariate	Main effect	
				$F_{(df)}$	*p*
leaf, rhizome root biomass	location	organic content	0.014	$10411.657_{(3,1)}$	0.007
leaf density	location	porewater NH_4^+	0.018	$297.404_{(1,3)}$	<0.001

Table 4.12 The significant outcomes of the MANOVA and ANOVA analyses that investigated the influence of location and the significant chemical parameters (adsorbed NH_4^+ and porewater $NO_2^- + NO_3^-$) on the seagrass abundance parameters (of biomass and leaf density respectively) of *Halophila ovalis* within the rhizospheres of seagrass meadows characterized by *Halophila ovalis* within the central region of the Great Barrier Reef World Heritage Area.

Dependent variables	Independent variable	Covariate(s)	*p* of covariate	Main effect	
				$F_{(df)}$	*p*
total biomass	location	none		$121.925_{(1,4)}$	0.002
leaf, rhizome root biomass	location	adsorbed NH_4^+	0.010	$417.672_{(3,1)}$	0.036
rhizome	location	porewater $NO_2^- + NO_3^-$	0.028	$653.728_{(1,3)}$	<0.001

Table 4.13 The model structure of the MANOVA analyses that evaluated the concept of seagrass tissue nutrients reflecting their nutrient environment within the rhizospheres of each seagrass species investigated from intertidal seagrass meadows within the central region of the Great Barrier Reef World Heritage Area.

Analysis	Dependent variables	Independent variable	Covariates
Concept 3: Plant tissue nutrient-sediment nutrient interaction			
	% leaf N	location	adsorbed $PO_4^{3-}{}_{(Bray)}$
	% leaf P		adsorbed $PO_4^{3-}{}_{(bicarbonate)}$
	% rhizome N		adsorbed NH_4^+
	% rhizome P		porewater PO_4^{3-}
	% root N		porewater NH_4^+
	% root P		porewater $NO_2^- + NO_3^-$
			pH
			Eh
			% carbonate
			% organic content

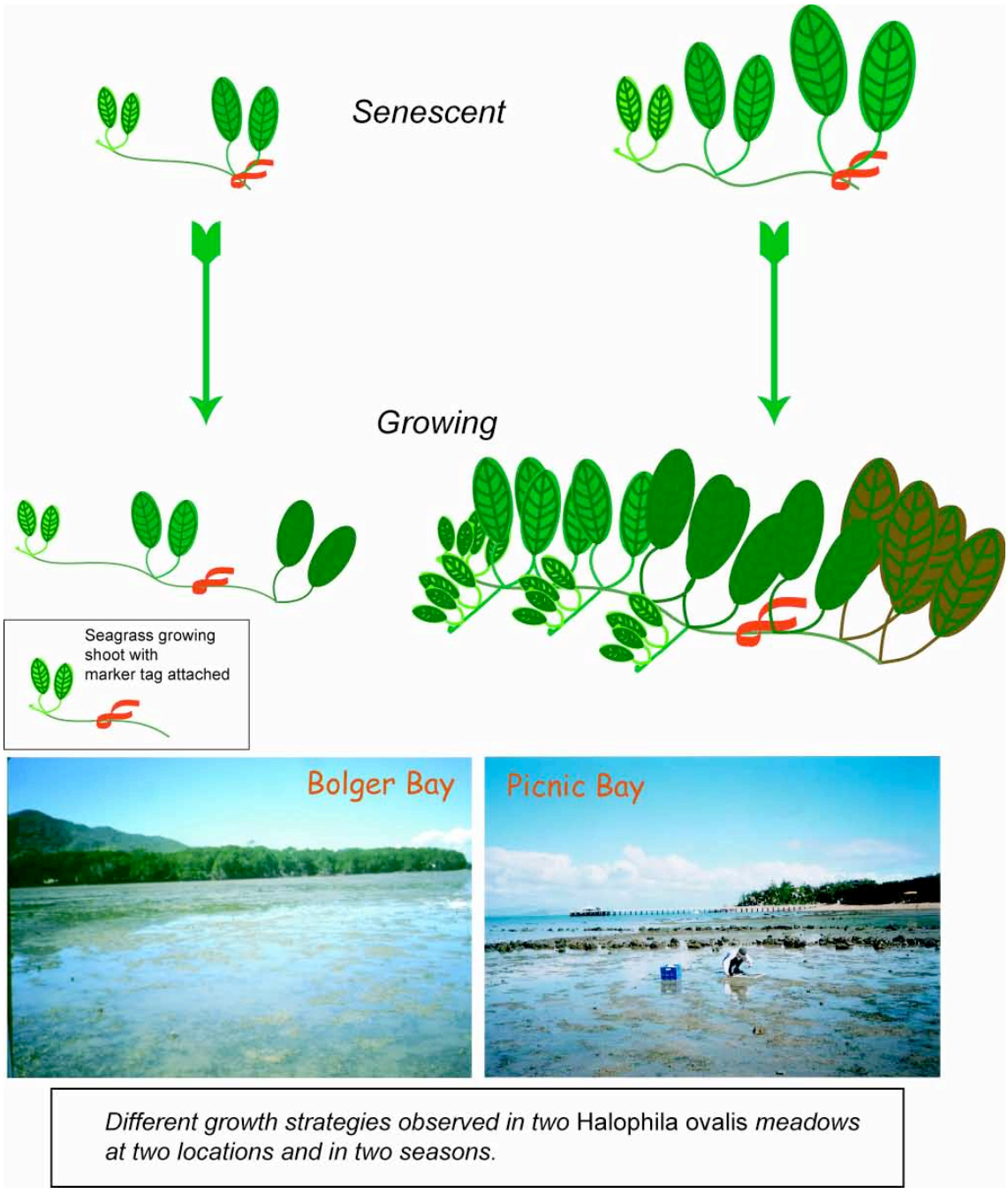
Table 4.14 The significant outcome for the univariate variable of % leaf P from the MANOVA analysis of plant tissue nutrients for *Halodule uninervis* and its relationship with location and the chemical environment of the rhizospheres of intertidal seagrass meadows characterized by *Halodule uninervis* within the central region of the Great Barrier Reef World Heritage Area.

Dependent variable	Independent variable	Covariate(s)	*p* of covariate	Main effect	
				$F_{(d.f)}$	*p*
% leaf P	location	Adsorbed $PO_4^{3-}{}_{(Bray)}$	0.002	$10.294_{(6,7)}$	0.004
		Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	0.036		
		Porewater NH_4^+	0.000		
		Porewater $NO_2^- + NO_3^-$	0.000		
		Carbonate	0.011		

Table 4.15 Summary of significant outcomes of my evaluation of the three concepts on ecological processes for meadows of *Halodule uninervis, Zostera capricorni* and *Halophila ovalis* in the central region of the Great Barrier Reef World Heritage Area.

Species	Significant outcomes	Support concept Yes/No
Concept 1: Sediment structure is affected by seagrass abundance		
Halodule uninervis	Significant differences between location moderated by rhizome biomass, but not in the manner expected	No
Zostera capricorni	No significant differences between locations even though seagrass abundance differed between locations	No but perhaps a species effect
Halophila ovalis	Significant differences between locations not moderated by seagrass abundance	No
Concept 2: Seagrass abundance is affected by the sediment chemical environment		
Halodule uninervis	Significant differences between locations not moderated by sediment geochemistry	No
Zostera capricorni	Significant differences between locations moderated by organic content and porewater ammonium	Yes
Halophila ovalis	Significant differences between locations moderated by levels of adsorbed ammonium however trends were conflicting	? conflicting trends
Concept 3: Plant tissue nutrients reflect sediment nutrients		
Halodule uninervis	Significant differences between locations moderated by the effect of sediment geochemistry on % leaf phosphate	Yes within location
Zostera capricorni	No significant differences between locations even though sediment geochemistry environment differed	No
Halophila ovalis	Not analysed	-

Subchapter 4.3 Intra-annual variation within two tropical intertidal meadows of the seagrass *Halophila ovalis*



Different growth strategies observed in two Halophila ovalis *meadows at two locations and in two seasons.*

Summary

Despite differences in sediment structure, nutrient status and plant parameters between two *Halophila ovalis* meadows, both meadows followed similar intra-annual patterns. This demonstrates that seasonality is important in tropical seagrass habitats. However, whilst growth increased during the warmer months of the year, at both locations, the strategies used for increasing biomass during the growing season differed. At Bolger Bay, biomass increase was due to an increase in all growth parameters: shoot production, rhizome extension, and number of new meristems. In contrast, growth at Picnic Bay resulted from an increase in the number of meristems and consequent increases in shoot density. These different growth strategies were consistent with the differing stages of meadow development at each location, that is, at Bolger Bay, the meadow was recovering from disturbance and at Picnic Bay the meadow was established.

4.3.1 Introduction

The fluctuations in biomass and productivity observed in temperate seagrasses follow seasonal changes in solar energy and temperature, with a strong increase in spring, a peak in the summer and a subsequent decline in autumn (Hemminga and Duarte 2000). In Australia, temperate and subtropical seagrasses also follow this pattern of biomass change (temperate: Bulthius and Woelkerling 1981, Kirkman *et al.* 1982, Larkum *et al.* 1984, Walker and McComb 1988, Hillman *et al.* 1989, subtropical: Young and Kirkman 1975, Walker and McComb, 1988). Seasonal fluctuations in abundance have also been observed in seagrass meadows in the tropics outside Australia. For example Brouns (1987) described the seasonal changes in the structure and physiology of tropical seagrass communities in Papua New Guinea waters. Intertidal seagrass meadows in Indonesian also showed conspicuous seasonal declines in biomass (Erftemeijer and Herman 1994). These authors attributed this result to desiccation and burning of leaves resulting from seasonal exposure of reef flats during daylight spring low tides.

Very little has been published on measurements of seasonal changes in standing crop of inshore seagrasses in tropical Australia. Lanyon and Marsh (1995) sampled every three months and found that the abundance of total seagrass and individual seagrass species fluctuated seasonally by a factor of between two and four, depending on the species. Minium abundance was observed in the dry season (August–September) with subsequent recovery of seagrass during the wet season (November–March). Lanyon and Marsh (1995) found consistent winter minima (June–August) for *Halophila ovalis*. McKenzie (1994) also found that in an intertidal *Zostera capricorni* meadow, the lowest biomass occurred from June to August, with highest biomass in September. Mellors *et al.* (1993) monitored intra-annual changes in seagrass standing crop over a twelve-month period at Green Island Reef on the Great Barrier Reef. They recorded a decrease in standing crop from May to August (winter) and an increase in standing crop from September to December. They could not establish whether the increase in standing crop resulted from an increase in leaf height, number of shoots, or an increase in growing tips, as they visually estimated standing crop.

Mellors *et al.* (1993) found that temporal variation in standing crop was positively correlated with day length and air temperature, and negatively correlated with number

of strong wind days. These variables were indirect measures of light availability and temperature, suggesting that temperature and light availability influenced fluctuations in seagrass standing stock. This meadow which Mellors *et al.* (1993) studied was subtidal and the changes in attenuation of light through water with season would have been important. Lanyon and Marsh (1995) also found seagrass standing crop of an intertidal meadow to be positively correlated with day-length and temperature, as well as rainfall. These studies support an earlier hypothesis of Bridges *et al.* (1982) and Coles *et al.* (1989) that seasonal rainfall may be an important factor influencing seagrass productivity in the Australian tropics. However rainfall is only likely to affect those beds that are directly influenced by terrestrial run-off or river discharge (Carruthers *et al.* 2002).

The research of Mellors *et al.* (1993), McKenzie (1994) and Lanyon and Marsh (1995) provides a baseline dataset that establishes the months from April to August as a senescent season and the months between September and December as a more active growing season for Australian tropical seagrasses. However, these studies did not investigate other aspects of seagrass meadow or plant seasonality, such as nutrient status of the meadow or plant growth dynamics.

The current study was undertaken to determine intra-annual differences in growth rates, sediment nutrient status, plant nutrient status and biomass accumulation. The two times of year sampled represent the growing season and the senescent season for *Halophila ovalis* growing in tropical eastern Australia on Magnetic Island, Cleveland Bay, near Townsville.

4.3.2 Material and methods

Study site description

Magnetic Island (19°11’E, 146°51’S, Fig. 4.8) is a continental island situated approximately 7 km off the coast from the city of Townsville in Cleveland Bay, Queensland, Australia. The seagrass beds I studied were in Picnic Bay and Bolger Bay and their biogeochemical status has been described in Chapter 3.

Picnic Bay faces south east and is characterized by headlands of large rounded granite boulders which are the parent rock for the granite-derived sediments found at this

location. Bolger Bay faces west and is fringed by mangroves on its landward edge (Pringle 1989). The rhizosphere was observed to be 2.5 cm in depth for *Halophila ovalis* growing at both of these bays.

Both bays are fringed by coral reefs on their seaward edge and have seagrass growing on their intertidal flats. The seagrass beds are made up of mono-specific stands of *Cymodocea serrulata* (lower intertidal, subtidal), *Halodule uninervis* (wide) (middle intertidal) and *Halophila ovalis* (upper intertidal). This study was undertaken within the stands of *Halophila ovalis* at the landward edge of each meadow.

Sampling design

Eighteen 0.25 m^2 quadrats were placed haphazardly within the *H. ovalis* stand at each location (Bolger Bay and Picnic Bay) during a month that was representative of each season: Senescent-August and Growing-October. Within each of those 18 quadrats, two porewater samples were taken for analysis of dissolved inorganic nutrients and averaged. Sediment core samples for the analysis of adsorbed inorganic nutrients were randomly assigned to eight of the eighteen quadrats. Of those eight quadrats, three were chosen randomly and excavated for the analyses of seagrass biomass and plant nutrient parameters. Three separate cores taken in the vicinity of the quadrats were used for the analyses of the abiotic parameters: sediment grain size, percent carbonate matter and percent vegetative matter. Eh and pH measurements were also taken in the general vicinity of sampled seagrass. Abiotic parameters were measured to characterize differences between locations and were not sampled seasonally. The placement of the sampling area differed in the two seasons although they were within the same seagrass meadow (Fig. 4.9).

Abiotic environment

Eh, pH, calcium carbonate, organic content and sediment grain size analysis were determined according to the protocols described in Chapter 2.

Nutrients

Porewater nutrients

Sediment porewater was collected *in situ* using sediment sippers (Chapter 2). Sippers were 2.5 cm in length, which was the depth of the rhizosphere associated with

Halophila ovalis at these locations. Porewater samples were analysed for dissolved inorganic nutrients, ammonium, nitrite + nitrate and phosphate as described in Chapter 2.

Sediment nutrients

Sediment samples were collected using 50 mL corers pushed to the depth of the rhizosphere (2.5 cm) at each location. Sediment samples were analysed for extractable inorganic ammonium, and phosphate. These inorganic nutrients were extracted and analysed using the techniques and methodologies outlined in Chapter 2.

Seagrass

Biomass and plant tissue nutrients were prepared and measured as outlined in Chapter 2. The plant nutrient state of each seagrass meadow was calculated by combining the % plant tissue nutrient of the whole plant with total biomass. The units for this derived measure of plant nutrient state are grams of nitrogen per m^2 of seagrass ($gN_{seagrass}\ m^{-2}$) and grams of phosphorous per m^2 of seagrass ($gP_{seagrass}\ m^{-2}$).

Seagrass growth

Within three separate smaller quadrats, 0.0625 m^2 (25 cm x 25 cm), ten growing tips were located by washing away sediment using a squeeze bottle. A tag made from electrical wire was placed directly behind the apical meristem (growing tip) with minimum disturbance. The sediment was then gently fanned back over the rhizome and the quadrat left undisturbed until the completion of the trial. During July (senescent season) growth trials lasted 16 days while the October (growing season) trails had a duration of ten days. At the end of each trial, the entire quadrat including the sediment was lifted as a single sod and taken back to the laboratory. The sediment was gently washed away from the sod, the tags retrieved and the number of apical meristems present in the quadrat counted. The data collected on each tag return included the number of shoots produced per meristem and the length (mm) of rhizome from the tag to the apical meristem. A mean was calculated for each quadrat.

Statistical methods

The main statistical analysis was performed to investigate the differences between locations and the differences between seasons, within a location. Exploratory analyses

showed that with respect to nutrients, the factor ‘Location’ (i.e. between Picnic Bay and Bolger Bay) consistently accounted for the majority of variance and would therefore mask any seasonal differences in any of the two-way analyses. Consequently, differences between locations at different times of the year and differences between seasons within location were analysed separately by MANOVA. If the data set was not large enough to conduct a MANOVA, an ANOVA was performed. The independent variable was either location or season depending on the analysis. The dependent variables were sediment grain size, other sediment characteristics, sediment nutrients, plant nutrients, plant biomass or plant growth, depending on the analysis. The experimental design had two deficiencies for logistical reasons: (1) each season was sampled in only one month and (2) the study was conducted of the course of a single year. In the tables (Table 4.16, 4.18, 4.19) the MANOVA and the ‘between subject tests’ are presented.

4.3.3 Results

Abiotic differences between locations

Sediment grain sizes were significantly different between locations as evidenced by comparison of the in the distribution of particle types (Fig. 4.10) and multivariate analysis (Table 4.16). The sediments of the rhizosphere were predominantly composed of clay sized particles (smaller grain sizes) in Bolger Bay, whereas those in Picnic Bay were much coarser (Table 4.16, Fig. 4.10). The percent calcium carbonate in sediments at Bolger Bay was 12.66%, significantly lower than that at Picnic Bay, 20.67% (Table 4.16). Bolger Bay had significantly more percent vegetative matter (1.82%) within the rhizosphere than Picnic Bay (0.97%) (Table 4.16).

Both Eh (127.4 mV) and pH (8.52) were significantly greater (Table 4.16) within the *Halophila ovalis* meadow at Picnic Bay than at the corresponding site at Bolger Bay (Eh = 43.38, pH 7.44). These results are consistent with Picnic Bay sediments being coarser and having a higher calcium carbonate content.

Sediment nutrients

Intra-annual differences in nutrient status between locations

Adsorbed nutrients

Nutrient levels in the *Halophila ovalis* meadow at Bolger Bay were generally and significantly (two times) higher than those at the corresponding site in Picnic Bay during both months sampled (Table 4.17, Fig. 4.11a).

Porewater nutrients

With some exceptions, the levels of porewater nutrients at Bolger Bay were generally double or higher, than those levels recorded at Picnic Bay (Table 4.17). There were no significant differences between locations in relation to $NO_2^- + NO_3^-$ during the senescent season. Porewater PO_4^{3+} was significantly higher at Picnic Bay than Bolger Bay during the growing season (Table 4.18, Fig. 4.11b).

Intra-annual differences in nutrient status within location

Bolger Bay

Sediment nutrients

Adsorbed nutrients

Levels of adsorbed nutrients were significantly different between seasons at Bolger Bay (Table 4.19). This outcome is attributed to the highly significant ANOVA result for adsorbed $PO_4^{3-}{}_{(Bray)}$ (Table 4.19). During the senescent season, levels of adsorbed $PO_4^{3-}{}_{(Bray)}$ were approximately double those of during the growing season (Table 4.17, Fig. 4.11a). The other adsorbed nutrients, $PO_4^{3-}{}_{(bicarbonate)}$ and NH_4^+ were not significantly different between seasons, however, there was a tendency for both nutrients to be slightly higher during the senescent season (Table 4.19, Table 4.17, Fig. 4.11a).

Porewater nutrients

The levels of porewater nutrients were also significantly different during seasons at Bolger Bay (Table 4.19). This is reflected in all the ANOVA results for each porewater

nutrient (Table 4.19). Porewater PO_4^{3-} and NH_4^+ levels were three times higher during the senescent season than the growing season (Table 4.17, Fig. 4.11b). The converse was true for porewater $NO_2^- + NO_3^-$ with levels being significantly four times higher during the growing season (Table 4.17, Fig. 4.11b).

Picnic Bay

Sediment nutrients

Adsorbed nutrients

Adsorbed nutrients were significantly different between seasons at Picnic Bay (Table 4.20, Fig. 4.11a). This is reflected in the highly significant ANOVA result for $PO_4^{3-}{}_{(Bray)}$ (Table 4.20). $PO_4^{3-}{}_{(Bray)}$ levels during the senescent season were double the levels recorded for the growing season (Table 4.17, Fig. 4.11a). In contrast, levels of $PO_4^{3-}{}_{(bicarbonate)}$ were significantly greater during the growing season (Table 4.20, and Fig. 4.11a). No significant difference was observed for adsorbed NH_4^+ (Table 4.20).

Porewater

Porewater nutrients were also significantly different between seasons at Picnic Bay (Table 4.20), probably due to the highly significant result for NH_4^+ (Table 4.20). Levels of porewater NH_4^+ were six times greater during the senescent season than levels recorded for the growing season (Table 4.17, Fig. 4.11b). Levels of porewater PO_4^{3-} and $NO_2^- + NO_3^-$ were not significantly different between seasons (Table 4.20, Fig. 4.11b).

Seagrass parameters

Intra-annual differences in seagrass status between locations

Biomass

Picnic Bay recorded significantly higher biomass for all plant components than Bolger Bay for both seasons (Table 4.21). During the senescent season, biomass at Picnic Bay was on average six fold greater than that at Bolger Bay and was also less variable (Table 4.22, Fig. 4.12a). No epiphytic algae were present at either location during the senescent season. Epiphytic algae were recorded at both locations during the growing season, with Picnic Bay recording significantly higher biomass than Bolger Bay (Table 4.21, Table 4.22). Whilst biomass measurements were significantly greater at Picnic

Bay also during the growing season, seagrass biomass was on average only six times greater than that recorded for Bolger Bay.

Shoot number

The number of seagrass shoots per m^2 at Picnic Bay was significantly higher than that recorded for Bolger Bay during both seasons (Table 4.21). Shoot numbers at Picnic Bay were one and a half fold greater than at Bolger Bay, during the senescent season, while double the density during the growing season (Table 4.22, Fig. 4.12b)

Plant nutrients

The only significant result for plant nutrients on per weight basis was that for % leaf N for both seasons with Bolger Bay recording higher % leaf N than Picnic Bay (Table 4.21, Table 4.22, Fig. 4.13a). There was a trend for seagrass plant nutrients at Bolger Bay to be higher than those recorded for Picnic Bay (Table 4.22, Fig. 4.13a). As % whole plant N approached significance in both seasons, % whole plant P neared significance only in the senescent season (Table 4.21). However, when the nutrient status (grams of nitrogen (gN) and grams of phosphorus (gP) m^{-2} of seagrass) of the seagrass beds for each location, at each season were analysed, a contrasting result emerged. For both seasons, the nutrient status of the Picnic Bay seagrass meadow had significantly higher $gN_{seagrass}\ m^{-2}$ and $gP_{seagrass}\ m^{-2}$ than at Bolger Bay (Table 4.21, Table 4.22). The low amount of plant material from Bolger Bay means this results needs to be interpreted cautiously.

Plant growth

The only statistically significant result, for plant growth, was rhizome extension at Bolger Bay, which was greater than that at Picnic Bay during the growing season (Table 4.21). The larger number of apical meristems at Bolger Bay compared to Picnic Bay, during the senescent season approached statistical significance (Table 4.21). Productivity (increase in shoot production per day) tended to be greater at Picnic Bay than Bolger Bay during the senescent season with the converse being true during the growing season (Table 4.21, Fig. 4.14b).

Intra-annual differences in seagrass status within location

Because of the low number of replicates with respect to all plant parameters at both locations, no multivariate analyses were attempted.

Bolger Bay

Biomass

All plant parameters had significantly higher biomass during the growing season at this location (Table 4.23). The differences in biomass between seasons ranged from almost 15 times greater to just under 25 times greater for the different plant components (Table 4.22, Fig. 4.13a).

Shoot number

Shoot number was also significantly higher during the growing season at this location (Table 4.23). Shoot count per m^2 was 13 times higher during the growing season than during the senescent season (Table 4.22, Fig. 4.12a).

Plant nutrients

Becaue of the small amount of plant material retrieved from each excavated quadrat, this data set is limited, and interpretation of the results is cautious. No statistical significant difference was detected between seasons at Bolger Bay for any plant nutrient material on a per weight basis (Table 4.23). This may be the result of low replication as a trend was evident for both % N and %P to be slightly higher during the growing season (Table 4.22, Fig. 4.13). However when the nutrient state of the seagrass meadow on a per m^2 basis was calculated for each season at this location, $gN_{seagrass}\ m^{-2}$ and $gP_{seagrass}\ m^{-2}$ of seagrass were significantly greater during the growing season (Table 4.22, Table 4.23).

Plant growth

The growth parameters, shoot production and rhizome extension, were significantly higher during the growing season (Table 4.23). Shoot production doubled through the growing season while rhizome extension trebled (Table 4.22, Fig. 4.14a,b). Even though the number of apical meristems was not statistically different between seasons,

the number of meristems produced in the growing season was one and half times more than that for the senescent season (Table 4.22, Fig. 4.14c).

Picnic Bay

Biomass

Algal and total biomass were significantly different between seasons (Table 4.24), with average biomass being higher in the growing season (Table 4.22, Fig. 4.12a). Leaf biomass and root biomass approached significance (Table 4.24). These biomass measures were also higher in the growing season (Table 4.22, Fig. 4.12a).

Shoot number

Shoot number between seasons was not significantly different. However, shoot numbers were one and a half times greater in the growing season than counts recorded for the senescent season (Table 4.22, Fig. 4.12b).

Plant nutrients

All plant nutrient parameters showed a trend towards higher percentages in the growing season than in the senescent season (Table 4.22, Fig. 4.13). The only significant result for the set of analyses involving % tissue nutrient was that for % whole plant P, though % leaf N approached significance (Table 4.24). The nutrient state of the *Halophila ovalis* bed at Picnic Bay was significantly greater in the growing season with respect to both nutrients N and P (Table 4.24). This outcome reflects the trend of an increase for both plant nutrients and biomass at this location in the growing season.

Plant growth

The number of apical meristems differed significantly between seasons (Table 4.24). The number present during the growing season was treble that present during the senescent season (Table 4.22, Fig. 4.14c). The other production parameters of rhizome extension and shoot production showed no difference between seasons at this location.

4.3.5 Discussion

This study demonstrated that Bolger Bay and Picnic Bay on Magnetic Island are significantly different from each other with respect to sediment nutrient status, *Halophila ovalis* biomass, number of *Halophila ovalis* shoots, *Halophila ovalis* % leaf N and gN and gP m^{-2}. Despite % leaf N being significantly higher at Bolger Bay, the nitrogen nutrient state (gN m^{-2}) of the seagrass meadow was higher at Picnic Bay. This result was mirrored by gP m^{-2} of seagrass even though on a per plant basis %P was not significantly different between locations. I also demonstrated consistent seasonal differences across bays with respect to porewater NH_4^+, *Halophila ovalis* biomass and nutrient state (gN and gP m^{-2} of *Halophila ovalis*). Levels of porewater NH_4^+ at both locations were lower during the growing season consistent with the significant increase in total plant biomass. Whilst not statistically significant, there was a matching trend for plant nutrients to be greater during the growing season within each location. This trend (%N and %P), combined with significant increases in biomass during the growing season resulted in the plant nutrient status (gN and gP m^{-2} of seagrass) of both locations being significantly greater during the growing season.

Another aspect of seasonality within location observed during this study was the significant increase in epiphytic algae during the growing season. This may result from an increase in water column nutrients or simply an increase in substrate availability for colonization as shoot numbers increased during the growing season.

Differences between location are related to their physical differences determined by local geography. Bolger Bay sediments are extremely muddy with a high percentage of silt and clay. In contrast the sediments of Picnic Bay are dominated by larger sediment particles with a higher percentage of calcium carbonate. As expected from these dissimilar sediment profiles, pH and Eh also differed between locations. These two bays also recorded dissimilar percentages of non-seagrass organic matter within their respective rhizospheres. In comparison with Picnic Bay, the higher percentage of non-seagrass organic matter within the sediments at Bolger Bay would be expected to support a larger population of microbial organisms with a greater capacity for nutrient cycling (Moriarty and Boon 1989).

The potentially larger microbial population, and higher proportion of silt and clay, known for their capacity to integrate nutrients (Garrels and Christ 1965, Friedman 1978), may, in part, explain the sediments at Bolger Bay being higher in nutrients than those at Picnic Bay. Whilst the majority of results for plant tissue nutrients were not significant, the trend was for Bolger Bay to have higher plant tissue nutrients. This is a reflection of high sediment nutrients resulting in high plant nutrients (Gerrloff and Kromholz 1966, Mengel and Kirkby 1987, Fourqurean *et al.* 1992). The higher sediment nutrients at Bolger Bay were reflected in significantly higher % leaf N than that recorded for Picnic Bay, rather than a larger biomass.

While Bolger Bay is not urbanized, the catchment of this bay is greater than that of Picnic Bay and is made up of small hobby farms specializing in tropical fruit and nursery plant production. This type of land-use is usually accompanied by significant fertilizer application (Pulsford 1991, Moss *et al.* 1992). In contrast, the urban surrounds of Picnic Bay may be responsible for an increase in nutrient input to the seagrass beds as a result of septic tanks leaching into the ground water as described by Short *et al.* (1996) for other places in the world. Thus, the differences between these two bays go beyond sediment structure and encompass ongoing difference in nutrient inputs.

At the beginning of this study, the seagrass biomass at Bolger Bay was greatly reduced compared to previous observations (Chapter 2). Consequently, the dramatic increase in biomass (10 times greater) between seasons at Bolger Bay could, in part, be due to a recovery of this seagrass bed, rather than a seasonal increase *per se*. In addition, the seagrass dieback prior to this analysis would have influenced the sediment nutrient status of the *Halophila ovalis* meadow at Bolger Bay to an unknown extent. These low biomass *Halophila ovalis* meadows are typical of the meadows on the coastal zone of the central GBRWHA (Lee Long *et al.* 1993). Thus, I expect the seasonal increases in biomass observed at Picnic Bay from the senescent season (August) to the growing season (October) (1.5 times greater between season) to be typical of seagrass habitat in this region.

Differences in new meristem formation observed between the seagrass meadows in these two bays may reflect the ability of the seagrass plant to occupy available space. A well recognized feature of seagrass growth is the ability to occupy more space and increase in biomass, which reflects increased activity of the apical meristems

(Hemminga and Duarte 2000). In temperate regions, this growth strategy varies seasonally (Sand-Jensen 1975). The activity of seagrass meristems or the ability to switch growth strategies affects how seagrass plants respond and adapt to disturbance or resource availability and allows them to accommodate varying resource levels and moderate the rates at which they occupy space (Marba and Duarte 1998). For example increased horizontal rhizome extension enables a plant to occupy new areas, while an increase in the number of apical meristems leads to an increase in the number of shoots and roots in the same area and enables greater use of local resources.

The strategies used for increasing biomass during the growing season were different between Picnic Bay and Bolger Bay. At Bolger Bay, biomass increase resulted from an increase in all growth parameters measured, particularly rhizome extension and shoot production. The production of new ramets is a key component of space occupation by seagrasses particularly during the colonization of new habitats or their recovery from disturbance (Duarte and Sand-Jensen 1990). This result supports my observation that the seagrass bed at Bolger Bay was recovering from die-back. In contrast, the growth strategy in Picnic Bay was attributable to a significant increase in the number of apical meristems and an accompanying increase in number of shoots (approaching significance $p = 0.056$) in the growing season. This strategy is consistent with an established meadow producing more biomass on a seasonal basis rather than a seagrass meadow trying to establish over a greater area. Both growth strategies are consistent with strategies used for rapid shoot turnover in species of seagrass such as *Halophila* and contrast with the traditional models of shoot elongation associated with higher biomass temperate seagrasses such as *Zostera* and *Posidonia* (see life history model in Walker *et al.* 1999).

4.3.6 Conclusions

Ambient nutrient levels at Bolger Bay were generally higher than those recorded for Picnic Bay. This difference was reflected in the higher tissue nutrients within the seagrass plants at Bolger Bay. In contrast, seagrass biomass was greater at Picnic Bay, which translated into significantly higher amounts of gN and gP m^{-2} of seagrass. These significant differences in sediment and plant tissue nutrients are related to the differences in sediment profiles at each location with respect to the proportion of silt clays, calcium carbonate and organic content present within the rhizosphere. The

significant differences in plant biomass and subsequent measure of gN and gP m^{-2} of seagrass at each location is probably a consequence of the disappearance of seagrass noticed at Bolger Bay through the course of this study. Similarly the differences in growth strategy observed between these locations were probably related to the recovery status of the seagrass meadow in Bolger Bay.

This chapter demonstrates that intra-annual differences in nutrients in both the sediments and plants. Intra-annual differences in biomass, shoot number and growth parameters were also observed. These results provide further evidence of the importance of seasonality in tropical seagrass habitats. The increased growth in the growing season reflects elevated nutrients. The interactions between biomass and nutrient availability at different times of the year are addressed experimentally in Chapter 5.

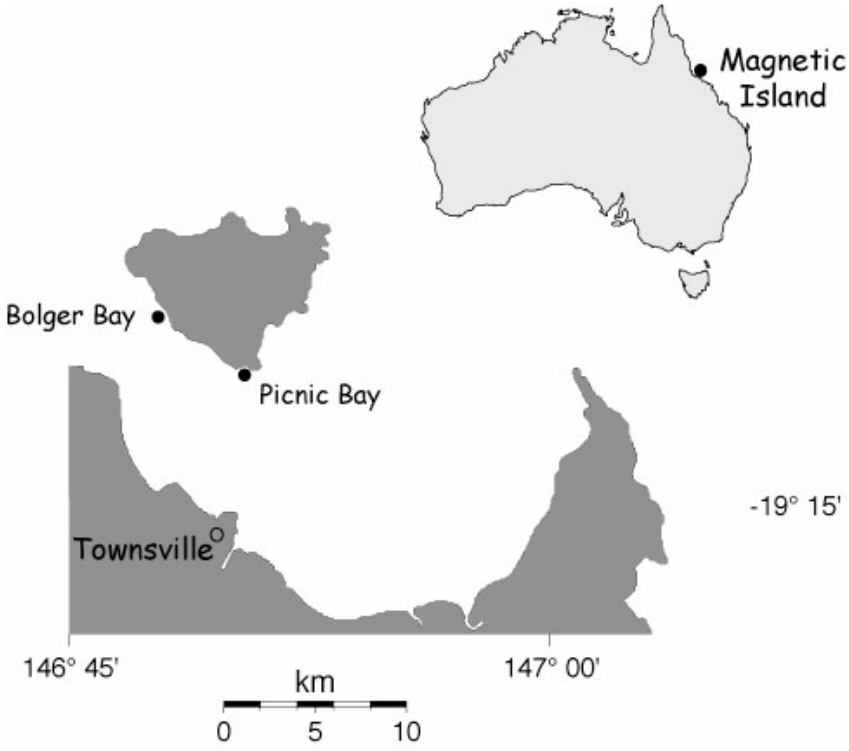


Figure 4.8 Map of Magnetic Island, off the coast of Townsville (open circle), Queensland, Australia with the locations of Picnic Bay and Bolger Bay indicated by solid circles.

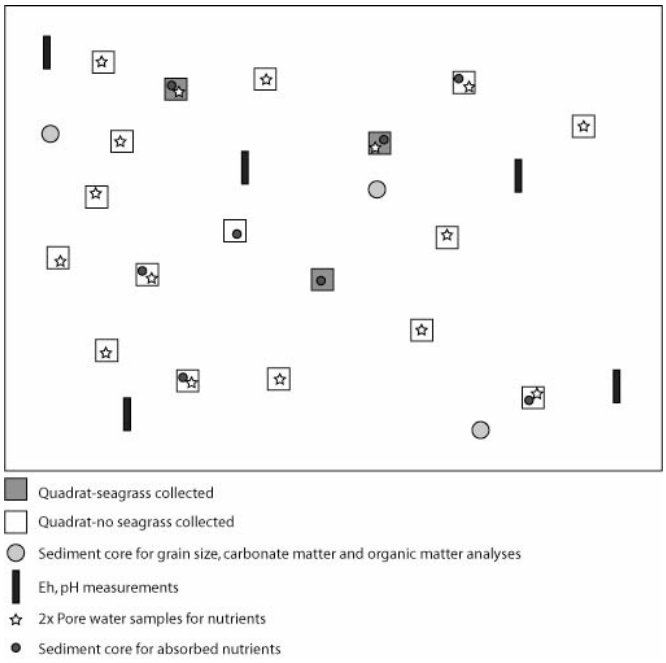


Figure 4.9: Schematic diagram of sampling design for all samples taken (note: not to scale), quadrat location assigned haphazardly.

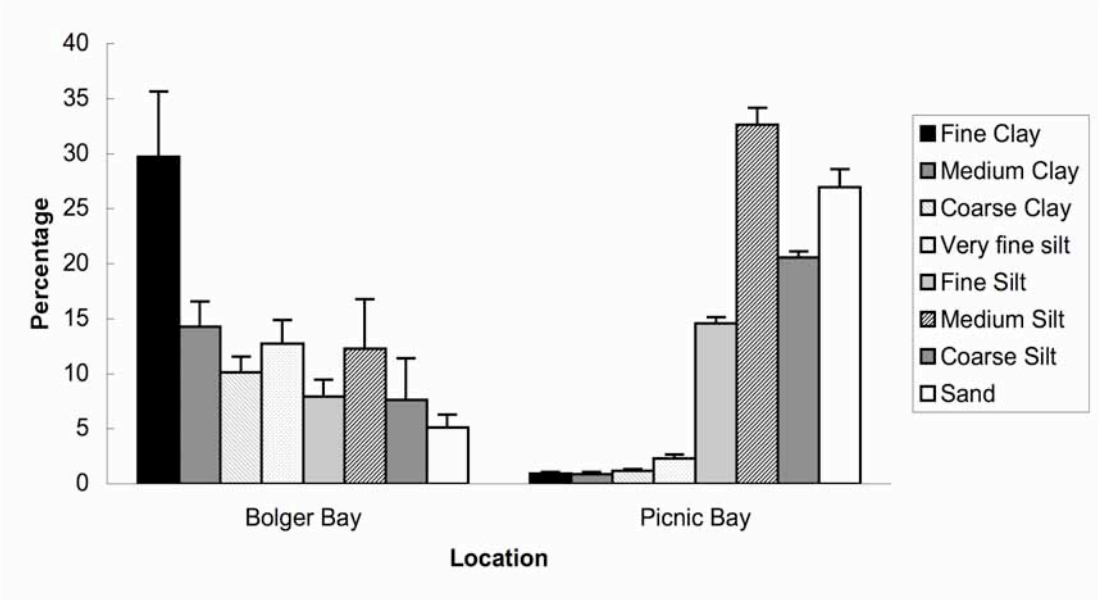
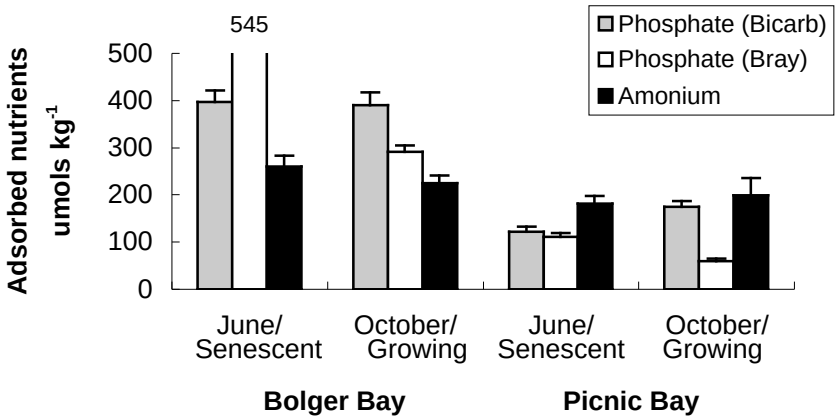


Figure 4.10 Sediment particle grain size distributions for Bolger Bay and Picnic Bay. Note that this graph has been presented previously in Chapter 4.2 as Fig.4.4. (mean and standard errors presented).

a).



b).

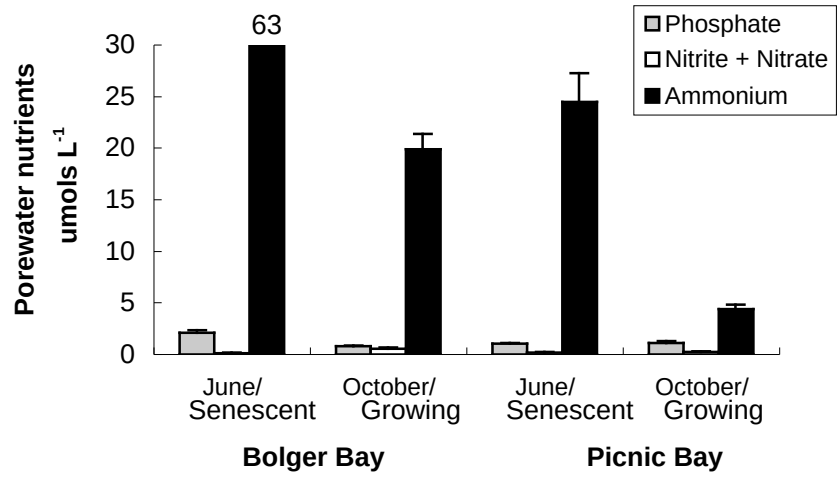
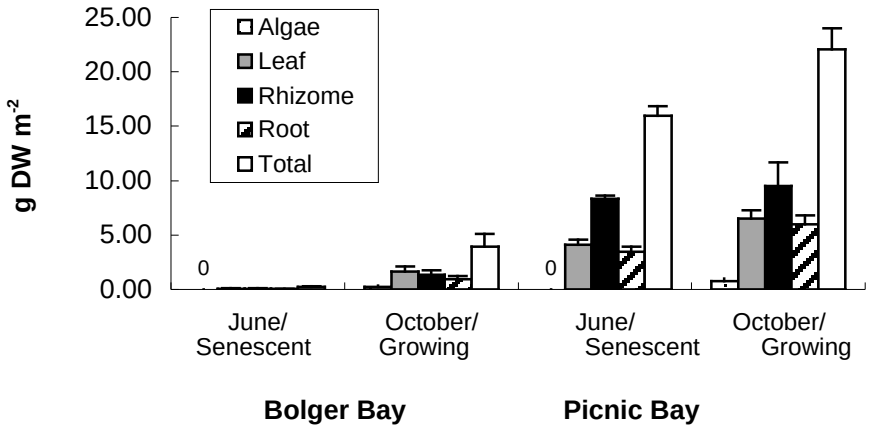


Figure 4.11 Intra-annual variation of sediment nutrients between Bolger Bay and Picnic Bay at different times of the year for **a)** adsorbed nutrients and **b)** porewater nutrients. (Mean and standard error presented). Where a number is displayed above a bar this represents the mean nutrient value of that bar which is beyond the scale of the y axis. Where no cross bar appears on top of the standard error line it means that the standard error was beyond the scale of the Y axis.

a).



b).

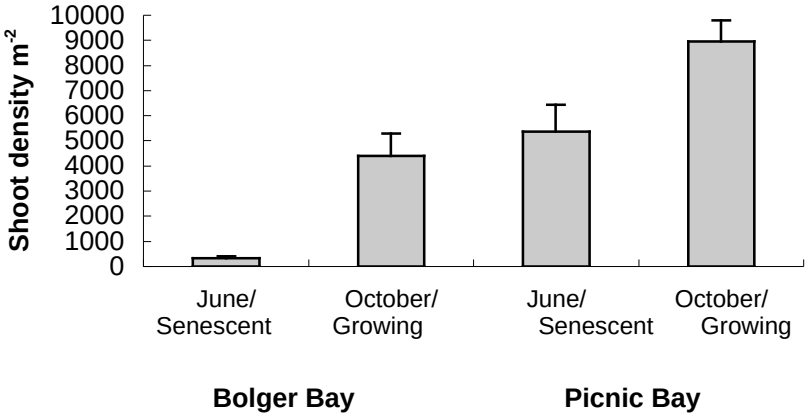
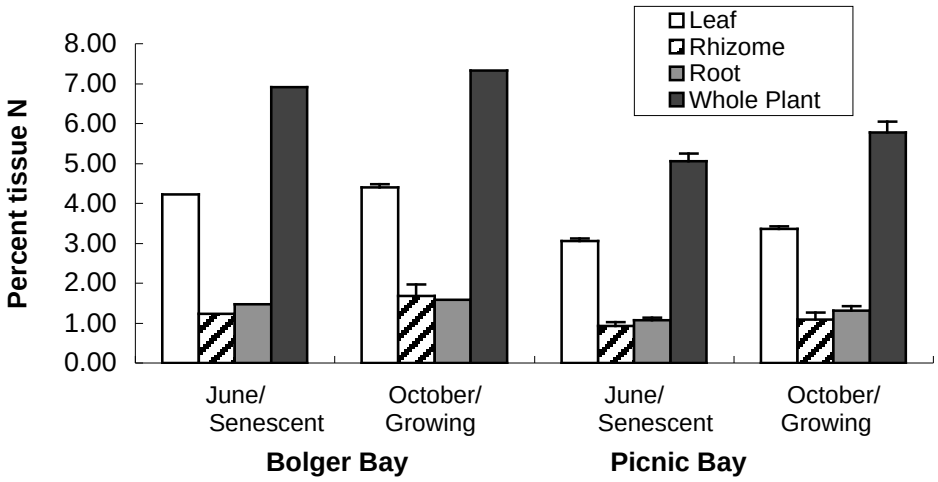


Figure 4.12 A comparison of the intra-annual variation in seagrass density measures between and within Bolger Bay and Picnic Bay for **a)** seagrass biomass and **b)** shoot density. (Mean and standard error presented).

a).



b).

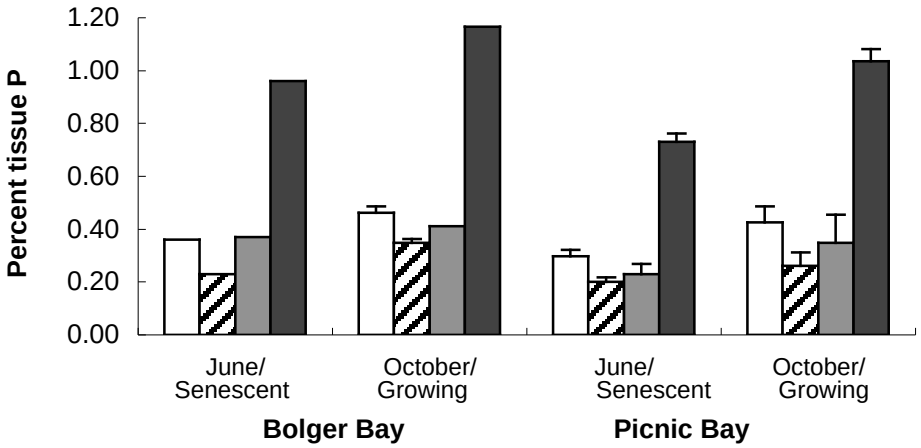
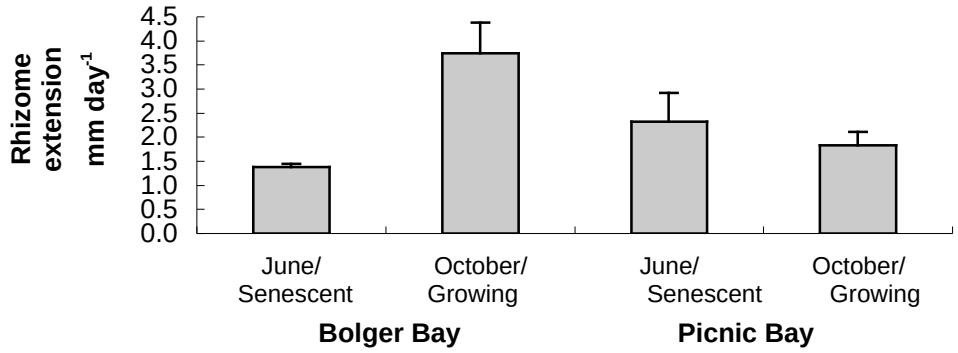
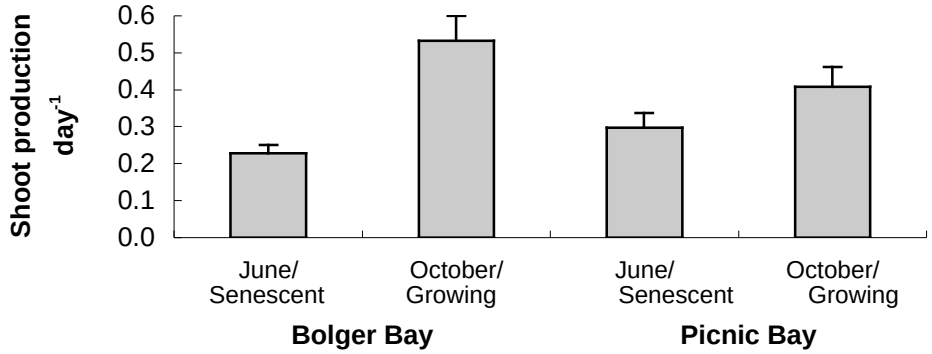


Figure 4.13 A comparison of the variation of plant tissue nutrients between and within the locations, Bolger Bay and Picnic Bay, for **a)** percent tissue N and **b)** percent tissue P. (Mean and standard error presented, where there are no standard errors, only a single sample was taken)

a).



b).



c).

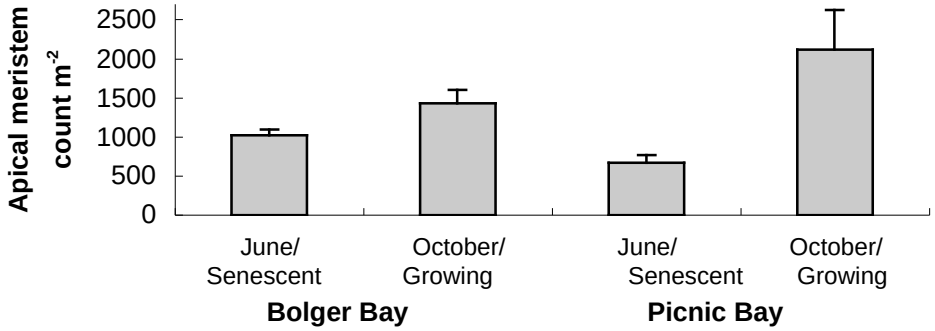


Figure 4.14 A comparison of intra-annual variation in plant growth parameters between and within the two locations, Bolger Bay and Picnic Bay for **a)** rhizome extension per meristem **b)** leaf production per meristem, **c)** apical meristem production.

Table 4.16 Statistical differences in abiotic parameters between Bolger Bay and Picnic Bay.

Analysis	Variables	$F_{(df)}$	*p*	Outcome
Grain Sizes				
MANOVA	All	$30.09_{(8,3)}$	0.009	
'Between subject tests'	Fine clay	$154.64_{(1,10)}$	< 0.001	> Bolger Bay
	Medium clay	$103.75_{(1,10)}$	< 0.001	> Bolger Bay
	Coarse clay	$120.80_{(1,10)}$	< 0.001	> Bolger Bay
	Very Fine silt	$56.89_{(1,10)}$	< 0.001	> Bolger Bay
	Fine silt	$8.96_{(1,10)}$	0.014	> Picnic Bay
	Medium silt	$9.708_{(1,10)}$	0.011	> Picnic Bay
	Coarse silt	$8.427_{(1,10)}$	0.016	> Picnic Bay
	Sand	$48.59_{(1,10)}$	< 0.001	> Picnic Bay
Chemically derived parameters				
MANOVA	All			
'Between subject tests'	Carbonate	$8.558_{(1,10)}$	0.015	> Picnic Bay
	Vegetative	$18.728_{(1,10)}$	0.001	> Bolger Bay
MANOVA	All	$7.525_{(2,7)}$	0.018	
'Between subject tests'	Eh	$0.959_{(1,8)}$	0.036	> Picnic Bay
	pH	$14.311_{(1,8)}$	0.005	> Picnic Bay

Table 4.17 Measurements of sediment nutrients (mean ± s.e.) for the two different times of the year (representative of the different seasons) at Bolger Bay and Picnic Bay.

Parameter	June—senescent season		October—growing season	
	Bolger Bay	**Picnic Bay**	**Bolger Bay**	**Picnic Bay**
Adsorbed (µmol kg^{-1})				
$PO_4^{3-}{}_{(Bray)}$	545.34 ± 41.65	110.97 ± 8.03	291.44 ± 13.42	59.49 ± 5.33
$PO_4^{3-}{}_{(bicarbonate)}$	396.87 ± 24	121.32 ± 11.05	390.15 ± 27.49	174.72 ± 12.49
NH_4^+	259.80 ± 22.95	224.62 ± 16.26	182.17 ± 15.50	199.21 ± 36.09
Porewater (µmol L^{-1})				
PO_4^{3-}	2.13 ± 0.22	1.046 ± 0.07	0.787 ± 0.094	1.113 ± 0.203
NH_4^+	63.131 ± 4.56	24.49 ± 2.81	19.869 ± 1.51	4.41 ± 0.40
$NO_2^- + NO_3^-$	0.153 ± 0.05	0.588 ± 0.118	0.21 ± 0.04	0.245 ± 0.05

Table 4.18 Differences in the levels of sediment nutrients between the two locations (Bolger Bay and Picnic Bay) at different times of the year representative of the different seasons.

Season/Analysis	Variables	$F_{(df)}$	*p*	Outcome
June/Senescent				
Adsorbed nutrients				
MANOVA	All	$89.20_{(3,12)}$	<0.001	
'Between subject tests'	Adsorbed $PO_4^{3-}{}_{(Bray)}$	$239.83_{(1,14)}$	<0.001	> Bolger Bay
	Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	$136.49_{(1,14)}$	<0.001	> Bolger Bay
	Adsorbed NH_4^+	$9.99_{(1,14)}$	0.007	> Bolger Bay
Porewater				
MANOVA	All	$26.35_{(3,72)}$	<0.001	
'Between subject tests'	PO_4^{3-}	$22.73_{(1,74)}$	<0.001	> Bolger Bay
	NH_4^+	$61.99_{(1,74)}$	<0.001	> Bolger Bay
	$NO_2^- + NO_3^-$	$1.23_{(1,74)}$	0.272	No difference
October/Growing				
Adsorbed Nutrients				
MANOVA	All	$113.243_{(3,12)}$	<0.001	
'Between subject tests'	Adsorbed $PO_4^{3-}{}_{(Bray)}$	237.88	<0.001	> Bolger Bay
	Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	$60.82_{(1,14)}$	0.001	> Bolger Bay
	Adsorbed NH_4^+	$1.27_{1,14)}$	0.279	No difference
Porewater				
MANOVA	All	$64.244_{(3,76)}$	<0.001	
'Between subject tests'	PO_4^{3-}	$6.89_{(1,78))}$	0.010	> Picnic Bay
	NH_4^+	$165.32_{(1,78)}$	<0.001	> Bolger Bay
	$NO_2^- + NO_3^-$	$11.40_{(1,78)}$	<0.001	> Bolger Bay

Table 4.19 Intra-annual differences in sediment nutrients, adsorbed and porewater at Bolger Bay.

Season/Analysis	Variables	$F_{(d.f)}$	*p*	Outcome
Senscent				
Adsorbed nutrients				
MANOVA	all	$17.21_{(3,12)}$	0.001	
'Between subject tests'	Adsorbed $PO_4^{3-}{}_{(Bray)}$	$47.10_{(1,14)}$	<0.001	> Senescent Season
	Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	$0.06_{(1,14)}$	0.814	No difference
	Adsorbed NH_4^+	$1.61_{(1,14)}$	0.225	No difference
Porewater nutrients				
MANOVA	all	$42.20_{(3,72)}$	<0.001	
'Between subject tests'	PO_4^{3-}	$37.42_{(1,74)}$	<0.001	> Senescent season
	NH_4^+	$94.54_{(1,74)}$	<0.001	> Senescent season
	$NO_2^- + NO_3^-$	$20.55_{(1,74)}$	<0.001	> Growing season

Table 4.20 Intra-annual differences in sediment nutrients at Picnic Bay.

Analysis	Variables	$F_{(d.f)}$	*p*	Outcome
Adsorbed nutrients				
MANOVA	all	$19.87_{(3,12)}$	<0.001	
'Between subject tests'	Adsorbed $PO_4^{3-}{}_{(Bray)}$	$30.11_{(1,14)}$	<0.001	> Senescent season
	Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	$9.86_{(1,14)}$	0.007	> Growing season
	Adsorbed NH_4^+	$0.01_{(1,14)}$	0.926	No difference
Porewater nutrients				
MANOVA	all	$84.29_{(1,76)}$	<0.001	
'Between subject tests'	PO_4^{3-}	$3.29_{(1,77)}$	0.074	No difference
	NH_4^+	$166.04_{(1,77)}$	<0.001	> Senescent season
	$NO_2^- + NO_3^-$	$0.32_{(1,77)}$	0.570	No difference

Table 4.21 Summary of statistically significant results for plant parameters between the two locations Bolger Bay and Picnic Bay during the different months that were chosen to be representative of the different seasons. N.B. Due to the high number of analyses performed, 5% of tests would be expected to be significant based on chance alone.

Analysis/Season	Variables	$F_{(d.f)}$	*p*	Outcomes
Biomass				
Senescent				
ANOVA	Leaf	$80.11_{(1,4)}$	<0.001	> Picnic Bay
	Rhizome	$880.72_{(1,4)}$	<0.001	> Picnic Bay
	Root	$59.34_{(1,4)}$	0.002	> Picnic Bay
	Whole plant	$241.06_{(1,4)}$	<0.001	> Picnic Bay
Growing				
ANOVA	Algae	$9.82_{(1,5)}$	0.035	> Picnic Bay
	Leaf	$28.88_{(1,5)}$	0.006	> Picnic Bay
	Rhizome	$21.49_{(1,5)}$	0.010	> Picnic Bay
	Root	$35.05_{(1,5)}$	0.004	> Picnic Bay
	Whole plant	$64.17_{(1,5)}$	0.001	> Picnic Bay
Shoot number				
Senescent				
ANOVA	Number of shoots	$127.58_{(1,4)}$	<0.001	> Picnic Bay
Growing				
ANOVA	Number of shoots	$14.20_{(1,5)}$	0.020	> Picnic Bay
Plant nutrients				
Senescent				
ANOVA	% leaf N	$63.37_{(1,3)}$	0.015	> Bolger Bay
	% leaf P	$1.72_{(1,3)}$	0.320	No difference
	% rhizome N	$2.75_{(1,3)}$	0.239	No difference
	% rhizome P	$0.75_{(1,3)}$	0.477	No difference
	% roots N	$8.15_{(1,3)}$	0.104	No difference
	% roots P	$3.15_{(1,3)}$	0.218	No difference
	% whole plant N	$15.43_{(1,2)}$	0.059	No difference
	% whole plant P	$12.79_{(1,2)}$	0.070	No difference
	*gN m^{-2} of seagrass	$210.25_{(1,4)}$	<0.001	> Picnic Bay
	*gP m^{-2} of seagrass	$215.60_{(1,4)}$	<0.001	> Picnic Bay
Growing		-	-	
ANOVA	% leaf N	$52.25_{(1,5)}$	0.002	> Bolger Bay
	% leaf P	$0.35_{(1,5)}$	0.586	No difference
	% rhizome N	$4.17_{(1,4)}$	0.134	No difference
	% rhizome P	$1.89_{(1,4)}$	0.263	No difference
	% root N	$2.55_{(1,3)}$	0.251	No difference
	% root P	$0.17_{(1,3)}$	0.719	No difference
	% whole plant N	$16.10_{(1,3)}$	0.057	No difference
	% whole plant P	$3.67_{(1,3)}$	0.196	No difference
	*gN m^{-2} of seagrass	$24.44_{(1,4)}$	0.008	> Picnic Bay
	*gP m^{-2} of seagrass	$89.67_{(1,4)}$	<0.001	> Picnic Bay
Plant growth				
Senescent				
	Rhizome extension	$2.66_{(1,4)}$	0.217	No difference
	Apical meristems	$7.21_{(1,4)}$	0.055	No difference
	Shoot growth	$4.17_{(1,4)}$	0.114	No difference
Growing				
	Rhizome extension	$10.42_{(1,4)}$	0.032	> Bolger Bay
	Apical meristems	$1.73_{(1,4)}$	0.258	No difference
	Shoot growth	$1.43_{(1,4)}$	0.298	No difference

*constant %N and %P used in calculations for Bolger Bay.

Table 4.22 All plant parameter measurements (means and s.e.) for both locations Bolger Bay and Picnic Bay during different months that were chosen to be representative of the different seasons.

Parameter	Bolger Bay		Picnic Bay	
	Senescent season	**Growing season**	**Senescent season**	**Growing season**
***Biomass*[1]**				
Algae	0	0.02 ± 0.01	0	0.75 ±0.26
Leaf	0.09 ± 0.03	1.64 ± 0.47	4.13 ± 0.45	6.49 ± 0.77
Rhizome	0.08 ± 0.02	1.33 ± 0.43	8.33 ± 0.28	9.54 ± 2.14
Root	0.04 ± 0.01	0.95± 0.29	3.48 ± 0.46	6.00 ± 0.80
Whole plant	0.25 ± 0.06	3.95 ± 1.17	15.99 ± 0.859	22.08 ± 1.936
Number of shoots	343 ± 57	4392 ± 895	5379 ± 1067	8969 ± 822
Plant nutrients				
% leaf N	4.22	4.407 ± 0.08	3.06 ± 0.07	3.36 ± 0.11
% leaf P	0.36	0.30 ± 0.02	0.46 ± 0.02	0.43 ± 0.06
% rhizome N	1.23	1.68 ± 0.30	0.93 ± 0.09	1.10 ± 0.17
% rhizome P	0.23	0.35 ± 0.01	0.20 ± 0.02	0.26 ± 0.05
% root N	1.47	1.59	1.07 ± 0.07	1.31 ± 0.11
% root P	0.37	0.41	0.23 ± 0.04	0.35 ± 0.11
% whole plant N	6.92	7.33	5.05 ± 0.20	5.77 ± 0.28
% whole Plant P	0.96	1.17	0.73 ± 0.03	1.04 ± 0.05
$gN_{seagrass}\,m^{-2}$	1.70± 0.40	28.94 ± 8.60	80.02 ± 2.82	126.43 ± 5.65
$gP_{seagrass}\,m^{-2}$	0.24 ± 0.06	4.59 ± 1.36	11.53 ± 0.34	22.74 ± 1.47
Plant growth				
Rhizome extension[2]	1.38 ± 0.07	3.75± 0.63	2.33 ± 0.591	1.83 ± 0.28
Apical meristems[3]	1024.00 ±76.00	1429.00 ± 175	672.00 ± 97.00	2123.00 ± 501
Shoot growth[4]	0.23± 0.02	0.53± 0.67	0.30 ± 0.04	0.41 ± 0.05

[1]g DW m^{-2}
[2]mm day^{-1}/mersitem
[3]count m^{-2}
[4]number produced day^{-1}/mersitem

Table 4.23 Summary of statistically significant results for plant parameters at Bolger Bay during the different times of the year that were chosen to be representative of the different seasons.

Analysis/Season	Variables	$F_{(d.f)}$	*p*	Outcomes
Biomass				
ANOVA	Algae	Zero Biomass		
	Leaf	$31.51_{(1,4)}$	0.005	> Growing season
	Rhizome	$40.04_{(1,4)}$	0.003	> Growing season
	Root	$31.90_{(1,4)}$	0.003	> Growing season
	Whole plant	$47.53_{(1,4)}$	0.002	> Growing season
Shoot number				
ANOVA	Number of shoots	$31.39_{(1,3)}$	0.005	> Growing season
Plant nutrients				
ANOVA	% leaf N	$1.42_{(1,2)}$	0.355	No difference
	% leaf P	$6.20_{(1,2)}$	0.130	No difference
	% rhizome N	$1.03_{(1,1)}$	0.490	No difference
	% rhizome P	$28.39_{(1,1)}$	0.118	No difference
	% root N	insufficient replication		
	% root P	insufficient replication		
	% whole plant N	insufficient replication		
	% whole Plant P	insufficient replication		
	*$gN_{seagrass}\,m^{-2}$	$42.07_{(1,4)}$	0.003	> Growing season
	*$gP_{seagrass}\,m^{-2}$	$46.12_{(1,4)}$	0.002	> Growing season
Plant growth				
	Rhizome extension	$34.97_{(1,4)}$	0.004	> Growing season
	Apical meristems	$4.67_{(1,4)}$	0.097	No difference
	Shoot growth	$18.96_{(1,4)}$	0.012	> Growing season

*a constant %N and %P used in this calculation

Table 4.24 Summary of statistically significant results for plant parameters at Picnic Bay during the different times of the year that are representative of the different seasons.

Analysis	Variables	$F_{(d.f)}$	*p*	Outcomes
Biomass				
ANOVA	Algae	$10.56_{(1,4)}$	0.031	> Growing season
	Leaf	$7.04_{(1,4)}$	0.057	> Growing season
	Rhizome	$0.606_{(1,4)}$	0.606	No difference
	Root	$7.41_{(1,4)}$	0.053	> Growing season
	Total	$8.23_{(1,4)}$	0.045	> Growing season
Shoot number				
ANOVA	Number of shoots	$7.11_{(1,4)}$	0.056	No difference
Plant nutrients				
ANOVA	% leaf N	$5.94_{(1,4)}$	0.071	No difference
	% leaf P	$3.85_{(1,4)}$	0.121	No difference
	% rhizome N	$0.71_{(1,4)}$	0.446	No difference
	% rhizome P	$1.28_{(1,4)}$	0.321	No difference
	% root N	$3.58_{(1,4)}$	0.131	No difference
	% root P	$1.06_{(1,4)}$	0.362	No difference
	% whole plant N	$4.62_{(1,4)}$	0.098	No difference
	% whole plant P	$32.3_{(1,4)}$	0.005	> Growing season
	gN m^{-2} of seagrass	$53.94_{(1,4)}$	0.002	> Growing season
	gP m^{-2} of seagrass	$91.88_{(1,4)}$	<0.001	> Growing season
Plant growth				
	Rhizome extension	$0.38_{(1,4)}$	0.573	No difference
	Apical meristems	$10.81_{(1,4)}$	0.030	> Growing season
	Shoot growth	$2.75_{(1,4)}$	0.172	No difference

Chapter 5.0 Evaluating the biogeochemical status and responses to nutrient enhancement of the sediments and plants in two *Halophila ovalis* meadows

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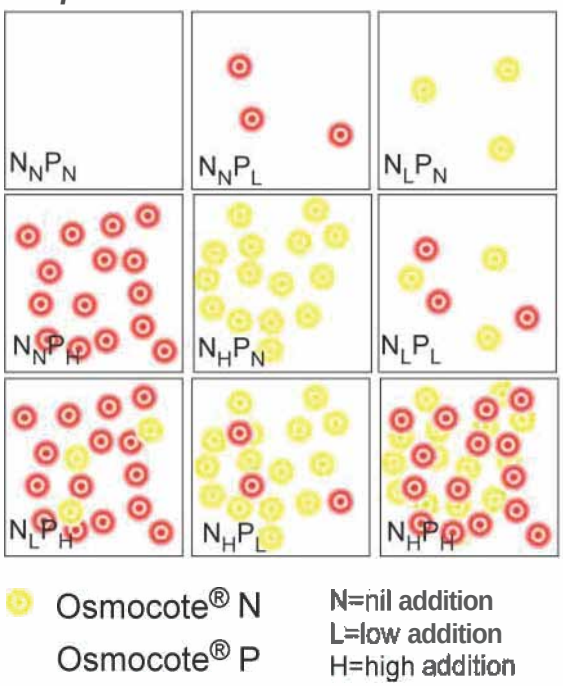
Experimental treatments



Summary

Unlike most nutrient enhancement studies of seagrasses, this experiment examined different locations, different seasons and different levels of fertilizers. Sediment nutrient levels were raised above ambient conditions using different application rates of Osmocote ®N only, Osmocote® P only, and combinations of Osmocote® N only + Osmocote® P only, at both locations during both experiments. Low and high levels of fertilizer addition did not consistently raise sediment nutrients incrementally, however, they did allow for observations of plant response to enhanced nutrients at locations with different sedimentary regimes and at different times of the year. Overall, the response of plant biomass to increased nutrients was limited and complex. Seagrasses at Bolger Bay, displayed primary P limitation during the senescent season and a trend for P limitation during the growing season. This location had a sedimentary regime dominated by clay mineralogy with small sediment grain sizes, high ambient nutrient levels and low seagrass biomass. Plant tissue nutrients were also higher in Bolger Bay. All these factors are thought to play a role in how *Halophila ovalis* responded to nutrient additions at Bolger Bay. In contrast seagrass at Picnic Bay showed no nutrient limitation during the senescent season, but in the growing season there was primarily N limitation with secondary P limitation. The factors thought to influence this seagrass response at Picnic Bay, was the sedimentary regime (sediments dominated by carbonate mineralogy with coarser grain particle sizes, higher Eh, higher pH, lower percent organic content, higher percent carbonate content, lower ambient nutrient levels) and the higher ambient seagrass biomass and lower percentage of plant tissue N and P compared to Bolger Bay. Other factors that influenced the overall outcomes of the experiment included the behaviour of Osmocote®, the amount of Osmocote® presented to the rhizosphere, the experimental effect of disturbing the rhizosphere with the application of the fertilizer, and the time of year.

5.0.1 Introduction to the nutrient enhancement experiment

Considerable industrial, urban and agricultural development (catchment modification) has occurred adjacent to the Great Barrier Reef Lagoon (GBRL) over the past century (Bell 1991, Schaffelke *et al.* 2001, Furnas 2003). Run-off from these activities can contribute large loads of nutrients and other contaminants into the Great Barrier Reef Lagoon and near shore environments. This phenomena has concerned scientists, managers and the public and has led to the growing realisation that changes in the water quality of terrestrial runoff is one of the most significant anthropogenic threats to the Great Barrier Reef (GBR) region (Yellowlees 1991, Bell 1991, Baldwin 1992, Brodie 1992, Williams 2001, Furnas 2003).

The effects of this terrestrial habitat modification on corals have been of primary concern to managers, researchers and the general public. Recently, awareness that the nutrient-enriched water entering the GBR lagoon from land-based sources is concentrated and effectively entrained along the coastline due to prevalent south-easterly winds (Wolanski *et al.* 1981a, Gagan *et al.* 1990, Larcombe *et al.* 1996), has lead to a growing concern for near shore habitats and inner reef areas. These near-shore habitats typically consist of mangroves and seagrass beds. Mangrove and seagrass communities have the ability to absorb increased quantities of nutrients and can act as a nutrient buffer between freshwater and marine systems (Hatcher *et al.* 1989, Hemminga *et al*. 1995, Subchapter 4.1). Above certain nutrient thresholds (which can vary according to a number of biological and physical factors), these coastal wetlands lose the ability to efficiently cycle nutrients, as the nutrient assimilation capacity of the community is exceeded (Gabric and Bell 1993).

In the last twenty years, substantial declines in seagrass meadows have occurred worldwide. These declines are considered to have been caused by several anthropogenic activities (Cambridge and McComb 1984, Larkum and West 1990, Gabric and Bell 1993, Preen *et al.* 1995). Diffuse or non-point sources of pollution entering the coastal marine environment are largely the result of inappropriate land-use practices and are now considered to be the most serious threat to the health of seagrass beds (Short 1987, Walker and McComb 1992, Preen *et al.* 1995). Research into the effects of pollutants has shown that seagrass plants can accumulate contaminants in their tissues (Chaphekar

1991, Lovett Doust *et al*. 1994). Consequently seagrasses are useful bioindicators of the concentration and geographical spread of heavy metals and other contaminants in the marine environment (Ward 1987, Tiller *et al.* 1989). Nutrients in seagrass plant tissue, particularly phosphate, have also been used as an indicator of the bioavailable phosphorus status of an area (Gerloff and Krombholz 1966, Fourqurean *et al.* 1992). The relationship between nutrients and seagrasses is complex.

The role of nutrients in seagrass growth has been evaluated through three different approaches:

i) assessment of the nutrient content of their tissues (e.g. Duarte 1990, Fourquearan *et al.* 1992);

ii) analysis of nutrient budgets (e.g. Patriquin 1972, Bulthius and Woelkerling 1981, Pedersen and Borum 1993); and

iii) nutrient addition experiments (Orth 1977, Powell *et al.* 1989, Short *et al.* 1990, Erftemeijer *et al.* 1994, Udy and Dennison 1997a, Udy and Dennsion 1997b, Udy *et al.* 1999).

In situ nutrient additions have provided the most conclusive evidence of the effects of enhanced external nutrient loadings on seagrass, as they test the plant's response to increased nutrients (see Table 5.1). Some researchers broadcast or inject fertilizer into the water column (Harlin and Thorne Miller 1981). These studies recorded modest seagrass growth, stimulated by the addition of the nutrients. The modest growth was attributed to the nutrient release into the water column rather than into the sediments, increasing the likelihood of the excess nutrients being diluted and moved from the source. Other studies have added or injected nutrients directly to sediments (e.g. Bulthius and Woelkerling 1981, Kenworthy and Fonseca 1992, Murray *et al*. 1992). Some studies have used timed, slow release fertilizer (manufacturers' description) to imitate the gradual nutrient build-up occurring in many coastal seagrass meadows as a result of anthropogenic impact (Roberts *et al.* 1984, Kenworthy and Fonseca 1992, Short *et al*. 1990). These studies have used granular, controlled release Osmocote® in N and P only forms. This type of fertilizer is designed for nutrient enrichment of terrestrial plants utilising freshwater, whereby contact with water triggers the release and temperature controls the rate of release. In contrast, the movement and behaviour of

Osmocote® in marine sediments is dependent upon the overall climatic regime of the study area, the salinity of the ambient water and the physical and chemical nature of the sediment in question.

In general these experimental studies did not: a) undertake in depth assessment of the mineralogy of the sediments being fertilized, b) investigate the effect of sediment geochemistry on the bioavailability of nutrients, c) test the effects of time of year when seagrass nutrient requirements may differ, or d) examine the response of structurally small seagrass species (see Table 5.1). As a result, the results from these earlier experiments cannot be extrapolated to infer broader processes due to differences in: a) species-specific nutrient requirements, b) locality mineralogy/sediment geochemistry and nutrient history of the locality where the experiment took place, c) seasonality, which may affect the 'availability' of the nutrient under question, and d) seasonal changes in nutrient requirements of the seagrass species being investigated.

As discussed below, this experiment does not profess to answer questions of mineralogical and seasonal influence on the response of *Halophila ovalis* in an optimum manner because of the acknowledged lack (due to financial and logistical constraints) of replication at the levels of location (sedimentary regime) and seasons. Rather, it is a first step at elucidating and comparing the responses of biomass and tissue nutrient status of *Halophila ovalis* (R.Br.) Hook., a structurally small seagrass, associated with different sedimentary regimes (mineralogy, sediment nutrients, sediment grain size) at different times of the year to varying levels of N, P and N+P enrichment. The scope and organization of the experiment is illustrated in Figure 5.1 as a conceptual flow chart of the study.

For clarity and ease of interpretation, this chapter has been arranged by topic into four subchapters. Each subchapter deals with a theme within the overall experiment as follows:

Subchapter 5.0 **A nutrient enrichment experiment: design and methodology.** This Subchapter outlines the experiment. It describes the study site in detail, the methodologies common to all sections of this study, including the experimental design, statistical analyses and discusses the behaviour of Osmocote® in the marine environment.

Subchapter 5.1 Assessing the mineralogy of two intertidal seagrass meadows of *Halophila ovalis*. This subchapter compares the sedimentary regimes (mineral composition and sediment particle size) of the experimental plots at the bay scale, within bay scale (different times of year), the block scale and at the treatment level.

Subchapter 5.2 Evaluating the response of sediment nutrients to Osmocote® additions. This subchapter evaluates the responses of ambient sediment nutrients (porewater and adsorbed) at the two locations (with dissimilar sedimentary regimes) to varying amounts and combinations of N and P Osmocote® at different times of the year and determines whether the ambient levels of nutrients were raised by the addition of Osmocote®.

Subchapter 5.3 Evaluating the response of *Halophila ovalis* to nutrient enrichment during different seasons. This subchapter deals with the response of this structurally small species of seagrass to changed sediment nutrient status as dictated by the addition of Osmocote®. In particular, it examines biomass, shoot density and plant tissue responses for each plant component (leaves, rhizomes and roots)

The experiment was performed within intertidal areas of the central region of the Great Barrier Reef World Heritage Area (GBRWHA), an area under threat from anthropogenic eutrophication and where information on small-scale spatial and temporal fluctuations in seagrass beds is sparse (Schaffelke *et al.* 2001). These experiments highlight the complexity of field experimentation and the need to: a) assess any experimental effect on seagrass responses, b) be aware of the behaviour in an aquatic environment of the fertilizer being used (most fertilizers are formulated and tested for terrestrial uses), and c) use appropriate extraction techniques dependent on the type of sediment.

5.0.2 Material and methods for enhancement experiment

The method of sampling sediment nutrients, excavating seagrass, extracting adsorbed sediment nutrients and plant tissue nutrients and, the chemical determinations of sediment and plant nutrients have been previously described in Chapter 2: *General*

materials and methods. Only those materials and methods that are common to all sections of the experiment are presented in this subchapter, such as site description, experimental design, application of fertilizer, number of samples for each parameter and statistical analyses. Methodologies pertinent to each specific topic are described in the following subchapter where relevant.

Site description

This experiment was conducted at Magnetic Island (19°11'E, 146°51'S, Subchapter 4.3: Fig. 4.8 and title page of this subchapter), a continental island situated approximately 7 km off the coast from the City of Townsville in Cleveland Bay. The island has an area of approximately 5100 hectares, contains 21 bays, two coves and numerous granitic rocky headlands (Pringle 1989, Gutteridge *et al*. 1990). Permian age granite, known as Magnetic Island Granite, dominates the geology of the island (Trezise and Stephenson 1990). Weathering of the parent rock reduces large slabs and pieces of granite into small gravel size fragments that contribute to the sediment loading into the surrounding bays and coves. Further weathering causes Magnetic Island Granite to decompose the quartz and feldspar to clay minerals (illite, smectite, kaolinite) and iron and aluminium hydroxides.

The seagrasses manipulated in this study were located at Picnic and Bolger Bays (Chapter 4.3, Fig. 4.8). Picnic Bay is located at the southern end of Magnetic Island facing Cleveland Bay. It is exposed to the south easterly winds and is characterized by headlands of large rounded granite boulders. At the time of my experiments, this bay was the commercial centre for the island housing the main ferry terminal and a resort located directly opposite the experimental site. Bolger Bay is on the western side of the island opposite Cape Pallarenda and Shelley Beach. It is sheltered from the prevailing south-easterlies and is fringed by mangroves on its landward edge (Pringle 1989). There is one residence at this bay, which is not connected to either town water or electricity. Hobby farms surround the greater catchment to this bay. The small rivers that make up the Ross River–Black River catchment and the vast catchment of the Burdekin–Haughton rivers influence Cleveland Bay. Of these rivers systems the Burdekin River–Haughton River catchment and thus the Burdekin River has the largest influence over the study sites due to its size.

Both bays are fringed by coral reefs on their seaward edge and have seagrass growing on their intertidal flats. The seagrass meadows at these sites are made up of monospecific stands of *Cymodocea serrulata* (lower intertidal, subtidal), *Halodule uninervis* (wide) (middle intertidal) and *Halophila ovalis* (upper intertidal). The experiments were undertaken within these stands of *Halophila ovalis* at the landward edge of the bed.

The experiments

Four experiments were conducted to test the response of *H. ovalis* to enhanced nutrient input, whilst also comparing plant responses to nutrient enhancement under different sedimentary regimes (location effects), and the plant's response during different growing seasons (Table 5.2). Each experiment ran as close as possible to 90 days. The exact number of days for each experiment was determined by tidal regimes at each location as sampling was undertaken during the lowest tide of the month.

Experimental design

To maximize the likelihood that light regimes were comparable between the two locations, the experimental units were set up at the landward edge of the intertidal seagrass beds. Thus sites were in similar depths so that exposure to light would be similar. In addition, the duration of exposure at low tide and hence desiccation should also have been similar. Three replicate blocks in a randomized block design were established for each experiment. The experimental treatments were blocked because of a perceived gradient in tidal exposure between each block. The blocks were organized with their long axes parallel to the shore (Fig. 5.2). Blocks were 2 m apart and quadrats approximately 1–1.5 m apart, depending on the distribution of the seagrass, which was patchy in both bays. The between-quadrat distance was chosen to reduce the impact of: i) diffusion of nutrients between quadrats, and ii) seagrass damage or sediment compaction caused by trampling while sampling.

Each block consisted of 10 x 0.25 m^2 quadrats incorporating eight fertilizer treatments of N and P combinations and two controls (Table 5.3): a field control (ambient conditions–no manipulation/lifting of rhizosphere: N_AP_A) and an experimental control (seagrass rhizosphere lifted and then replaced without addition of fertilizer: N_NP_N). I lifted the rhizosphere before adding the fertilizer and then replaced it to prevent the

Osmocote® floating away on the next tide. Before lifting the rhizosphere, I established its depth to be 2.5 cm. I then angled a trowel from the edge of quadrat to this depth in order to raise the entire rhizosphere with minium disturbance to the rhizome root mat. Whilst the rhizosphere was on the trowel, the fertilizer was scattered underneath the sod.

Once the fertilizer was in place, the sod was replaced and the trowel slid out. An experimental control was included in the design to determine whether the handling and disturbance of the rhizosphere affected the seagrasses' response. Treatments were assigned to quadrats within each block by lottery. To define the working area of each quadrat, each of the four corners was marked by a tent peg with coloured plastic coated electrical wire. Porewater, and sediment samples and seagrass were collected from each quadrat/treatment at the conclusion of the experiment.

Justification of levels of fertilizer used

A pilot study at Picnic Bay from (October 1994–January 1995) using a retail preparation of Osmocote supplied the quadrats with a combination of N and P at loadings of 100 g N m^{-2} and 32 g P m^{-2} respectively. At the conclusion of this pilot study, the response of the seagrass was visually obvious. The fertilizer loadings also translated into a ten-fold increase in adsorbed sediment nutrients between the fertilized plots and the control plots. Fertilizer obtained for subsequent experiments was Osmocote P only 0:18:0 (N:P:K) and N only 23:0:0 (N:P:K). For these experiments, I decided to test the response of the seagrasses to a 'low' loading of fertilizer (which the pilot study suggested should have resulted in a five-fold increase in adsorbed sediment nutrients), and a 'high' loading of fertilizer (which should have resulted in a fifteen-fold increase in adsorbed sediment nutrients). The analysis codes and actual loadings of fertilizer for each treatment are listed in Table 5.3 and Table 5.4 respectively.

Fertilizer application

The fertilizer was applied by lifting the seagrass from below the rhizosphere, approximately 2.5 cm deep at each location, and inserting the Osmocote®. Each 0.25 m^2 quadrat was divided into nine sections, as was the total amount of fertilizer. This procedure ensured equal coverage of fertilizer in the quadrat.

Sampling

Porewater—dissolved inorganic nutrients

The sippers, 2.5 cm in length (described in Chapter 2) were used to sample porewater nutrients in this experiment at both Picnic Bay and Bolger Bay. Two replicate samples were taken from haphazardly selected positions within each 0.25 m^2 quadrat. As I was primarily interested in variations between treatments rather than variation within quadrats, the replicates were averaged. Treatment of the sample and chemical analyses of the nutrient within the sample are described in Chapter 2.

Sediment—extractable inorganic nutrients

Due to the cost of chemical analyses, one sediment core was taken per quadrat and treated as a depth integrated sample of the rhizosphere. The methodologies used in extracting the nutrient and the chemical analyses of the nutrient are described in Chapter 2.

Seagrass

At the completion of each experiment, the entire quadrat was excavated and biomass and shoot density determinations were made and plant tissue nutrients were determined as described in Chapter 2.

Physical environment

In addition to collecting data on sediment grain size, carbonate content and organic content from each location (see Chapter 4.3), information on the mineralogical status of each location was also analysed. Methodologies pertaining to sediment grain size, % carbonate and organic content, Eh and pH are described in Chapter 2. Techniques used to determine the mineralogy of each location are described in full in the next chapter, which deals solely with the mineralogy of the experimental sites.

Statistical methods

In Subchapter 4.3, I established that each location was unique and that seasonal patterns observed within location were consistent across locations. Preliminary analyses of the nutrient factors also showed that Bolger Bay and Picnic Bay were significantly different from each other with respect to sediment grain size, Eh, pH, % organic content and

% carbonate content, and ambient nutrient levels. If location had been included in the analyses of nutrient enhancement, the resultant residual would have been too small to test for differences in nutrient treatments, the paramount question of this study. Consequently, with the exception of the mineralogy data which had not been analysed previously, no further analyses were required to demonstrate the differences between locations in this chapter, thus I analysed the data separately for each location.

Differences between Season within Location and N and P could not be analysed, as the experimental plots at each location were not replicated within season at each location or across years at each location. My approach was necessitated by the destructive sampling undertaken within each quadrat at the completion of the experiment for tissue nutrients. I moved the experimental area to an independent site to avoid the confounding effects of plant recolonisation and its associated growth. This is not the ideal design to test for seasonal effects, however, it was dictated by financial and logistical constraints and the eco-ethical requirements of the management agency. Consequently, the effects of nutrient enhancement (N and P) on *Halophila ovalis* were analysed separately for each location (Bolger Bay, Picnic Bay) and for each time of year (Experiment 1: senescent season and Experiment 2: growing season).

The ANOVA model (GenStat) included a manipulation term so that the interactions between manipulation (lifting of the rhizosphere) and enhancement could be examined. Because only one quadrat per block was not manipulated, individual Least Significant Differences were re-calculated and tested for significant terms other than the three-way interaction (Manipulation*N*P) because the computer-generated LSD results (GenStat) did not take uneven replication into account[1]. Summarised tables and outcomes are presented in each relevant subchapter. Full statistical tables can be found in Appendix C.

[1] Advice form Angela Reid, Biometrician at Queensland Department of Primary Industries

5.0.3 An examination of Osmocote® behaviour in the marine environment

Osmocote® is granular in form and consists of water-soluble nutrients coated with an organic resin. The resin coating around each granule controls the daily release of plant nutrients. After application, water vapour penetrates the coating and dissolves the nutrients inside the coating, which are released gradually into the soil. According to the manufacturer, the rate of release is determined only by soil temperature and is not influenced by pH, microbiological activity, soil moisture levels, soil type or external salt concentration. The manufacturer identified the longevity of the product by reference to the rate of release at 21°C. Higher temperatures give a faster release and decrease the longevity period, while lower temperatures slow the release rate and increase the longevity period. However, this fertilizer is designed for the nutrient enrichment of terrestrial plants, utilising freshwater and may well act differently in a marine environment where the salinity of the ambient water and the physical and chemical nature of the sediments are quite different from those encountered in terrestrial situations.

The information supplied by the manufacturers of Osmocote® indicated that the daily release of Osmocote® products used in these experiments should be consistent over 5 to 6 months with an initial increase followed by the maintenance of a stable level in the porewater over time at 21°C. Following Udy and Dennison (1997a and b), I decided that the experiments should have a duration of three months due to the unknown nature of the behaviour of Osmocote® in a marine environment. During the senescent season, temperatures ranged from 25.1–16.6°C (May–August, average temperature 20°C) and for the growing season, 18–33°C (August–November, average temperature 25°C). If Osmocote® followed the release pattern described by the manufacturers, release rates should have been slower during the senescent season than during the growing season.

However that assumption was not valid and the viable longevity of the Osmocote® beads in the marine environment differed from expectation. For these experiments Osmocote® N only (23:0:0), was delivered as 11.5% NH_4^+ and 11.5% NO_2^- while Osmocote® P only (0:18:0) was delivered as mono-calcium phosphate (Scotts® Australia Pty Ltd, manufacturers of Osmocote®). At the completion of each experiment, Osmocote® beads found in the excavated seagrass samples were analysed for total

nutrient content. At the end of Experiment 1 (May–August) Osmocote® N had 4.63 ± 0.65%N, while beads at the end of Experiment 2 (August–November) had 3.66 ± 0.53%N. Whilst this suggests N was released more quickly during Experiment 2, a comparison of these means showed that there was no significant difference in the amount of N retained inside the beads between experiments ($p = 0.314$, d.f. = 1,5). Similarly, there was no significant difference between experiments for Osmocote® P ($p = 0.311$, df = 1,5) Experiment 1—8.01 ± 0.31%P and Experiment 2—7.59 ± 0.19 %P. These results suggest that the release rate of Osmocote® N was faster than that of Osmocote® P due to the differences in the proportion of the nutrient retained in the Osmocote® bead and that time of year had no effect on the rate of release.

However, the duration of the experiment had an effect on the amount of N or P released and made available to the seagrass. Jenkins (1995) specifically studied the behaviour and movement of Osmocote® through the intertidal marine sediments of Picnic Bay in the same experimental plots as this study, and showed that while phosphorus Osmocote® displayed an initial rapid release of P followed by slow release over time, similar to manufacturer's specifications, the nitrogen Osmocote® had an initial rapid release of N followed by pulse-like releases that decreased in magnitude over time. Jenkins (1995) predicted that this release rate pattern of N Osmocote® would be highly dependent on the sediment characteristics including grain size and mineralogy and ambient concentrations of N and P in the marine environment rather than on temperature alone as specified by the manufacturers.

Osmocote® has been used for many studies, which aimed to assess the effects of enhanced nutrients on seagrass beds (Roberts *et al.* 1984, Short *et al*. 1990, Kenworthy and Fonseca 1992, Erftemeijer *et al*. 1994, Udy and Dennison 1997a,b, Udy *et al*. 1999). These studies assumed that Osmocote® released nutrients to marine sediments slowly over three to six months depending on the temperature. These studies occasionally took into account the particle grain size of the sediments but did not analyse the mineralogy of the sediments beyond classifying the experimental sites as either terrigenous or carbonate (Kenworthy and Fonseca 1992, Erftemeijer *et al*. 1994). In contrast, Jenkins (1995) did not address the effect of seagrass uptake on depleting the N sediment pool, which may have accounted for the decline of N. Consequently many factors can affect the release rates of fertilizer, therefore I conclude that any

interpretation of fertilization experiments within seagrass meadows should include a full examination of the chemical and physical characteristics of the sediment and consideration of the role of seagrasses in nutrient uptake. This experiment is in an attempt to investigate these issues in a single integrated manipulation.

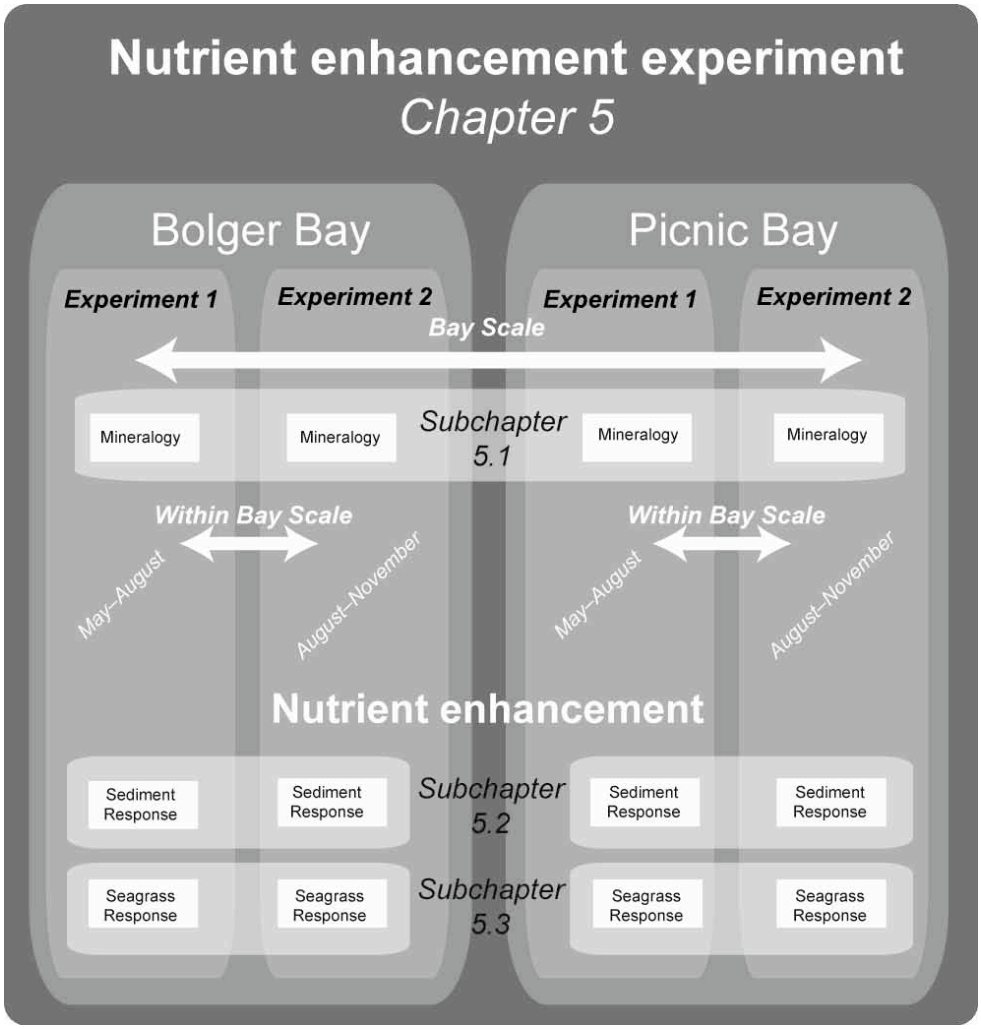


Figure 5.1 A conceptual flow chart of the scope and organization of the nutrient enhancement experiment conducted at Bolger Bay and Picnic Bay over two seasons.

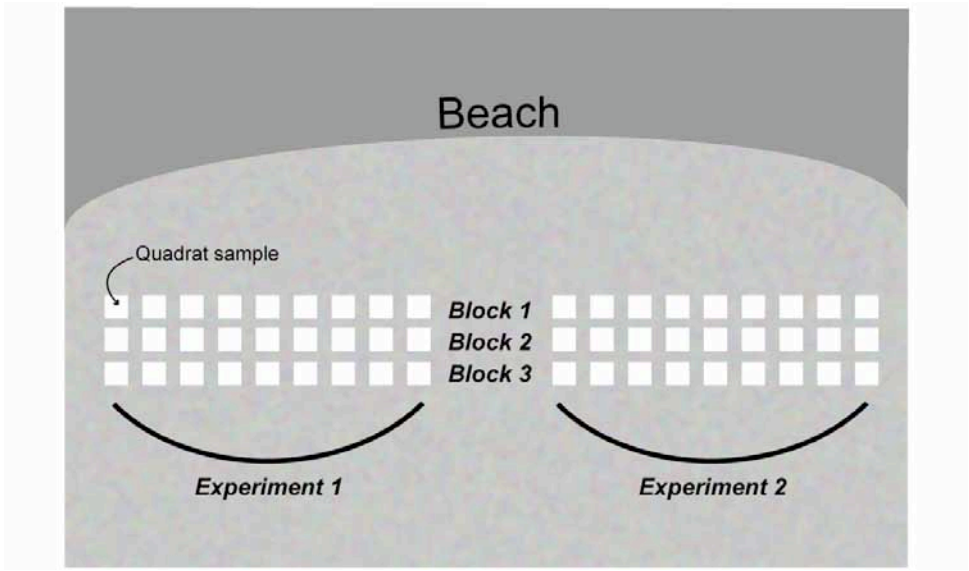


Figure 5.2 A schematic diagram of the experimental design for both nutrient enhancement experiments at each site, three replicate blocks, parallel to shore in a randomised block design (N.B. Not to scale).

Table 5.1 Summary of previously published nutrient enhancement experiments on seagrass beds globally.

Author(s)	Year	Nutrient added	Location	Seagrass species	Sediment type	Outcomes
Orth, RJ	1977	N & P	Chesapeake Bay, Virginia, USA	*Zostera marina*	Terrigenous	Increase in leaf length, biomass and total number of turions
Bulthius, DA & Woelkerling, WJ	1981	N & P	Western Port Bay, Victoria, Australia	*Heterozostera tasmanica*	Terrigenous	N increased level of nitrogen in rhizomes and leaves N increased leaf growth rate No significant increase in standing crop of leaves or in density in response to N & P additions
Harlin, MM & Thorne-Miller, B.	1981	N & P	Rhode Island coastal lagoon, USA	*Zostera marina*	Water column	N increased leaf, root and rhizome biomass and leaf length P increased leaf, root and rhizome biomass and leaf length
Roberts, MH, Orth, RJ & Moore, KA	1984	N & P	Lab study: seagrass transplants from York River Virginia, USA	*Zostera marina* seedlings	Terrigenous	Increased leaf length Increased vegetative production of shoots
Dennison, WC, Aller, RC & Alberte, RS	1987	N	Great Harbor Massachusetts, USA	*Zostera marina*	Terrigenous	No significant effect, possibly P limiting
Short, RT	1987	N	Mesocosm study: seagrass transplants from Great Bay, New Hampshire, USA	*Zostera marina*	Terrigenous	Increased biomass, shoot length, leaf area and tissue N
Williams, SL	1987	N & P	St Croix, Virgin Islands, USA	*Syringodium filiforme*	Carbonate	Increased shoot density and below ground biomass
Short, FT, Dennison, WC & Capone, DG	1990	P	San Salvador Island, Bahamas, USA	*Syringodium filiforme*	Carbonate	Increased growth, biomass and tissue P Increased rhizosphere N fixation

Table 5.1 cont'd

Author(s)	Year	Nutrient added	Location	Seagrass species	Sediment Type	Outcomes
Kenworthy, WJ & Fonseca, MS	1992	N & P	Back Sound, North Carolina, USA	*Zostera marina*	Carbonate	N additions increase shoot production
Murray, L, Dennison, WC and Kemp, WM	1992	N & P	SE shore of Chesapeake Bay, USA	*Zostera marina*	Terrigenous	N addition increased tissue N in roots and rhizomes P addition increased tissue P in leaves, roots and rhizomes.
Erftemeijer, PLA, Stapel, J, Smekens, MJE & Drossaert, WME	1994	N & P	South Sulawesi, Indonesia	*Cymodocea rotunda*, *Cymodocea serrulata*, *Syringodium isoetifolium*, *Thalassia hemprichii*	Terrigenous Carbonate	Seagrass in terrigenous sediments did not respond to N & P additions N added to carbonate sediments resulted in increases in tissue C and tissue N
Perez, M, Duarte, CM, Romero, J, Sand-Jensen, K, & Alcoverro, T	1994	P	Alfracs Bay north-east Spain	*Cymodocea nodosa*	Terrigenous	Increased shoot length and increased tissue P in roots and rhizomes
van Lent, F, Verschehurre, JM & van Veghel, MLJ	1995	N	South-west, The Netherlands	*Zostera marina*	Terrigenous	Increased above ground biomass, growth rates and flowering.

Table 5.2 Timing of the fertilization experiments conducted at Bolger Bay and Picnic Bay, Magnetic Island, Queensland Australia, during May–August 1995 (Experiment 1) and August–November 1995 (Experiment 2).

	Experiment 1			Experiment 2		
	Seagrass senescing, May–August			Seagrass growing, August–November		
Location	**Start**	**Finish**	**Duration (days)**	**Start**	**Finish**	**Duration (days)**
Bolger Bay	12 May 95	6 Aug 95	86	7 Aug 95	4 Nov 95	89
Picnic Bay	14 May 95	10 Aug 95	88	8 Aug 95	2 Nov 95	86

Table 5.3 Experimental treatments for the nutrient enhancement experiment conducted at Bolger Bay and Picnic Bay, Magnetic Island, Queensland, Australia, during May–August 1995 (Experiment 1) and August–November 1995 (Experiment 2) showing fertilizer combinations, the presence or absence of lifting treatment, and the corresponding codes used in statistical analysis.

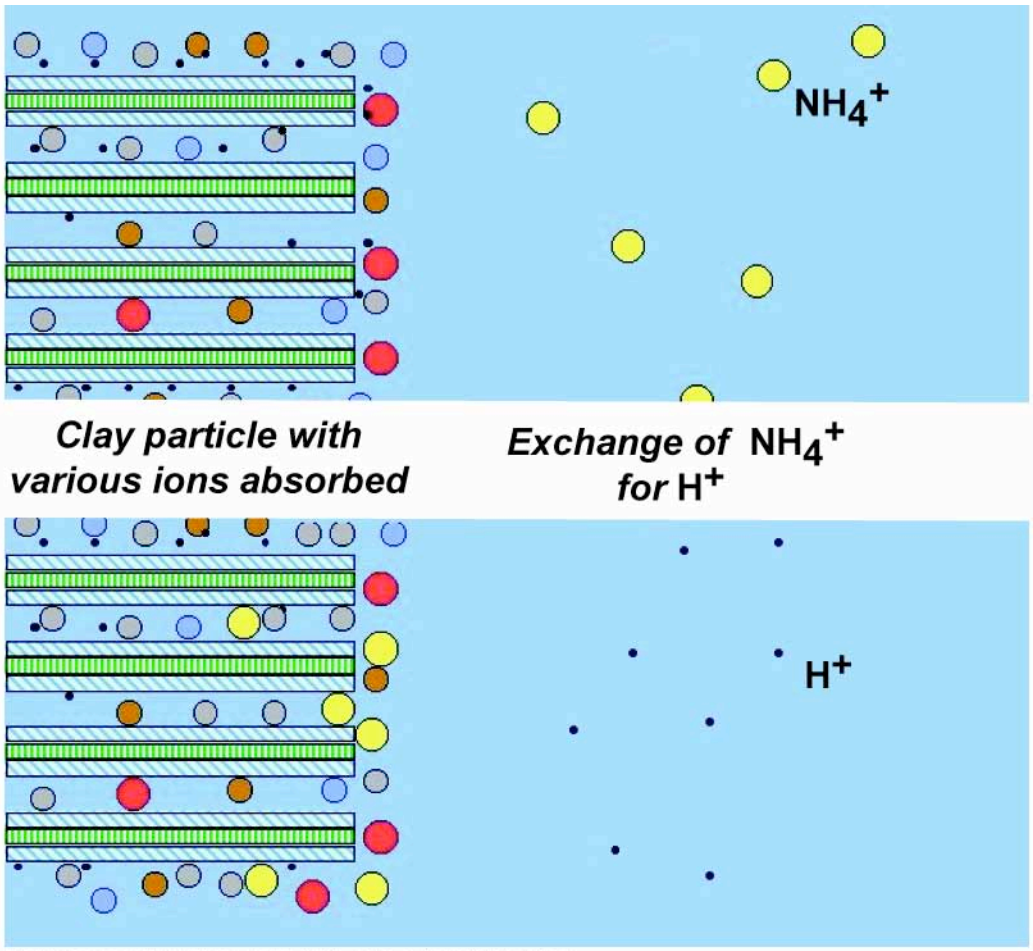
Treatment	**Treatment codes used in analysis***	**Manipulation**
Ambient (field control)	N_AP_N	No Lifting
Nil Addition (experimental control)	N_NP_N	Lifting
Low nitrogen	N_LP_N	Lifting
High nitrogen	N_HP_N	Lifting
Low phosphorus	N_NP_L	Lifting
High phosphorus	N_NP	Lifting
Low nitrogen, low phosphorus	N_LP_L	Lifting
Low nitrogen, high phosphorus	N_LP_H	Lifting
High nitrogen, low phosphorus	N_HP_L	Lifting
high nitrogen, high phosphorus	N_HP_H	Lifting

* A = Ambient, N = Nil Addition, L = Low loading, H = High Loading

Table 5.4 Fertilizer loads used in the experiment conducted at Bolger Bay and Picnic Bay, Magnetic Island, Queensland Australia, during May–August 1995 (Experiment 1) and August–November 1995 (Experiment 2), and the equivalent loading m^{-2} and ha^{-1} for each fertilizer.

Fertilizer	**High N (N_H)**	**Low N (N_L)**	**High P (P_H)**	**Low P (P_L)**
N or P only Osmocote (g)	150	50	66	22
Actual mass of N or P added to $0.25m^2$ (g)	34.5	11.5	11.88	3.96
Concentration of N or P added (g m^{-2})	138	46	47.52	15.84
Equivalent loading (t ha^{-1})	1.38	0.46	0.48	0.16

Subchapter 5.1 Assessing the mineralogy of two intertidal seagrass meadows of *Halophila ovalis*



Cation exchange process for the absorption of ammonium into a clay mineral.

Summary

Twelve mineral types were identified by X-ray diffraction within the sediment profiles at Bolger and Picnic bays, on Magnetic Island near Townsville. These types were grouped into four mineral phases: granite derived phases, carbonate phases, clays and evaporites. Granite derived phases dominated at both locations, which is not surprising as the parent rock of Magnetic Island is granite based. After the granite derived phases, Bolger Bay's sediment profile was dominated by clay minerals, while Picnic Bay's sediment profile was dominated by carbonate derived phases. This difference in mineralogy between locations/bays was consistent for both experiments (between bay scale).

Differences within bay (i.e. between experiments/time) were also apparent at each location, though negligible compared to differences between locations. At Bolger Bay, clay minerals were more abundant during Experiment 1 (seagrass senescing, May–August), than during Experiment 2 (seagrass growing, August–November). At Picnic Bay, the proportions of clay minerals were less and the proportions of carbonate minerals higher during Experiment 1 than Experiment 2. This may be due to spatial heterogeneity within the bay as the experiments were conducted at slightly different sites, or due to changes in sediment profile through the resuspension of fine sediments by wind and tides.

No differences in mineralogical profile were detected at the quadrat/treatment scale. Consequently, I predict that the greatest influence that mineralogy will have on the behaviour of nutrients and the response of seagrass to these nutrients will be at the Bay/Location scale and not at smaller spatial scales (within bays or between quadrats).

5.1.1 Introduction

Sediments are usually the ultimate sink for the dispersion, accumulation, and modification of nutrients in marine systems, therefore, they form a crucial link for the cycling, transport and availability of nutrients (Eyre and McConchie 1993). Adsorption of ammonium and phosphate to sediment particles occurs in all seagrass beds, but the nature of this process is strongly dependent on sediment characteristics (Hemminga and Duarte 2000). Most seagrass species colonize benthic habitats that are characterized by fine-grained sediments i.e. sand (siliceous or carbonate) and mud (Odum 1971, McRoy and Helfferich 1977, Phillips and Meñez 1988, Erftemeijer and Koch 2001). The close packing of fine-grained sediments decreases exchange between the porewater and the overlaying water column. This may result in increased nutrient concentrations within the rhizosphere (Kenworthy *et al.* 1982, Koch 2001). At the other extreme, when seagrasses colonize coarser sandy sediments, the exchange of porewater with the overlying water column is higher than in finer sediments and nutrient availability in the sediment may be lower.

The bioavailability of nutrients to seagrass may also be limited by the adsorptive capacity of the sediment rather than the sediments particle grain size *per se.* Adsorption of NH_4^+ and PO_4^{3-} to sediment particles occurs in all seagrass beds, but the importance of this process is dependent on sediment characteristics such as mineralogy. Those seagrass studies that have classified sediments have typically categorized the mineralogical composition of the sediments either as carbonate or terrigenous (see Short 1987, Fourqurean *et al.* 1992, Udy and Dennison 1996, Udy and Dennison 1997a, Udy *et al.* 1999 and Table 5.1). Much has been written about the high affinity of phosphate ions for carbonate minerals resulting in low phosphate concentrations compared to ammonium in sediment porewaters (Short *et al.*1985, 1990, Fourqurean *et al.* 1992, Erftemeijer 1994). Clay rich sediments also show a high adsorptive potential for PO_4^{3-} (Folk 1974, Blake and Chivas 1994). Consequently, the consideration of sediment structure and composition in seagrass related studies has the potential to contribute to a better understanding of the factors that affect nutrient dynamics, sediment geochemistry and seagrass health (Erftemeijer and Koch 2001).

Subchapter 4.3 demonstrated that the ambient conditions at Bolger Bay and Picnic Bay were significantly different with respect to sediment nutrient status, plant biomass, number of shoots, % leaf N and gN and gP m^{-2} of seagrass. Eh and pH also differed between these locations, as did the percentages of organic content and carbonate content. I attributed these differences to the different sediment regimes at each location. Bolger Bay is extremely muddy with a high percentage of silt and clay grain sized particles. In contrast, the sediment profile of Picnic Bay is dominated by larger sediment particles with a higher percentage of calcium carbonate (see Subchapter 4.3, Fig. 4.10). Sediments with a higher proportion of silt and clay are known for their capacity to integrate nutrients into their mineral structure (Garrels and Christ 1965, Friedman 1978) and this may, in part, explain the higher levels of ambient sediment nutrients measured at Bolger Bay (Subchapter 4.3). Consequently the mineralogical composition of these locations and its variability within bay (between experiments) and at the quadrat level is of interest. This study will provide further insights into the influence of sediment regimes on nutrient processes that affect nutrient bioavailability to seagrasses, and how this will influence the mobility and bioavailability of the additional nutrients delivered by Osmocote® to the sediments at Bolger Bay and Picnic Bay.

5.1.2 Material and methods

Sediments were collected for mineral analysis using cut-off 50 mL syringes as sediment corers. One core per quadrat was collected for mineralogical analyses as in the experimental design explained in Subchapter 5.0.

Mineralogy

Samples were dried at 60°C for 24 hours to remove loose surface water and minimize any changes to the mineral phases present. The samples from Picnic Bay were then crushed with a mortar and pestle to a fine, smooth powder (i.e. approximately < 20 μm). The samples from Bolger Bay were washed and air-dried before analysis, as the clay fraction needed to be free of all salt crystals. Mineral phases in the sediment were identified with X-Ray Diffraction (XRD) using the following protocol.

The prepared samples were placed in aluminium pack mounts for analysis on a Rigaku 2155D5 X-ray diffractometer and processed at the Advanced Analytical Centre, James Cook University. Each XRD trace was interpreted by Michelle Jenkins and Dr Chris

Cuff (School of Earth Sciences, James Cook University) to determine the major mineral phases present. A computer program, Siroquant©, was used to calculate semi-quantitatively the relative weight percent of each mineral phase.

Statistical methods

The main statistical analysis was performed to investigate the differences between location and differences between experiments, within a location. Differences between locations at different times of the year and differences between experiments within location were analysed separately by MANOVA (SPSS 10). The independent variable was either location or experiment depending on the analysis. The dependent variables were each of the mineral phases (i.e. granite, clay, carbonate, evaporite) depending on the analysis. MANOVA was run for 'between Bay' (i.e. location, Table 5.6) and 'within Bay' (i.e. experiment, Table 5.8) comparisons. A series of ANOVAs was used to test for differences within quadrats for each dependent variable (i.e. granite, clay, carbonate, evaporite; Table 5.9).

5.1.3 Results

Between bay scale: mineralogical differences between location for each experiment

X-ray diffraction identified 12 minerals within the sediment profile at both of these locations. For ease of analysis, these minerals were grouped into four mineral phases: granite derived phases, carbonate phases, clays and evaporites (Table 5.5). All further analyses are based on these mineral phase groupings.

Mineral phases were significantly different between locations and across experiments (Table 5.6). Granite-derived minerals dominated the mineralogical profile of both locations. The proportion of granite was significantly greater at Picnic Bay for the first experiment but no statistical difference was detected between locations for Experiment 2 (Table 5.6, Fig. 5.3). Apart from granite, Bolger Bay consistently had a greater proportion of clay and evaporite within its mineralogical profile than the profile at Picnic Bay for both experiments (Table 5.6, Fig. 5.3).

Comparisons of the mineralogy and other sediment parameters (e.g. grain size, Chapter 4.3), between the two bays confirms that the sediment regime at Bolger Bay differed from the regime at Picnic Bay (Table 5.7).

Within bay scale: mineralogical differences between experiments within locations

Significant differences in mineralogical profiles were detected between sites where the experiments were conducted at each location (Table.5.8 respectively). At Bolger Bay, the granite and clay minerals were more abundant at the site selected for Experiment 1 (May–August) than they were at during Experiment 2 (August–November) (Table 5.8, Fig. 5.3). At Picnic Bay, clay minerals were in greater abundance within the profile at the site of Experiment 2, whilst the proportion of carbonate minerals was significantly lower than percentages found within the sediment profile at the site used for Experiment 1 (Table 5.8, Fig. 5.3).

Quadrat scale: mineralogical differences within experiments

Because of the significant differences of mineralogical profiles between locations (Between Bay Scale, Table 5.6) and also at the scale of 100 m within each location (Within Bay Scale, Table 5.8), I decided to evaluate the mineralogical profiles of each quadrat (Quadrat Scale) which equates to fertilizer treatments across blocks within each experiment at each location.

At this scale, the distribution of minerals was not significantly different between individual quadrats during either experiment at either location (Table 5.9). This means that the behaviour of individual fertilizer treatments should not have been unduly influenced by the mineralogical profile of the particular quadrat to which they were applied. Comparison of the F ratio for the blocking term with that of the Treatment/Quadrat F ratio revealed that the data were variable across blocks within experimental sites at each location (Table 5.9). This means there were changes in the mineralogical profiles possibly in accordance with the tidal exposure or intensity of bioturbation, however, once the differences in block are accounted for, mineralogical differences between quadrats/treatments were not significant.

5.1.4 Discussion

Granite comprised the largest proportion of minerals at both sites. This result was expected as Magnetic Island is a granite outcrop and consequent weathering of this mother rock ends up in the sediments of the surrounding bays. Once the granite proportion of the mineralogical profile had been accounted for, the results support what is visually obvious. Bolger Bay is a muddy site with a high proportion of silt and clay, whereas Picnic Bay is a reefal site with a small clay component and a larger carbonate proportion in its mineralogical profile. Differences with respect to clay and carbonate proportions between locations were constant across experiments (Between Bay Scale: Table 5.6). Slight differences were noted in mineralogical profile between experiments within location (Within Bay, Table 5.8), with no significant differences in mineralogical profile detected at the quadrat/treatment scale (Table 5.9).

Mineralogical differences between bays

The mineralogical differences between sites were sufficient for Bolger Bay to be designated as a terrigenous site and Picnic Bay a carbonate site. Whilst much has been written in the seagrass literature about the ability of carbonate minerals to affect the mobility of P, clay minerals also have the ability to adsorb P. By using different mechanisms of adsorption, clay minerals can render P unavailable for plant uptake. Clay also has the capacity to sequester anions within its matrix, thereby decreasing N availability. Consequently, both the clay fraction at Picnic Bay and the carbonate fraction at Bolger Bay, both of which form only minor components by volume of their sediments, potentially contribute to the immobility of N and P.

Mineralogical differences within bays

Differences in mineralogical profile were detected between the experiments conducted in each bay in different seasons. *Post priori*, it is impossible to determine whether these differences are attributable to a shift in mineralogical profiles caused by the timing of the experiments (e.g. resuspension or influx of new sediments caused by seasonal south-easterly winds) or whether this difference is a reflection of spatial heterogeneity. Experimental plots covered approximately 77 m^{-2} and were located approximately 100 m from each other. At this ‘within bay scale’, it is possible that the seasonal shift in wind direction made subtle changes to the individual bay’s hydrology causing the re-

suspension and redistribution of the mineral phases and grain sizes according to the finer scale topography within each bay.

Mineralogical differences between quadrats

As differences in mineralogical profile were apparent within-bays, it was pertinent to assess mineralogical profiles at a quadrat scale level. Small differences were observed between quadrats and block, which could be attributed to tidal depositional processes distributing mineral phases according to the micro-topography within each bay. However, the differences in mineralogical profile detected at this scale (tens of metres) were not significant. Therefore each fertilizer treatment could be assessed as a response to the fertilizer rather than as a co-varying response to differences in sediment types within each quadrat during each experiment at both locations.

Differences in sediment regimes

Mineralogical differences were examined at various scales. As no significant mineralogical differences were detected at the quadrat scale, the assumption that fertilizer treatments would not be affected by differences in mineralogy within a quadrat is robust and as such fertilizer treatments were replicated within each experiment. However, differences were reported in the mineralogical profiles between experiments within each location. A comparison of the F ratios associated with the 'within bay scale' with those of the 'between bay scale' (Tables 5.8 and 5.6 respectively) revealed that most of the mineralogical variation was at the Bay scale. I consider that the dramatic seasonal response of meristem activity (new growing shoots, see Chapter 4.3) would have a greater influence on cycling of nutrients than the subtle mineralogical differences associated with the timing of each experiment within each bay. Consequently, any differences in the response of sediment nutrients or *Halophila ovalis* to enrichment should occur at the level of location (Bay Scale i.e. a scale of 1000s of metres) for this study.

The scope of this study might have underestimated the relationship between individual minerals and nutrients at these scales, as I grouped together individual minerals under the broad categories of clay and carbonate (Table 5.5). The three clay minerals, kaolinite, smectite and illite, that made up the clay category are quite different in their cation/anion exchange capacity (Brady 1996), as are the aragonite and calcite minerals

which made up the carbonate category. As these minerals may vary greatly between locations, lumping the individual minerals into one category may well mask their influence on nutrient processes. The effect of individual minerals on the mobility of nutrients warrants further investigation in order to understand the cause and effect of the differences in nutrients observed at the scale of locations.

5.1.5 Conclusions

Differences in mineralogical profiles at the quadrat scale were non-significant and the differences at the 'within bay scale' were negligible compared to differences observed 'between bays'. Differences in mineralogical and grains size profiles were reflected in differences in the physico-chemical environment of the rhizosphere between Bolger Bay and Picnic Bay. A comparison of sedimentary regimes between the two locations showed that Bolger Bay had larger quantities of finer grain sizes; was dominated by clay minerals; recorded lower Eh, pH and percent carbonate matter; but had higher levels of percent vegetative matter and sediment nutrients than Picnic Bay. How these differences in sediment regime at the bay scale affect nutrient enhancement processes will be examined in the next Subchapter.

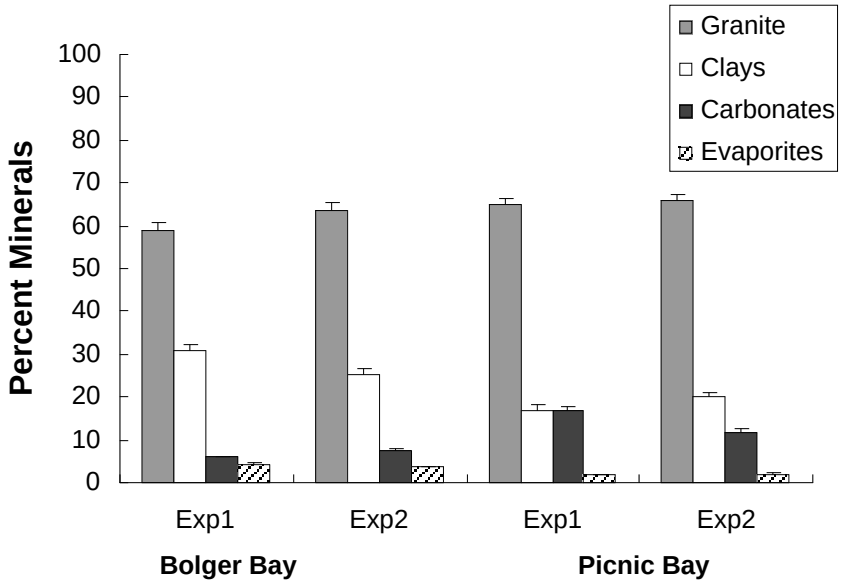


Figure 5.3 Differences in the four categories of mineral phase (mean ± se) between Bolger Bay and Picnic Bay, Magnetic Island, Queensland, Australia, during Experiment 1 (May–August 1995) and Experiment 2 (August–November 1995).

Table 5.5 List of mineral phases identified by X-ray diffraction for the minerals detected at Bolger Bay and Picnic Bay, Magnetic Island, Queensland Australia, during May–August 1995 (Experiment 1) and August–November 1995 (Experiment 2).

Granite-derived	Carbonate	Clays	Evaporites
Quartz	Calcite	Kaolinite	Halite
Low Albite	High Mg Calcite	Smectite	Gypsum
Max microcline	Aragonite	Illite	
Hornblende			

Table 5.6 Outcomes of statistical analysis for mineralogical differences detected at the 'between bay scale' (Bolger Bay and Picnic Bay, Magnetic Island, Queensland, Australia) during Experiment 1 (Seagrass senescing, May–August 1995) and Experiment 2 (seagrass growing, August–November 1995).

Analysis	Mineral Phase	$F_{(d.f)}$	*P*	Outcome
Experiment 1 (seagrass senescing, May–August)				
MANOVA	All	$30.293_{(4,55)}$	<0.001	
'Between subject tests'	Granite	$6.104_{((1,58)}$	0.016	> Picnic Bay
	Clay	$50.425_{(1,58)}$	<0.001	> Bolger Bay
	Carbonate	$80.156_{(1,58)}$	<0.001	> Picnic Bay
	Evaporite	$23.160_{(1,58)}$	<0.001	> Bolger Bay
Experiment 2 (seagrass growing, August–November)				
MANOVA	All	$15.482_{(4,55)}$	<0.001	
'Between subject tests'	Granite	$1.040_{(1,58)}$	0.312	n.s.
	Clay	$7.817_{(1,58)}$	0.007	> Bolger Bay
	Carbonate	$40.753_{(1,58)}$	<0.001	> Picnic Bay
	Evaporite	$10.200_{(1,58)}$	0.002	> Bolger Bay

Table 5.7 Summary of previously analysed physical and chemical parameters that constitute the sediment regimes of Bolger Bay and Picnic Bolger Bay, Magnetic Island, Queensland, Australia.

Comparison of parameters that make up the sedimentary regime[1]	Bolger Bay	Picnic Bay
Rhizosphere depth	2.5 cm	2.5 cm
Dominant grain size (see Fig. 6.2)	Fine clay[2]	Medium silt
Dominant mineral	Clay[2] minerals	Carbonate minerals
Eh	43.38 mV	127.4 mV
pH	7.44	8.52
Percent carbonate	12.66%	20.67%
Percent organic matter	1.82%	0.97%
Porewater–PO_4^{3-}	2.13 ± 0.22 μmol L^{-1}	1.046 ± 0.07 μmol L^{-1}
NH_4^+	63.13± 4.56 μmol L^{-1}	24.49 ±2.81 μmol L^{-1}
Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	396.87 ±24 μmol kg^{-1}	121.32 ± 11.05 μmol kg^{-1}
Adsorbed $PO_4^{3-}{}_{(Bray)}$	545.34 ± 41.65 μmol kg^{-1}	110.97 ± 8.03 μmol kg^{-1}
Adsorbed NH_4^+	259.80 ± 22.95 μmol kg^{-1}	182.17 ± 15.50 μmol kg^{-1}

[1] all measurement cited from a sampling trip in May 1994

[2] There are two geological definitions of clay: a) term used in grain size analysis, based simply on size, i.e. anything smaller than 4 μm; b) based on composition defined as hydrous aluminium silicates (kaolin, montmorillonite illite) and fine grained muscovite and even the hydrous aluminium oxides e.g. bauxite and gibbsite (Folk 1974).

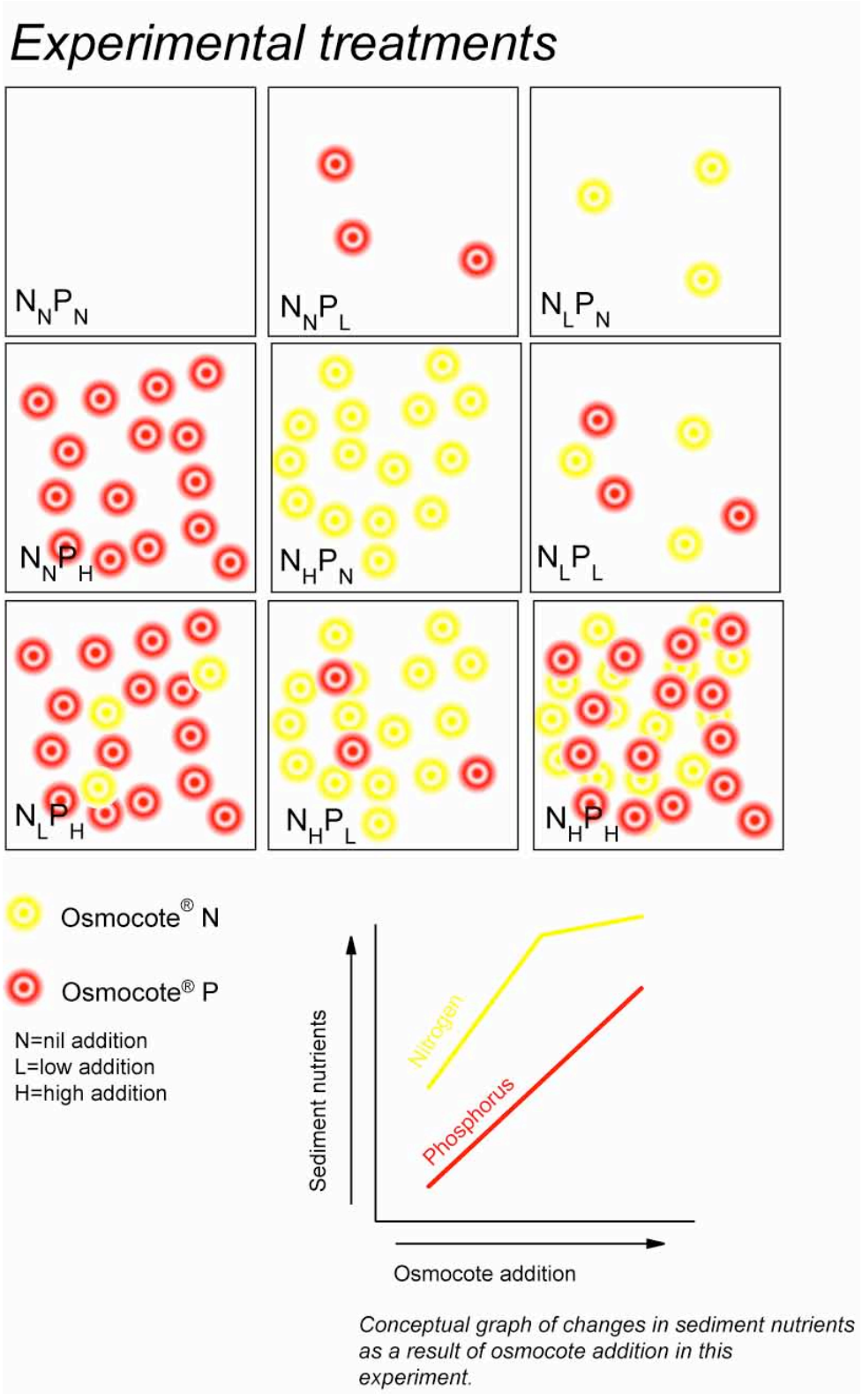
Table 5.8 Outcomes of statistical analyses for mineralogical differences detected between experiments ('within bay scale') at Bolger Bay and Picnic Bay, Magnetic Island, Queensland Australia, during May–August 1995 (Experiment 1) and August–November 1995 (Experiment 2).

Analysis	Variables	$F_{(d.f)}$	*p*	Outcome
Bolger Bay				
MANOVA	All	$5.98_{(4,53)}$	<0.001	
'Between subject tests'	Granite	$4.08_{(1,56)}$	0.048	> Experiment 1
	Clays	$7.87(_{1,56)}$	0.007	> Experiment 1
	Carbonate	$5.63_{(1,56)}$	0.0021	> Experiment 2
	Evaporite	$0.31_{(1,56)}$	0.577	n.s.
Picnic Bay				
MANOVA	All	$5.60_{(4,53)}$	<0.001	
'Between subject tests'	Granite	$0.34_{(1,56)}$	0.561	
	Clay	$3.15_{(1,56)}$	0.081	> Experiment 2
	Carbonate	$13.34_{(1,56)}$	<0.081	> Experiment 1
	Evaporite	$1.14_{(1,56)}$	0.289	

Table 5.9 Outcomes of statistical analyses for each mineralogical phase within Quadrats/Treatment between Experiment 1 (seagrass senescing, May–August 1995) and Experiment 2 (seagrass growing, August–November 1995) at Bolger Bay and Picnic Bay, Magnetic Island, Queensland Australia, respectively.

Analysis	Variables	Block $F_{(d.f)}$	Treatment $F_{(d.f)}$	*p*
Bolger Bay—Experiment 1 (seagrass senescing, May–August)				
ANOVA	Granite	$2.57_{(1,18)}$	$0.89_{(9,18)}$	0.551
	Clay	$1.76_{(2,18)}$	$1.06_{(9,18)}$	0.436
	Carbonate	$1.36_{(2,18)}$	$1.43_{(9,18)}$	0.248
	Evaporite	$3.55_{(2,18)}$	$1.40_{(9,18)}$	0.261
Bolger Bay—Experiment 2 (seagrass growing, August–November)				
ANOVA	Granite	$0.20_{(2,18)}$	$1.473_{(9,18)}$	0.231
	Clay	$0.28_{(2,18)}$	$1.21_{(9,18)}$	0.348
	Carbonate	$0.30_{(2,18)}$	$1.98_{(9,18)}$	0.105
	Evaporite	$0.28_{(2,18)}$	$1.03_{(9,18)}$	0.451
Picnic Bay—Experiment 1 (seagrass senescing, May–August)				
ANOVA	Granite	$0.14_{(2,18)}$	$0.37_{(9,18)}$	0.934
	Clay	$1.00_{(2,18)}$	$0.33_{(9,18)}$	0.952
	Carbonate	$2.77_{(2,18)}$	$0.21_{9,18)}$	0.989
	Evaporite	$1.80_{(2,18)}$	$0.78_{(9,18)}$	0.639
Picnic Bay—Experiment 2 (seagrass growing, August–November				
ANOVA	Granite	$1.16_{(2,18)}$	$1.23_{(9,18)}$	0.339
	Clay	$0.75_{(2,18)}$	$1.19_{(9,18)}$	0.358
	Carbonate	$1.06_{(2,\ 18)}$	$0.72_{(9,18)}$	0.687
	Evaporite	$0.32_{(2,18)}$	$0.33_{(2,18)}$	0.954

Subchapter 5.2 Evaluating the response of sediment nutrients to Osmocote® additions



Conceptual graph of changes in sediment nutrients as a result of osmocote addition in this experiment.

Summary

The response of sediment nutrients within the different sedimentary regimes (between locations) to the different levels and combinations of Osmocote® fertilizer was investigated at different times of the year. Throughout this yearlong study, Bolger Bay remained a higher nutrient site than Picnic Bay even with maximum nutrient additions. Using different application rates of Osmocote® N only, Osmocote® P only, and combinations of Osmocote® N only + Osmocote® P only, I raised sediment nutrient levels during both experiments (Experiment 1 seagrass senescing May–August, and Experiment 2 seagrass growing August–November) at both locations (Bolger Bay and Picnic Bay, Magnetic Island). A qualitative comparison of the response of the porewater nutrients to fertilizer inputs indicated that the response was similar at both locations, despite the differences in sedimentary regime.

Additions of Osmocote® N raised porewater N above ambient levels but not in concert with the incremental increase in Fertilizer N, at both locations and at both times of the year. Responses of adsorbed NH_4^+ reflected those of porewater N. Levels were raised with the addition of Osmocote® N, but not incrementally for both locations (between bay scale) and at both times of the year/experiments (within bay scale).

In contrast, additions of P fertilizer raised porewater PO_4^{3-} incrementally in proportion to the incremental increase in Osmocote® P. The response of adsorbed PO_4^{3-} was dependent on location, time of year and extraction method. At Bolger Bay, $PO_4^{3-}{}_{(Bray)}$ levels were significantly raised above ambient levels, incrementally during Experiment 1 and non-incrementally during Experiment 2. There was no significant response from $PO_4^{3-}{}_{(Bray)}$ at Picnic Bay for either experiment. This was attributed to the inability of the Bray method to extract PO_4^{3-} under alkaline/carbonate conditions.

Levels of $PO_4^{3-}{}_{(bicarbonate)}$ were significantly raised by the combination addition of Osmocote® N and P at Bolger Bay during Experiment 1. No significant response of $PO_4^{3-}{}_{(bicarbonate)}$ was detected during Experiment 2 at Bolger Bay. At Picnic Bay, levels of $PO_4^{3-}{}_{(bicarbonate)}$ were significantly raised by the addition of P fertilizer, incrementally during Experiment 1 but not incrementally during Experiment 2. A number of possible reasons for this result are discussed.

5.2.1 Introduction

The major nutrient elements required for plant growth are carbon, nitrogen and phosphorus. Carbon in the form of bicarbonate is abundant in seawater and is used quite readily as the inorganic carbon source by a variety of seagrass genera including *Halophila* (Hemminga and Duarte 2000). Inorganic nutrient nitrogen (N) in the form of ammonium and nitrate and inorganic phosphorus (P) in the form of phosphate are compounds found in both the water column and sediments. As concentrations of these nutrients in sediments are usually greater than those in seawater, it is generally accepted that seagrasses derive most of their nutrition from the sediments (McRoy and McMillan 1977, Iizumi and Hattori 1982, Thursby and Harlin 1982, Brix and Lyngby 1985, Short 1987, Fourqurean *et al.* 1992, Kenworthy and Fonseca 1992, Eftemeijer and Middelburg 1993).

Sediment nutrients available for seagrass uptake can be either adsorbed to sediment particles or dissolved in the porewater (Rosenfeld 1979a). The levels found in the adsorbed pool or the porewater pool are dependent on a concentration gradient between these two pools, which can be influenced by biological (plant uptake, bioturbation and bacterial activity), physical (sediment grain size) and chemical factors (sediment mineralogy, redox and pH). Hence, differences in species–specific uptake of nutrients, and sediment characteristics that differ between locations and within seasons are a source of variability for nutrient levels within seagrass meadows (Hemminga and Duarte 2000).

The aim of this component of the overall enhancement study was to establish whether:

i) the addition of varying levels and combinations of Osmocote® N and P enhanced the nutrient content at the different Locations/Bays;

ii) this enhancement was affected by the different types of sedimentary regimes experienced at the different Locations/Bays; and if

iii) the time of year when the experiments were conducted had an effect on the sediment enhancement process.

Addition of Osmocote® to the sediment rhizosphere of two *Halophila ovalis* meadows, successfully raised nutrient levels of N and P above ambient levels. The success of this part of the experiment provides an essential base for the interpretation of the response of *Halophila ovalis* to nutrient enrichment (Subchapter 5.3).

5.2.2 Material and methods

Methodologies relevant to this chapter only, such as the number of samples collected for each component of the sediment nutrient pool are described below. General methodologies such as the extraction and analysis of inorganic nutrients are described in Chapter 2–*General materials and methods.*

Sampling sediment nutrients

Porewater—dissolved inorganic nutrients

The 2.5 cm sippers were used in this experiment as dictated by the depth of the rhizosphere at Picnic Bay and Bolger Bay. Two replicate samples were taken from haphazardly selected positions within each 0.25 m^2 quadrat. As I was primarily interested in the variation between treatments rather than variation within quadrats, the two replicates were averaged and the resultant averaged concentrations used in the subsequent statistical analyses (see section below—statistical analysis).

Sediment–extractable inorganic nutrients

Because of the cost of chemical analyses, one sediment core was taken per quadrat and treated as a depth integrated sample of the rhizosphere. Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$, $PO_4^{3-}{}_{(Bray)}$ and NH_4^+ were extracted from this depth integrated core.

Physico chemical environment of the sediments

For mineralogy refer to Subchapter 5.1. Methodologies for grain size analysis, Eh, pH percent organic and carbonate content as outlined in Chapter 2. Specific results of these parameters for Bolger Bay and Picnic Bay are presented in Subchapter 4.3.

Statistical methods

The small amount of mineralogical variability between quadrats/treatments, suggests that the broad categories of mineral phases, (granite, clay, carbonate and evaporite) that

I assigned to groups of minerals should not affect the levels of nutrients within the sediments at this fine scale (Subchapter 5.1). To confirm this, ANOVAs in GenStat were used to test for the effect of sediment minerals on fertilizer treatments at the fine scale level of quadrat. This trial series of ANOVAs used the mineral phases as covariates with all 10 fertilizer treatments as the dependent variables for each experiment at each location (full statistical tables in Appendix C). The mineral phase covariates were not significant supporting the assumption that at this fine scale, mineral phase had no effect on levels of sediment nutrients. This result also validated the hypothesis that the major influence on the response of the sediments to enhanced nutrients was Location, the surrogate used in analyses for the large differences in the mineralogical profile observed within each meadow. Thus, my subsequent analyses of individual experiments did not include mineral phase as a co-variate.

Statistical analyses conducted to test the affect of fertilizer on sediment nutrients followed the general model outlined in Subchapter 5.0. To recap, the ANOVA model used in GenStat was (Lifting/(N*P)) within Block. The term 'Lifting' was a comparison of quadrats that were not lifted (N_AP_A: field control) and quadrats that were lifted and had no fertilizer added (N_NP_N: experimental control) and those that did have fertilizer added (fertilizer treatments) (Chapter 5.0. Table 5.3). As the computer generated Least Significant Differences (LSDs) were calculated based on an orthogonal design, the LSDs had to be recalculated for significant second order interactions (Lifting*N or Lifting*P) because of the unequal replication for the term Lifting. (i.e. only three quadrats per experiment were not lifted compared to 27 quadrats lifted and the various fertilizer treatments added). Summarized statistical tables are presented in this subchapter, full statistical tables can be found in Appendix C.

5.2.3 Results

The response of sediment nutrients to enhanced nutrients

Addition of fertilizer successfully raised the sediment nutrient pool above ambient levels at both sites and during both experiments. Responses of the relevant nutrient pool to the different loadings of N and P fertilizer were variable. In some instances, the levels of nutrients increased significantly with the incremental loadings of fertilizer. In other

instances the levels of nutrients were not significantly different between the different loadings of fertilizer but were significantly different from the controls (ambient and nil additions) (Table 5.10, Fig. 5.4, Fig. 5.5).

N additions

Porewater and adsorbed NH_4^+, $NO_2^- + NO_3^-$

Addition of N fertilizer significantly increased NH_4^+ and $NO_2^- + NO_3^-$ levels in the absorbed and porewater nutrient pools at both locations during both Experiment 1 (Senescent Season: May–August) and Experiment 2 (Growing Season: August–October). Whilst the addition of N fertilizer raised the different forms of N (NH_4^+ and $NO_2^- + NO_3^-$) within the nutrient pool, these nutrients were not raised incrementally (Table 5.10, Fig. 5.4). In three instances only, the high loading of N managed to significantly raise the levels of NH_4^+ and $NO_2^- + NO_3$ above control levels (ambient and nil addition) (Bolger Bay—Experiment 2: adsorbed NH_4^+ ; Picnic Bay—Experiment 1: adsorbed NH_4^+ and Picnic Bay—Experiment 2: porewater $NO_2^- + NO_3^-$, Table 5.10).

P additions

Porewater P

Addition of P fertilizer increased levels of PO_4^{3-} in the porewater at both locations and during both experiments. Levels of PO_4^{3-} were raised incrementally with increased loadings of P Fertilizer (Table 5.10).

Adsorbed P

$PO_4^{3-}{}_{(Bray)}$

Levels of $PO_4^{3-}{}_{(Bray)}$ increased significantly but not incrementally at Bolger Bay with the addition of P fertilizer during both experiments (Table 5.10, Fig. 5.5b). The addition of P fertilizer at Picnic Bay did not produce a significant result for $PO_4^{3-}{}_{(Bray)}$ for either experiment (Table 5.10, Fig. 5.4b).

The bicarbonate extraction method gave slightly different results than the results obtained using the Bray extractions technique. Adsorbed PO_4^{3-}(bicarbonate) was significantly raised at Picnic Bay during both experiments, incrementally during Experiment 1 (Fig. 5.5c), but not incrementally during the latter half of the year (Experiment 2, Fig. 5.5c, Table 5.10). At Bolger Bay, levels of PO_4^{3-}(bicarbonate) during Experiment 1, increased significantly in response to combined additions of N and P fertilizer. The highest response occurred in quadrats that had dosages of N_LP_H and N_HP_H. Other statistically significant responses recorded during Experiment 1 at Bolger Bay included the non-incremental increase in PO_4^{3-}(bicarbonate) to the loading of N fertilizer and an incremental increase in PO_4^{3-}(bicarbonate) with increased loadings of P fertilizer. No significant response was detected for PO_4^{3-}(bicarbonate) during Experiment 2 at Bolger Bay, however, PO_4^{3-}(bicarbonate) tended to be higher in quadrats that had high loadings of P fertilizer added to them (Fig. 5.5c). While these results are mixed, I consider that applications of P fertilizer generally raised the level of PO_4^{3-} in both the porewater and adsorbed nutrient pool as the ANOVA term Lifting*P explained most of the variance within the data sets.

5.2.4 Discussion

In general, the addition of fertilizer successfully raised the levels of nutrients above ambient and nil additions, relevant to the nutrient fertilizer added. Applications of Osmocote® N raised sediment N levels above ambient but not incrementally between the different loadings of Osmocote® at both locations and at both times of the year. In contrast, applications of Osmocote® P raised porewater P incrementally but adsorbed P responses varied according to location, time of year, and extraction method used. It is possible that the differences in response observed between the two nutrients, N and P, are due to differences in the mobility of N and P in marine sediments. Nitrogen movement tends to be largely vertical i.e. moving up or down the profile depending on the direction of water movement (Brady 1996). Phosphorous compounds tend to move very little except in sandy soils and some organic soils (Brady 1996). Other factors that affect the concentration and fate of dissolved inorganic forms of N and P in marine environments are the level of microbial activity, diffusion to the overlying water column, uptake by seagrasses and other organisms, bioturbation and the physical and

chemical conditions of the sediment that affect precipitation and adsorption, e.g. redox state, temperature, oxygen content, ion exchange capacity and sediment depth (Kamp-Nielsen and Anderson 1975, Kaspar 1983, Barko *et al.* 1991, Erftemeijer *et al*. 1994). Any one of these factors or a combination of them may have acted on the processes of nutrient adsorption and desorption at these two locations.

Nitrogen

Additions of N fertilizer raised NH_4^+ and $NO_2^- + NO_3^-$ levels in the pore water and NH_4^+ in the absorbed nutrient pool, but did not raise levels to be significantly different between the low and high loadings of N fertilizer at both locations and during both seasons (Table 5.10). Of these two nitrogen species, NH_4^+ is the preferred source of N for plant nutrition (see Barko *et al*. 1991, Touchette and Burkholder 2000). Ammonium tends to be very mobile and can accumulate both in porewater and on sediment particles (Rosenfeld 1979a, Short 1983). Once NH_4^+ becomes attached to the surface of sediment particles via a cation exchange reaction, it can remain on the surface as exchangeable NH_4^+ (Kamp-Nielsen and Anderson 1975, Blackburn and Henrikson 1983, Erftemeijer and Middelburg 1993). It is this exchangeable NH_4^+ fraction that acts as a nitrogen reservoir for plant nutrition because it can diffuse across a concentration gradient into the porewater, where it is available for rapid uptake by plants (De Laune *et al.* 1980). If the NH_4^+ does not diffuse into the porewater it can be absorbed into the interlayers of the minerals present in the sediment profile. Here it becomes fixed and is not readily replaced by other ions (Rosenfeld 1979b). This may explain why the porewaters and sediment pools of N did not reflect the high loadings of Osmocote® N at either location or experiment. That is, once the NH_4^+ ions become fixed within the mineral's lattice they can no longer be desorbed and diffuse into the porewater explaining the non-incremental increases in NH_4^+ at Bolger Bay and Picnic Bay for both experiments. The non-incremental increases observed in the adsorbed NH_4^+ pool might also be explained by the fixation of the NH_4^+ ions within the mineral lattice at such a level that there was not enough K^+ in the KCl extractant to exchange place with, thereby recording similar levels of adsorbed NH_4^+ between quadrats dosed with different levels of Osmocote® N.

Another factor that has the capability to control the availability of nutrients is the redox potential or oxidation state of the sediments. Any extension of the oxidized zone to deeper layers by the action of benthic organisms may serve to decrease nutrient

availability to seagrass roots. An increase in the oxidized zone allows for a larger population of ammonium-oxidizing bacteria to exist, which in turn can lead to increased rates of ammonium oxidation to nitrite and nitrate (nitrification, Jenkins and Kemp 1984). Nitrate can then diffuse back in to nearby anaerobic zones where it can be reduced to nitrogen gas (denitrification), resulting in loss of nitrogen from the sediment. This process may have contributed to the loss of N at Bolger Bay. The low redox potentials recorded at this location indicated anaerobic sediments, consequently any bioturbation would promote NH_4^+ to be transformed into nitrate, which in turn, could be reduced to nitrogen gas and thereby lost from the system. At Picnic Bay, the redox potential indicated aerobic sediments. The transformation of NH_4^+ to nitrate would also have occurred at this location (Jenkins and Kemp 1984). Rather than be transformed into N gas, it is more likely the nitrate would have diffused into the water column and be lost from the sediments in this manner as the concentration gradient for nitrate would be in the direction of the water column. Consequently by these two different processes, both involving the redox potential of the sediments, it can be seen how excess N in the sediment nutrient pool (as delivered by high loadings of Osmocote® N) may not appear in the system and therefore not record levels significantly higher than levels recorded with quadrats dosed by low loadings of Osmocote® N.

It is also possible that during this experiment, the available surface adsorption sites for minerals became satiated at low loadings of N fertilizer, i.e. the diffusion rate between the adsorbed and porewater fractions were in equilibrium. The excess N as delivered by the high loadings of N fertilizer would then have been used in the processes of nitrification and denitrification by bacteria present in marine sediments (Grundmanis and Murray 1977, Seitzinger 1988). The process of denitrification results in the removal of nitrogen from sediment-water systems leading to an overall loss of nitrogen (Kamp-Nielsen and Andersen 1975, Koike and Hatori 1978, Caffrey and Kemp 1990). Alternatively, the excess N may have diffused directly into the water column during high tides and have been transported away from the sites when the tide receded. Ullman and Sandstrom (1987) found that the re-suspension of 1 cm of sediment could cause a four-fold increase in total nitrogen in the water column of a bay within the Great Barrier Reef Lagoon. Another explanation for the lack of significant differences in porewater N between the high and low loading of N fertilizer, is that the plants in quadrats dosed with high N assimilated more of the available N as evidenced by plant tissue %N

displaying an incremental increase with increasing levels of N fertilizer (result presented in Subchapter 5.3). Whatever the reason for the lack of incremental increase in sediment N with increasing loads of N fertilizer observed in this experiment, the kinetically complex and dynamic nature of N speciation in marine environments means that the N released by Osmocote® progresses through a variety of chemical transformations reducing the stability of the released N species.

Phosphorus

The response of sediment phosphorus to applications of P fertilizer was far more variable than that of sediment nitrogen to N fertilizer (Table 5.10). Results for porewater PO_4^{3-} were consistent across location and experiments. Levels of porewater PO_4^{3-} were raised significantly and incrementally, in synchronization with the different levels of P fertilizer. In contrast, results for adsorbed PO_4^{3-} were found to vary with location, time of year (experiment), and extraction method.

These differences are emphasised in locational difference between the adsorbed phosphate concentrations at Bolger Bay and Picnic Bay. At Bolger Bay during Experiment 1, levels of adsorbed $PO_4^{3-}{}_{(Bray)}$ increased significantly with the addition of P fertilizer but not incrementally, despite the differences in loadings of P fertilizer (Table 5.10). Levels of PO_4^{3-} at this location, as measured by the bicarbonate technique, $PO_4^{3-}{}_{(bicarbonate)}$, recorded significant increases with the addition of N and high loadings of P fertilizer during Experiment 1, but recorded no significant increase in $PO_4^{3-}{}_{(bicarbonate)}$ during Experiment 2 (latter part of the year), however quadrats dosed with high levels of P fertilizer recorded the highest levels of $PO_4^{3-}{}_{(bicarbonate)}$ (Table 5.10). In contrast at Picnic Bay (both experiments), no significant result was recorded for $PO_4^{3-}{}_{(Bray),}$ The non-significance of $PO_4^{3-}{}_{(Bray)}$ results at Picnic Bay (for both experiments) reflects the inability of the Bray method to efficiently extract PO_4^{3-} under alkaline conditions (Pailles and Moody 1995) that occur at this site as a result of the higher percentage of carbonate present in the sediments. Levels of $PO_4^{3-}{}_{(bicarbonate)}$ at Picnic Bay increased significantly with the application of P fertilizer (Table 5.10). These levels increased incrementally with increased loadings of P fertilizer during Experiment 1, but showed no significant difference between loadings during Experiment 2. The difference in the response to fertilizer loadings between $PO_4^{3-}{}_{(Bray)}$ and $PO_4^{3-}{}_{(bicarbonate)}$ within the same quadrat, highlights the need to select an appropriate

extraction technique relevant to the type of sediment being analysed. Regardless of how available the phosphorus is in the fertilizer, it may be rendered unavailable to the seagrass depending on the type of sediment it interacts with on release.

Phosphorus in the marine environment

Several studies have proposed that a phosphate buffering system in marine sediments (Froelich 1985, Sundby *et al.* 1992) influences the way in which sediments control the PO_4^{3-} concentrations in the overlying water at some equilibrium level between the sediment porewaters and the water column. This buffering activity has been suggested as the mechanism that keeps the bioavailability of PO_4^{3-} in the water column low (Froelich 1985, Portielje and Lijklema 1993). To maintain this buffer, processes of PO_4^{3-} adsorption and desorption in the sediments must occur. Consequently marine sediments can act either as a source or a sink of PO_4^{3-}, depending on water column PO_4^{3-} levels being higher (sediment sink) or lower (sediment source) than the equilibrium PO_4^{3-} concentration in the sediment porewater. In turn, the equilibrium PO_4^{3-} level in the porewaters is controlled by the adsorptive capacity of the mineral compounds in the sediments.

A general adsorption process for PO_4^{3-} onto sediments has been proposed that includes two steps: 1) the quick adsorption of the PO_4^{3-} onto a variably charged surface of a sediment particle, and 2) the slow diffusion of PO_4^{3-} along a gradient towards the interior of the sediment particle (Edzwald *et al*. 1976, Froelich 1985). The rates of adsorption, diffusion and fixing vary with the mineralogy of the receiving sediment. Three main groups of amorphous and crystalline compounds have been identified in the adsorption processes of phosphate. They are clay minerals: calcium compounds particularly calcium carbonate and iron and aluminium oxy/hydroxides (Krom and Berner 1980, Froelich 1985, Sundby *et al*. 1992, Moutin *et al.* 1993)

The oxyhydroxides involved in the processes of PO_4^{3-} adsorption are the hydrous oxides of iron and aluminium. They are the dominant sorbents in natural systems with a tendency to be finely dispersed and therefore easily resuspended (Dzomebak and Morel 1990). As such, they constitute the particulate matter in the water column and in the porewater. The mechanism by which PO_4^{3-} attaches to the oxyhydroxides is by surface complexation whereby the PO_4^{3-} causes displacement of the hydroxyl ions (Parfitt *et al*.

1975). After this initial complexation and coating of a sediment grain, the phosphate ion undergoes the two-step adsorption process described above (Edzwald *et al.* 1976, Froelich 1985) into the receiving mineral whether it is clay or carbonate. The displacement of hydroxyl ions in the porewater increases the tenure of the phosphate ions in the porewater. This phenomenon may account for the incremental increases in porewater PO_4^{3-} that were recorded at both locations and at both times of the year in concert with increasing loading of Osmocote® P.

Nutrient processes in clay sediments–Bolger Bay

Clay minerals have a layered structure and are classified according to the combinations of these layers (MacKinnon and Cuff 1992). The adsorptive reaction of PO_4^{3-} onto all clays involves the exchange between PO_4^{3-} in the porewater and the metal ions on the clay surface (Edzwald *et al*. 1976). The specific adsorptive area of the different clays controls their specific adsorptive capacity (i.e. the number and stacking of layers and varying degrees of crystallinity that affect their surface area (MacKinnon and Cuff 1992)). Consequently some clays have greater adsorptive powers than others due to their degree of electrostatic attraction or their cation exchange capacity (CEC) (Reichelt 1993). Smectite and illite clays (small particle size, large surface area, higher CEC) will have a higher capacity for the adsorption of P than kaolinite. Overall, Bolger Bay sediments had higher clay content than Picnic Bay (Chapter 5.1), therefore I predict that this mechanism for binding PO_4^{3-} predominated in Bolger Bay. The influence of the constituent clays that made up the category of clay in this study requires further investigation.

Nutrient processes in carbonate sediments—Picnic Bay

In carbonate sediments, phosphate can either adsorb onto calcium carbonate or co-precipitate with calcium carbonate (Bostrom *et al*. 1988). Both of these mechanisms produce calcium phosphate. The adsorption of PO_4^{3-} onto carbonate minerals occurs via an exposed surface with a positive charge. Water molecules, bicarbonate ions or hydroxyl ions often occupy these sites, however, they have a weaker charge and are readily exchanged for PO_4^{3-}. Once PO_4^{3-} has adsorbed onto the carbonate particles, precipitation of phosphate minerals such as apatite on their surface can occur (Gaudette and Lyons 1980). As with clay, the different carbonate minerals have different affinities for PO_4^{3-} as the capacity of carbonates to adsorb phosphate is directly related to the

reactive surface area, which in turn depends on the grain size of the sediment (Erftemeijer and Middelburg 1993). Sediments with smaller grain sizes will have greater surface areas and greater adsorptive capacities. The sediment summary for Picnic Bay showed that carbonates predominated over clays and that the mean particle size was large. I predict that the adsorption of PO_4^{3-} onto Picnic Bay sediments is governed by processes that apply to carbonate sediments but restricted by the large particle size that limits the adsorption capacity of PO_4^{3-} onto carbonate minerals. Consequently the lack of adsorption of Osmocote® PO_4^{3-} onto sediment particles may have contributed to the observed incremental increases in porewater PO_4^{3-} levels, as the Osmocote® released directly into the porewater and then was not adsorbed incrementally onto the sediments.

Geochemical processes

The differences in the response of $PO_4^{3-}{}_{(bicarbonate)}$ levels between experiments observed at Picnic Bay and Bolger Bay respectively, may have been caused by the slight change to the mineralogical profile that was observed with the 'within bay scale' shift in experimental sites during Experiment 2 (Picnic Bay more clay present, Bolger Bay lower percentage of clay but carbonate content increases, Subchapter 5.1). This change in response of $PO_4^{3-}{}_{(bicarbonate)}$ could also be associated with a seasonal change in the reactivity of calcium carbonate. Moutin *et al*. (1993) found that during the summer months i.e. the times of the year with higher temperatures, more phosphate was released from iron compounds allowing an increase in the formation of calcium phosphate; redox and pH conditions permitting. In winter, the reverse occurs because the Fe ions resume phosphate adsorption. If the redox potential is high, the reduction of the iron component in the sediments may not occur limiting the release of PO_4^{3-} (Krom and Berner 1980, Sundby *et al*. 1992) and if pH is high then adsorption of PO_4^{3-} onto sediments will not occur (Edzwald *et al*. 1976, Stirling and Wormald 1977).

The combination of clay and carbonate sediments at Picnic Bay and the slight differences in their proportions between experiments/sites (within bay scale) may explain the incremental levels of $PO_4^{3-}{}_{(bicarbonate)}$ during Experiment 2 as the carbonate and clay fractions in the quadrats rated with high P held on to their bound PO_4^{3-}. Conversely, the non-incremental levels of $PO_4^{3-}{}_{(bicarbonate)}$ at Picnic Bay (Experiment 2) and the non-significance of $PO_4^{3-}{}_{(bicarbonate)}$ levels at Bolger Bay (Experiment 2) may be

accounted for by Fe^{3+} fraction within the clay proportion giving up its bound PO_4^{3-} to the porewater pool. When viewed in combination with the high pH recorded at Picnic Bay, adsorption onto carbonate particles from the porewater may have been inhibited, hence the non-incremental increase of $PO_4^{3-}{}_{(bicarbonate)}$ at the high ratings of P fertilizer.

Biological processes

Alternatively, the difference in response between experiments may be attributed to a seasonal increase in biological activity, which could be suggestive of a temporal response of nutrient adsorption, rather than a difference caused by a change in mineralogy caused by the shift in site (within bay spatial scale). The phosphate that diffuses from the Osmocote® granules into the porewater could be used directly from the porewater as a result of a higher demand for P by seagrass, micro-flora and bacteria during Experiment 2 (Seagrass growing: August–November), thereby preventing PO_4^{3-} in solution (porewater) from being adsorbed onto sediment particles and causing adsorbed PO_4^{3-} to desorb into the porewater to maintain the concentration gradient between the two pools in order to sustain the higher biological demand for PO_4^{3-} at this time of year. This phenomenon may account for the incremental increases in porewater PO_4^{3-} and the non-incremental and non-significant response of the adsorbed PO_4^{3-} observed at both locations for this time of year (Experiment 2).

5.2.5 Conclusions

Throughout this yearlong study, Bolger Bay remained a higher nutrient site than Picnic Bay, an observation that persisted even with maximum nutrient additions throughout the experiment. The qualitative response of the porewater nutrients at both locations was similar despite differences in sedimentary regime and the nutrient release processes that drive nutrient availability. Given that the Osmocote® nutrients diffuse directly into the porewater, I propose that the responses of the adsorbed nutrients were influenced by:

i. the differing mobility of these nutrients within the rhizosphere;

ii. the different processes of adsorption of nutrients (particularly for PO_4^{3-}) as dictated by different sedimentary regimes;

iii. the differing seasonal requirement by seagrass for each of the nutrients;

iv. the seasonally changing reactivity of particular minerals caused by seasonal changes in temperature; and

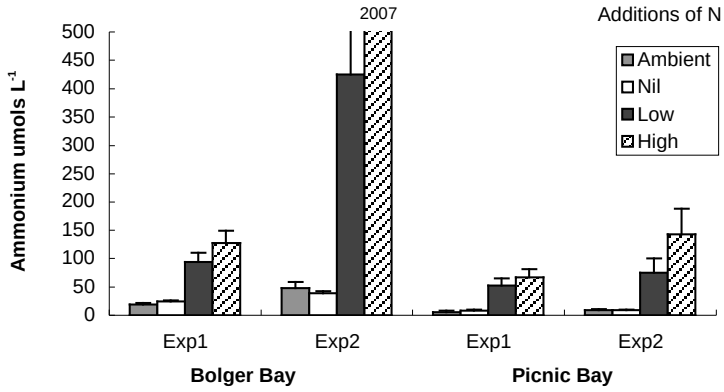
v. seasonally changing demands for nutrients by increased biological activity of plants and organisms other than seagrass.

These influencing factors suggest reasons why nitrogen levels were not incremental with increasing fertilizer application and why the phosphate responses varied according to time of year/experiment and location.

The methods used to measure the nutrient levels within the sediment pool may not necessarily represent the bioavailablity of that nutrient, particularly with adsorbed PO_4^{3-}. To be able to understand the responses displayed by the sediment nutrient pools to the addition of fertilizer within these seagrass meadows, there is a need to appreciate the actual nutrient levels available to the seagrasses. The presence of comparatively high concentrations of nutrients in the pore water does not mean that plant roots have unrestricted access to this reservoir as actual uptake rates can be limited by the slow diffusion rates of nutrients from the soil solution /porewater to the roots surface (Stapel *et al.* 1996). Competition between seagrasses and other flora (micro-, macro- and epiphytic algae) as well as bacteria within the seagrass community also limit the amount of nutrients available for seagrass uptake.

Despite these factors having the capacity to affect the levels of sediment nutrients, sediment nutrients were successfully raised above ambient levels in this study. Additions of N fertilizer tended to raise the nutrient pool (both adsorbed and porewater) above ambient but did not result in any incremental differences between the high and low loadings of N fertilizer. Addition of P fertilizer raised levels of porewater PO_4^{3-} incrementally above the controls. Results for adsorbed PO_4^{3-} were more variable depending on the extraction technique and the mineralogical profile at each location. In general, additions of P increased sediment levels of PO_4^{3-}. However, the actual amount of nutrient available for seagrasses may be substantially lower, hence evaluation of seagrass yield and physiological responses will be more indicative of the nutrient availability and limitation to seagrass plants themselves. This component of the experiment is examined in the next subchapter.

a).



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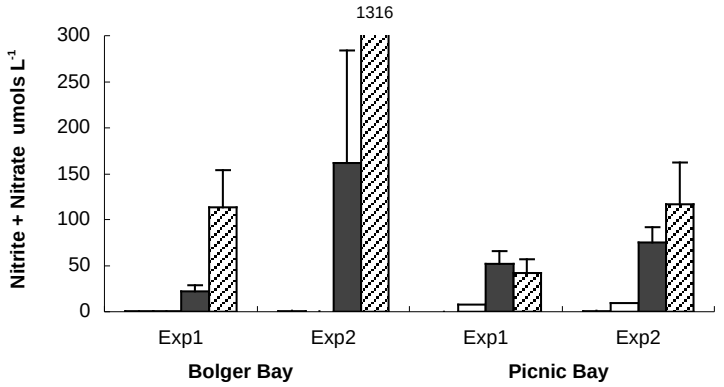


c).

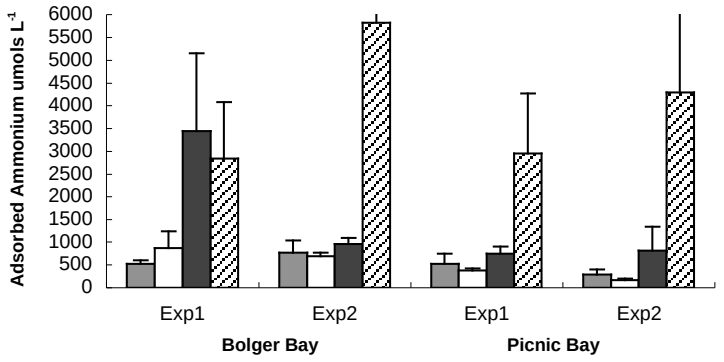
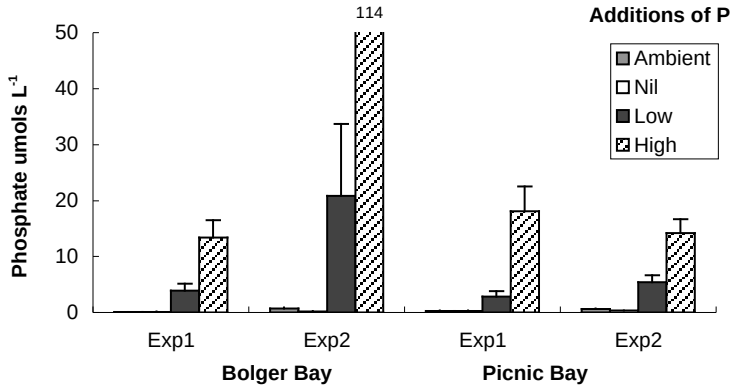
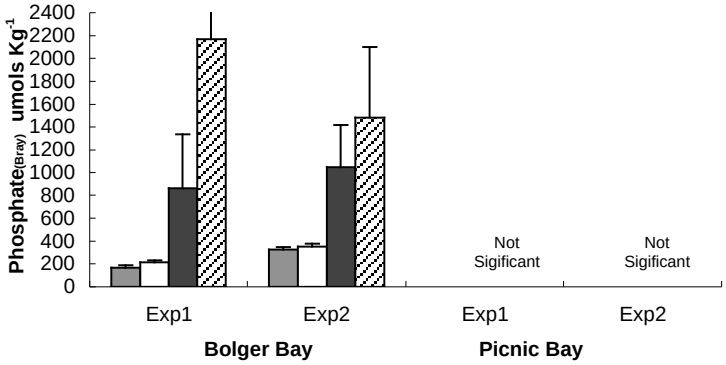


Figure 5.4 The effect of N fertilizer additions at Bolger Bay and Picnic Bay during Experiment 1 (seagrass senescing, May–August) and Experiment 2 (seagrass growing, August–September) for: **a)** porewater NH_4^+, **b)** porewater NO_2^- + NO_3^- and **c)** adsorbed NH_4^+ (KCl extracted). Note different scales on the Y axes. Means and standard errors are displayed. Where a number is displayed above a bar this represents the mean nutrient value of that bar which is beyond the scale of the y axis. Where no cross bar appears on top of the standard error line it means that the standard error was beyond the scale of the Y axis.

a).



b).



c).

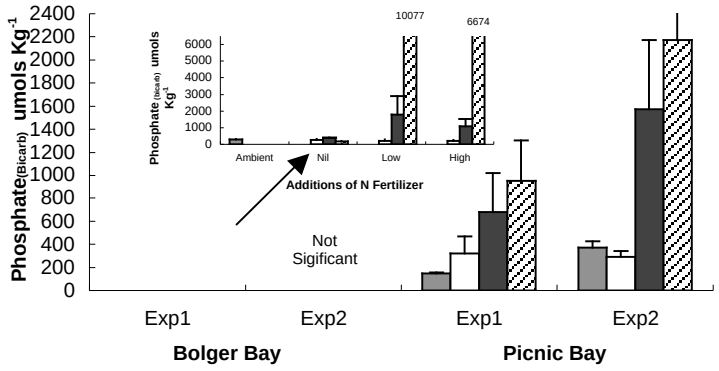


Figure 5.5 The effect of P fertilizer additions at Bolger Bay and Picnic Bay during Experiment 1 (seagrass senescing, May–August) and Experiment 2 (seagrass growing, August–September) for: **a)** Porewater PO_4^{3-}, **b)** adsorbed $PO_4^{3-}{}_{(Bray)}$ and **c)** adsorbed $PO_4^{3-}{}_{(bicarbonate)}$. Note different scales on the Y axis. Means and standard error are displayed. Where a number is displayed above a bar this represents the mean nutrient value of that bar which is beyond the scale of the y axis. Where no cross bar appears on top of the standard error line it means that the standard error was beyond the scale of the Y axis.

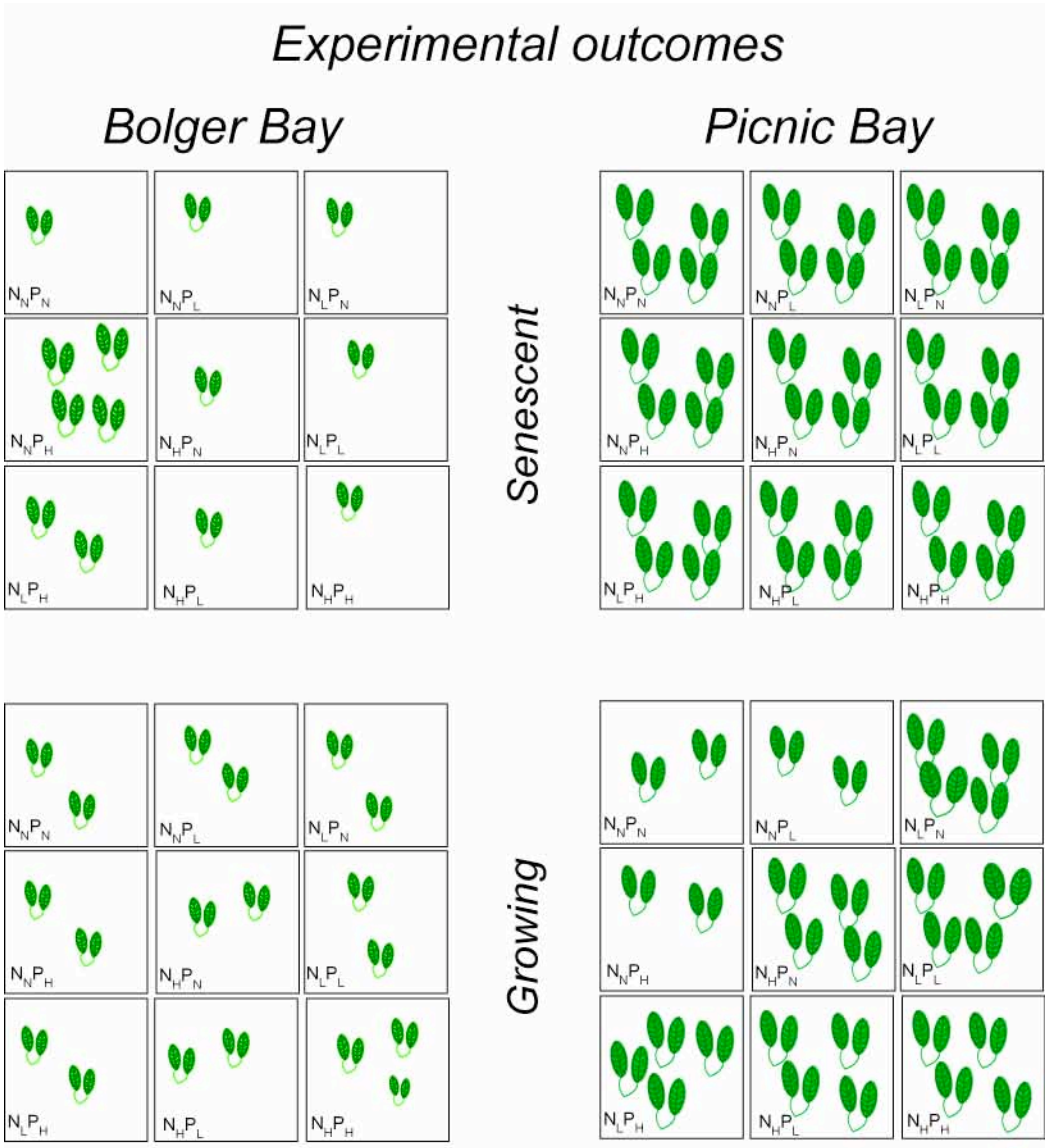
Table 5.10 Summaries of statistical analyses of sediment nutrients responses to applications of Osmocote® conducted at Bolger Bay for Experiment 1: (May–August 1995) and Experiment 2 (August–November 1995), and Picnic Bay, Experiment 1 (May–August 1995) and Experiment 2 (August–November 1995), Magnetic Island, Queensland, Australia, highlighting the statistically significant treatment term and the response of the parameter to that term.

Bolger Bay				
Parameter	**Significant term**	**Experiment 1 (seagrass senescing, May–August) *post priori* outcomes**	**Significant term**	**Experiment 2 (seagrass growing, August–November) *post priori* outcomes**
N additions				
Porewater NH_4^+	Lifting*N	Additions of N fertilizer increased levels of NH_4^+ but not incrementally	Lifting*N	Same as Experiment 1
Porewater $NO_2^- + NO_3^-$	Lifting*N	Additions of N fertilizer increased levels of $NO_2^- + NO_3^-$ but not incrementally	Lifting*N	Additions of N fertilizer increased levels of $NO_2^- + NO_3^-$ and incrementally
Adsorbed NH_4^+	Lifting*N	Additions of N fertilizer increased levels of NH_4^+ but not incrementally	Lifting*N	Only additions of high N (N_H) fertilizer increased levels of NH_4^+
P additions				
Porewater PO_4^{3-}	Lifting*P	Additions of P fertilizer increased levels of PO_4^{3-} and incrementally	Lifting*P	Same as Experiment 1
Adsorbed $PO_4^{3-}{}_{(Bray)}$	Lifting*P	Additions of P fertilizer increased levels of $PO_4^{3-}{}_{(Bray)}$ and incrementally	Lifting*P	Additions of P fertilizer increased levels of $PO_4^{3-}{}_{(bicarbonate)}$ but not incrementally
Adsorbed $PO_4^{3-}{}_{(bicarbonate)}$	Lifting*N*P	$PO_4^{3-}{}_{(bicarbonate)}$ response to combinations of N+P was variable with N_LP_H and N_HP_H being significantly higher than N_AP_H	ns	
	Lifting*P Lifting*N	Addition of P fertilizer incrementally raised levels of $PO_4^{3-}{}_{(bicarbonate)}$ while additions of N fertilizer increased levels of $PO_4^{3-}{}_{(bicarbonate)}$ but not incrementally.		

Table 5.10 continued.

Picnic Bay				
Parameter	**Significant term**	**Experiment 1 (seagrass senescing, May–August) *post priori* outcomes**	**Significant term**	**Experiment 2 (seagrass growing, August–November) *post priori* outcomes**
N additions				
Porewater NH_4^+	Lifting*N	Additions of N fertilizer increased levels of NH_4^+ but not incrementally	Lifting*N	Same as Experiment 1
Porewater $NO_2^- + NO_3^-$	Lifting*N	Additions of N fertilizer increased levels of $NO_2^- + NO_3^-$ but not incrementally	Lifting*N	Only additions of high N (N_H) fertilizer increased levels of $NO_2^- + NO_3^-$
Adsorbed NH_4^+	Lifting*N	Only additions of high N (N_H) fertilizer increased levels of NH_4^+	Lifting*N	Additions of N fertilizer increased levels of NH_4^+ but not incrementally
P additions				
Porewater PO_4^{3-}	Lifting*P	Additions of P fertilizer increased levels of PO_4^{3-} and incrementally	Lifting*P	Same as Experiment 1
Adsorbed $PO_4^{3-}{}_{(Bray)}$	ns		ns	
Adsorbed $PO_4^{3-}{}_{(Bicar)}$	Lifting*P	Additions of P fertilizer increased levels of $PO_4^{3-}{}_{(bicarbonate)}$ and incrementally	Lifting*P	Additions of P fertilizer increased levels of $PO_4^{3-}{}_{(bicarbonate)}$ but not incrementally

Subchapter 5.3 Evaluating the response of *Halophila ovalis* to nutrient enrichment



Conceptual diagram depicting the differences in seasonal response of Halophila ovalis *to nutrient additions at Bolger Bay and Picnic Bay.*

Summary

In this component of the nutrient enhancement experiments, the overall plant biomass response to increased nutrients was limited. Whilst the outcomes were complex, seagrass at Bolger Bay, with high clay mineralogy within the sediment profile, displayed primary P limitation during the Experiment 1 (seagrass senescing season) and a trend for P limitation during Experiment 2 (seagrass growing season). The responses could not be fully assessed due to the lack of data from plant tissue (%N and %P) resulting from the extremely low biomass in the quadrats sampled at the completion of the experiments. In contrast, seagrass at Picnic Bay, characterized by carbonate mineralogy, showed no significant yield response during Experiment 1 (seagrass senescing season) although there was a trend for changes in biomass to be greatest in quadrats that had low N:P fertilizer ratios indicating a preference for increased P nutrients. During Experiment 2 (seagrass growing season), *Halophila ovalis* at Picnic Bay displayed primarily N limitation with secondary P limitation. The experimental effect of disturbing the rhizosphere during the application of the fertilizer, the type of sediment, grain size, and particularly the time of year, influenced the responses of the *Halophila ovalis* to nutrient enhancement.

5.3.1 Introduction

Light is generally considered to be the primary resource that limits the growth and distribution of most seagrass species (McRoy and McMillan 1977, Dennison and Alberte 1986, Phillips and Meñez 1988), with nutrients a secondary factor limiting growth. While light availability controls the maximum depth to which seagrasses occur (Abal and Dennison 1996) and biomass accumulation at depth (Dennison and Alberte 1986), nutrient availability can be a major limiting factor for growth and biomass accumulation of submersed plants at any depth. In temperate seagrass meadows, light is also involved in pronounced seasonal fluctuations in biomass (and productivity) (Hemminga and Duarte 2000). The results of analysing plant growth at the two proposed study sites (Subchapter 4.3), demonstrated seasonal differences in sediment and plant nutrients, biomass, shoot number and plant growth. This supports the notion that contrary to expectations, seasonality is an important feature of tropical seagrass habitats. Subchapter 4.3 also identified a link between increased growth and plant nutrient uptake with elevated porewater nutrients at the time of year when *Halophila ovalis* is actively growing (September). As declining marine and coastal water/sediment quality is of concern in the GBRWHA (Zann 1995, Williams 2001), it is pertinent to evaluate the response of coastal seagrass in this region to nutrient addition and whether this response can change according to location and time of year.

Several authors have examined nutrient limitation to seagrass growth around the world with different conclusions. On the basis of earlier work, Short (1987) postulated that seagrasses growing in northern temperate climates (and in habitats with terrigenous sediments) typically experience nitrogen-limitation; where as those in tropical environments (and growing on carbonate sediments) appear to experience phosphorus limitation. The explanation for this contrast was the absorption of phosphate on to the carbonate sediments, thus making it less available to the plants (Short 1987). However, Erftemeijer and Middelburg (1993) found a relatively high availability of phosphate in porewater from tropical coarse-grained carbonate rich sediments. They concluded that the particle size distribution of sediment plays a crucial role in the nutrient adsorption-desorption process. If a large proportion of the sediment has a high coarse grain size and therefore relatively low surface area to volume ratio, the nutrient adsorption capacity of the sediment will be low, while the porewater contains high nutrient concentrations. A

predominantly fine grain size will increase the sediment adsorptive capacity, so porewater concentrations are reduced compared with coarser sediments (de Kanel and Morse 1978, O'Neil and Capone 1989, Slomp *et al.* 1993). The adsorptive capacity of fine-grained sediment is influenced also by the mineralogical composition of the grains. Clay rich sediments show a higher adsorptive potential for nutrients than fine-grained, quartz and feldspar rich sediments (Blake and Chivas 1994). Consequently, particle grain size, and mineralogy, both play important roles in the bioavailability of nutrients to seagrasses. A nutrient is bio-available if it: a) is present or can be transferred readily to the free ion species, b) can move to plant roots on a time scale that is relevant to plant growth and development, and c) once adsorbed by the roots affects the life cycle of the plant (Mengel and Kirkby 1987).

The role of nutrients in controlling seagrass growth has been evaluated most successfully through *in situ* nutrient enhancement experiments (Orth 1977, Powell *et al.* 1989, Short *et al.* 1985, Erftemeijer *et al.* 1994, Udy and Dennison 1997a,b, Udy *et al.* 1999). The purpose of this study was to examine the response of *Halophila ovalis* (R.Br.) Hook. f., a structurally small seagrass of great importance in the central regions of the Great Barrier Reef World Heritage Area as a nursery area for commercial prawns (Coles *et al.* 1987, Lee Long *et al.* 1993) and a food source for dugongs and green turtles (Lanyon *et al.* 1989) to nutrient enhancement by:

i) assessing the influence of an enriched nutrient environment on plant production and physiological parameters; and

ii) determining whether these influences change with time of year or differences in sedimentary regime.

5.3.2 Material and methods

The number of seagrass samples collected and the parameterisation of samples are described below. General methodologies pertaining to the digest and consequent nutrient analysis of plant tissue nutrients were described in Chapter 2.

Sampling seagrass parameters

Every 50 x 50 cm (0.25 m^{-2}) quadrat was excavated at the completion of both experiments (Experiment 1: Bolger Bay 30 quadrats + Picnic Bay 30 quadrats:

Experiment 2: Bolger Bay 30 quadrats + Picnic Bay 30 quadrats). Seagrass from each quadrat was separated into leaves, rhizomes, and roots. Epiphytes were removed from seagrass samples by gently scraping the plant matter with forceps. Each component was dried and weighed then prepared for plant tissue digest and analyses as described in Chapter 2.

Statistical methods

Statistical analyses conducted to test the affect of fertilizer on seagrass parameters followed the general model outlined in Subchapter 5.0. To recap, the ANOVA model used in GenStat was (Lifting/(N*P)) within Block. The term 'Lifting' was a comparison of quadrats that were not lifted (N_AP_A: field control) and quadrats that were lifted and had no fertilizer added (N_NP_N: experimental control) and those that did have fertilizer added (fertilizer treatments) (Chapter 5.0, Table 5.3). As the computer generated Least Significant Differences (LSDs) were calculated based on an orthogonal design, the LSDs had to be recalculated for significant second order interactions (Lifting*N or Lifting*P) because of the unequal replication for the term Lifting. (i.e. only three quadrats per experiment were not lifted compared to 27 quadrats lifted and the various fertilizer treatments added). Summarized statistical tables are presented in this subchapter, full statistical tables are in Appendix C.

5.3.3 Results

Plant production parameters

Bolger Bay

Experiment 1: Seagrass senescing, May–August

The above ground biomass of seagrass meadow at Bolger Bay started to decline during the May–August period of this experiment. My visual observations suggested that this decline was more than the natural cycle of senescence that I had observed at this location in previous years. The seagrass meadow was not only patchy, but was also exceedingly sparse. The plant biomass within the experimental plots was so depauperate, that there was insufficient plant material to perform tissue nutrient analyses. The highest total biomass recorded from any quadrat was less than 1 g DW 0.25 m^{-2}. As a result, statistical analyses were conducted on seagrass biomass and

density for each fertilizer treatment but additional plant tissue nutrient analyses were not possible.

Aberrant data points that were recognized as statistical outliers (identified by box plots and residual as described in Chapter 2) influenced the ANOVA results. These points represent real data from a variable environment making it difficult to determine whether the response was due to fertilizer addition, or the patchy distribution of the seagrass. Nevertheless some observational trends were apparent and are reported here. However, the statistical results should be interpreted conservatively due to the patchiness of the bed and the extremely low seagrass biomass.

Of the statistical analyses carried out on this data set three of the five analyses recorded a significant outcome (Table 5.11). The biomass of leaves and roots was higher in quadrats with high loadings of P fertilizer than quadrats with low loadings of P, but were not significantly different from quadrats that had no fertilizer added or the field control. (Fig. 5.6 a, c respectively). Root biomass declined concomitant with increases in N fertilizer (Fig. 5.6c). Shoot density showed a varying response to the different combinations of N+P fertilizer. At ambient and low loadings of P fertilizer, shoot density appeared to increase slightly with increases in N fertilizer. At high loadings of P, however, shoot density decreased with increasing dosages of N fertilizer (Fig. 5.6d). Though not significant, total biomass tended to increase with increasing loads of P fertilizer (Table 5.11). In general, the N_NP_H treatment recorded the highest average biomass for all plant production parameters except for rhizome biomass which recorded the highest average biomass within quadrats dosed with N_HP_H.

Experiment 2: Seagrass growing: August–November

The seagrass at Bolger Bay started to recover, during this second experiment. Biomass was still extremely low and the distribution patchy, even though the average biomass at ambient conditions was 14 times greater during this experiment than during Experiment 1 at this site.

None of the plant production analyses produced a statistically significant result (Table 5.11). All plant production parameters showed their largest increase in biomass and shoot density in quadrats that had N_HP_H loadings, with the exception of root biomass,

which had its greatest mean response in quadrats that had been loaded with $N_N P_H$ (Table 5.11).

Overall, the data were extremely variable reflecting the patchy distribution of the seagrass. This is also indicated by the high variance ratio for the blocking term. The interaction terms of the model (i.e. Lifting*N*P; Lifting*N; Lifting*P) explained very little of the variance. P additions tended to produce a greater response, as there was an increase at every level of N with increasing P fertilizer. At low additions of P, biomass and shoot density appeared to decrease with increases in the loading of N. This trend suggests, that during the growing season, seagrass yield at this location responded to increases in the nutrient pool from both N and P additions. The greatest increases in yield were observed in quadrats where the N:P ratio is low, that is a greater P nutrient pool relative to N. However these biomass measurements were in general lower then 1 g DW 0.25 m^{-2}. Consequently it is difficult to ascertain whether this observation has any ecological significance, principally due to the decline in seagrass cover at this site before the start of the experiment.

Picnic Bay

Experiment 1: Seagrass senescing May–August

The seagrass bed at Picnic Bay was less patchy than that at Bolger Bay and the biomass at ambient conditions was 60 times greater. The data gathered from replicate treatment plots were variable. As justified above, I included the outliers in the analyses.

No plant production parameter responded significantly to any of the fertilizer treatments or combinations at Picnic Bay during Experiment 1: seagrass senescing, May–August (Table 5.11). However there was a trend for the largest seagrass response to be associated with an increase in N fertilizer when combined with high loadings of P. Mean biomass of shoots, rhizomes and total plant were highest in quadrats with $N_L P_H$ fertilizer loadings. Root biomass and shoot density were both highest in quadrats dosed with $N_H P_H$.

Experiment 2: Seagrass growing, August–November

Under ambient conditions, biomass measurements in the growing season were on average double those during the senescent season and eight times greater than ambient

biomass measurements for Bolger Bay during the growing season. Rhizome biomass and shoot density responded significantly to increases in N fertilizer (Table 5.11). The significant difference was between loadings of N compared to nil additions—the ambient quadrats were not statistically different from any of the treatments (Fig.5.6).

Of the other three plant production parameters, leaf biomass and total biomass analyses approached significance in relation to additions of N fertilizer ($p = 0.079$ and $p = 0.079$ respectively). All three parameters recorded their highest average response to additions of $N_{H.}$ suggesting that *Halophila ovalis* may be N limited during the growing season at Picnic Bay.

Plant tissue nutrients

Bolger Bay

Experiment 1 and Experiment 2

No analyses were done on this parameter for Bolger Bay due to insufficient plant biomass.

Picnic Bay

Experiment 1: Seagrass senescing, May–August

The parameters % leaf N, % rhizome N and % whole plant N were significantly raised in quadrats that had been enhanced with N fertilizer with respect to the controls (Table 5.12). Only % rhizome N showed significant differences between low and high loadings of N (Fig. 5.7). All plant tissue %P parameters responded positively to applications of P fertilizer, (Table 5.12, Fig. 5.8), increasing incrementally with increasing dosages of P fertilizer, with the exception of $gP_{seagrass}$ 0.25 m^{-2} which did not respond incrementally. Both % leaf P and % rhizome P declined with additions of N fertilizer (Fig. 5.8). Quadrats that had been lifted without N fertilizer being added (N_N), had higher %P in their leaves and rhizomes than those plants in quadrats with N_L and N_H added. Those quadrats that had not been manipulated, were not significantly different from those quadrats that had been manipulated and fertilizer added (Fig. 5.8).

Experiment 2: Seagrass growing, August–November

Tissue percent nitrogen (%N)

Additions of N fertilizer significantly increased % leaf N, % rhizome N and $gN_{seagrass}$ 0.25 m^{-2}, though no incremental difference was detected in %N of these parameters between the high and low loadings of N fertilizer (Table 5.12). Whilst % leaf N and $gN_{seagrass}$ 0.25 m^{-2} showed an experimental effect by being significantly different from nil additions but not ambient conditions, % rhizome N showed significant differences between enhanced quadrats and both ambient and nil addition treatments (Fig. 5.7). Both % root N and % whole plant N recorded a significant result for the term Lifting*N*P (i.e. the third interaction term involving combinations of N and P fertilizer (Fig. 5.7c and d respectively).

A single high recording of % root N in N_HP_L quadrats influenced the result of the significant third order interaction term (Fig. 5.7c). The % root N was unaffected by increased loadings of N fertilizer within quadrats that had nil and high loadings of P. At low loadings of N, high additions of P also had no affect on % root N, however at low loadings of P the addition of a high rating of N fertilizer ($N_HP_{L)}$ significantly increased % root N in comparison to quadrats that had had nil N additions (N_NP_L) and those quadrats with low loadings of N (N_LP_L), (Fig. 5.7c).

The Lifting*N*P term was significant for % whole plant N. This third order interaction was significant because of the variable response of % whole plant N to the incremental loadings of P fertilizer at nil additions of N fertilizer (Fig. 5.7d). At low and high loadings of N the addition of low loadings of P fertilizer elicited the greatest response i.e. when the sediment N:P ratio was moderate and the fertilizer N:P was at its greatest (Fig. 5.7). The second order interaction term Lifting*N was also significant (Table 5.12). The % whole plant N increased incrementally with increased loadings of N fertilizer at all levels of P fertilizer.

Tissue percent phosphorous (%P)

The %P in all five plant components increased significantly with the addition of P fertilizer (Table 5.12). An experimental effect was observed for % leaf P, % rhizome P and % whole plant P. These parameters showed an incremental increase in %P from

quadrats that had been manipulated but no P fertilizer added (N_NP_N, experimental control) but no significant difference in %P was observed between the low loadings of P and the plants at ambient conditions (N_AP_A, field control, (Fig. 5.8a,b and d respectively). These three parameters also displayed a significant decrease in %P to additions of N fertilizer (Table 5.12, Fig. 5.8a,b and d). The % plant tissue P at high, low and ambient loadings of N fertilizer were significantly lower than %P in the experimental controls (i.e. quadrats that had been lifted but not fertilized with Osmocote® N).

The plant parameter $gP_{seagrass}0.25\ m^{-2}$ displayed a similar response to P additions as did %P of leaf, root and whole plant (Fig. 5.8). This parameter also displayed an experimental effect by being significantly less only in the experimental control (manipulation no fertilizer). No significant difference in $gP_{seagrass}0.25\ m^{-2}$ was observed between the different loadings nor between quadrats at ambient conditions. Root %P and $gP_{seagrass}0.25\ m^{-2}$ were significantly affected only by the addition of P fertilizer (Table 5.8). The % root P in quadrats of high and low P loadings had significantly more %P in roots than the controls. Differences between % root P in quadrats of low and high loadings of P fertilizer were not detected.

5.3.4 Discussion

The response of *Halophila ovalis* to experimental nutrient enhancement varied according to location and season. At Bolger Bay, *Halophila ovalis* responded to inputs of P fertilizer during Experiment 1: Seagrass senescing (May–August). In contrast, the response of *Halophila ovalis* at Picnic Bay differed from that at Bolger Bay in that it responded physiologically to inputs of fertilizer during Experiment 1: Seagrass senescing, (May–August) while both plant abundance and plant tissue parameters responded to additions of N fertilizer during Experiment 2: Seagrass growing, (August–November) only. The response to nutrient enhancement at Picnic Bay suggests that the plant nutrient requirements associate with plant growth influence sediment nutrient dynamics. As the plants start to grow more rapidly in response to some seasonal cue there is a need for more nutrients, particularly nitrogen.

Experimental manipulation of the rhizosphere also played a significant role in the seagrass responses to nutrient enhancement. Enhanced nutrients and disturbance had an

effect on various growth and nutrient parameters of *Halophila ovalis* relative to the effects of the experimental disturbance *per se* (Tables 5.11 and 5.12, Figs 5.6, 5.7 and 5.8). The addition of fertilizer was more often significantly different to the 'nil addition' (manipulation–no-fertilizer) treatment than to the 'ambient' (no-manipulation–no-fertilizer) treatment.

My experiments were unable to measure the effect of enhancing sediment nutrients without disturbance because of the manipulation involved in introducing fertilizer to the rhizosphere. However, the responses of disturbance plus nutrients on the plants were usually not very different from ambient, suggesting that the effects of nutrient enhancement tended to counteract the effects of disturbance *per se*. Any effect of disturbance was relatively small, as the field control (ambient) and the experimental control (manipulation–no-fertilizer) were not significantly different from each other for many of the observed responses.

The results of this experiment suggest that the different sedimentary regimes, the different sedimentary nutrient status and the differing modes of growth (see Subchapter 4.3) that occurred at these meadows at Bolger Bay and Picnic Bay are the factors responsible for the varying response of *Halophila ovalis* to nutrient enhancement. During Experiment 1 (senescing: May–August), both locations showed evidence of increasing biomass when the sediment nutrient N:P ratio was small (Bolger Bay significantly, Picnic Bay a trend). Leaf biomass at Bolger Bay decreased with the addition of N fertilizer (N:P large) suggesting nitrogen toxicity may have been affecting *Halophila ovalis* at this site. At Picnic Bay, P limitation is supported by the decrease in % tissue P with increases in N fertilizer with no concomitant increase in biomass. This increase also suggests that another factor was limiting growth e.g. light (Hillman *et al.* 1995, Abal and Dennison 1996), water temperature (Bulthius 1987) or possibly another nutrient (Hemminga and Duarte 2000). Desiccation/exposure has also been suggested as a disturbance factor limiting seagrass growth and succession in this region (Bridges *et al.* 1982, Coles *et al.* 1989). Hence desiccation from over exposure and lack of light as a result of turbidity may be the drivers for limiting plant growth in these systems. During Experiment 2 (growing, August–November) there was significant seagrass response to nutrient input at Bolger Bay, presumably, because as the plants started to grow they were able to utilize the overabundance of N and therefore just show a trend for P limitation. In contrast at this time, the meadow of *Halophila ovalis* at Picnic Bay

showed evidence of primary N limitation with secondary limitation of P as evidenced by the increase in biomass and decrease in plant tissue %P with increasing levels of N fertilizer. As plant biomass increases there is an increase in demand for cellular P to be involved in the metabolic activities associated with the assimilation of N into cell production and other cellular growth activities (Touchette and Burkholder 2000).

Implications for interpreting other studies

I found that the significant differences were between disturbance + fertilizer additions and disturbance + nil addition rather than between disturbance + fertilizer additions and ambient. This result suggests that the physical act of raising the rhizosphere whilst not having a significant effect on the sediment nutrient profiles (Subchapter 5.2), had an effect on the seagrass plants within the manipulated quadrats.

The use of both an ambient (field) control and an experimental control (nil addition) is clearly essential to the interpretation of any form of rhizosphere manipulation. I believe that previous experiments (Bulthius and Woelkerling 1981, Udy and Dennison 1997a and b, Udy *et al*. 1999) have been deficient in not clearly addressing: (1) the relationship between ambient N and P within the sediment pool, (2) the complexity of the geochemical process occurring in the sediments, (3) the time of year of the experiment, and/or (4) the manipulation required to introduce the excess nutrients into the experimental plots.

For example, if I had followed the experimental approach of Udy and Dennison (1997a, b) and compared my treatments of fertilizer addition only to an experimental control at the same time of year their experiments were conducted, I would have concluded (as Udy and Dennison did), that the seagrass in this region is N limited. Alternatively, if like Bulthius and Woelkerling (1981), I had combined my controls because there was no significant difference between them I would have concluded (as Bulthius and Woelkerling did) that sediment nutrient enrichment had little direct effect on the standing crop and that seagrass in this area had sufficient nutrients for growth. The results of previous enhancement experiments clearly need to be interpreted very cautiously.

Implications for future work

As pointed out by Duarte (1999), most of the available information about seagrass nutritional physiology in Australia has been obtained from studies of only a few species and a few locations, notably Western Port Bay: Bulthius and Woelkerling (1981), Moreton Bay: Udy and Dennison (1997a, b), Rottnest Island: Udy and Dennison (1999) and Green Island: Udy *et al*. (1999). The basic nutritional characteristics of many seagrass species remains to be determined and compared across geographic regions. Recent gains in the general understanding of the seasonal physiological response of seagrass species to nutrient gradients should strengthen the scientific basis of management efforts to protect seagrass meadows. However, my work demonstrates a need to go beyond the single factor study, we need assessments of the interactions between nutrients and light, and nutrients and water temperature. To be able to achieve an understanding of such complex interactions without the complication of factors that cannot be controlled, I suggest that such interactive experiments be preformed in a mesocosm environment, where light, temperature and nutrients can be controlled. This approach will enhance the interpretation of subsequent field experiments.

5.3.5 Conclusions

- This study evaluated the response of structurally a small seagrass, *Halophila ovalis,* a species that is common along the Queensland coastline, to various levels of nutrient enhancement under dissimilar sedimentary regimes during different seasons.

- The response of *Halophila ovalis* in two bays on the same island to inputs of N and P nutrients differed according to the different sedimentary regime and nutrient state within each meadow (i.e. location).

  - The meadow at Bolger Bay showed statistically significant evidence of P limitation during Experiment 1 (senescing, May–August) and towards P limitation during Experiment 2 (growing, August–November).

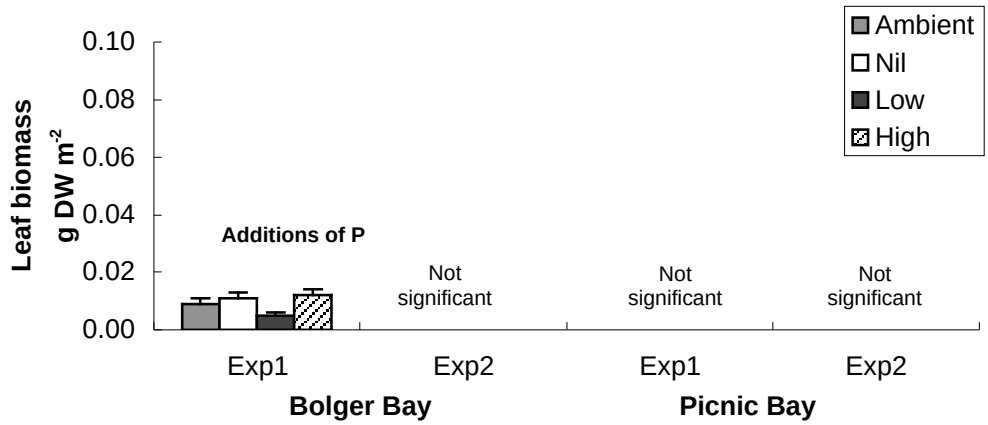
  - The general decline of seagrass in Bolger Bay from mid-1993 may have been caused by an imbalance of the sediment N:P ratio in favour of N (high levels of NH_4^+ and $NO_2^- + NO_3^-$) hence inputs of P redressed this situation.

- Whilst a trend of P limitation (physiologically) was evident at Picnic Bay during Experiment 1 (senescing, May–August), some other parameter may have limited growth at this time, as plant yield showed no sign of significant limitation, in spite of an increase in biomass within quadrats that had a small sediment N:P ratio.
- During Experiment 2 (growing, August–November) the seagrass at Picnic Bay responded positively by increasing in abundance to additions of N at the cost of P tissue content suggesting primary N limitation, with secondary P limitation.

- Because factors other than nutrients can limit seagrass growth, inferring nutrient limitation from growth and tissue content is difficult under field conditions.
- Consequently, experiments to test nutrient limitation may be conducted in mesocosms. Once the specific plant responses have been investigated, field experiments, with rigorous experimental approaches that incorporate experimental controls that test the effect of nutrient introduction, differences in the time of year, geochemistry of the sediments and nutrient history of the meadow should be conducted.
- The design of many field based nutrient enhancement experiments is inadequate and their results must be interpreted with caution due to the lack of appropriate controls.

See over for figures…

a).



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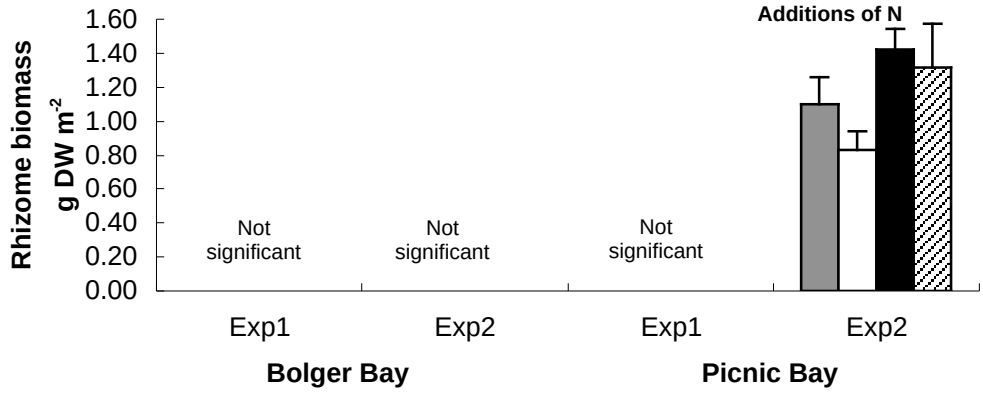

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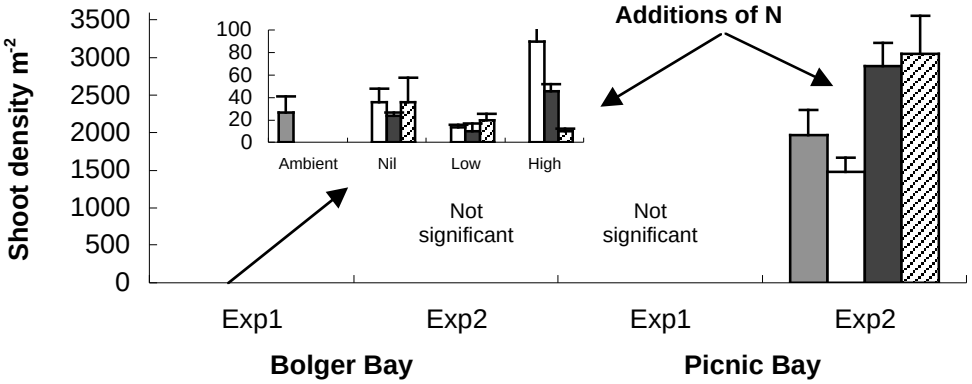
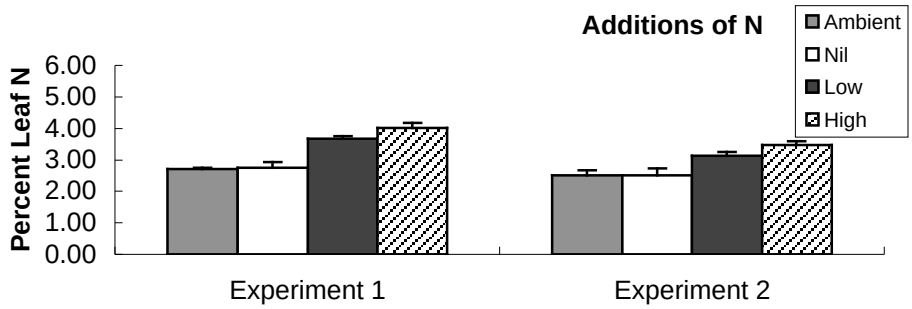


Figure 5.6 Significant plant production responses to additions of Osmocote® at Bolger Bay and Picnic Bay for during Experiment 1 and Experiment 2 for **a)** leaf biomass, **b)** rhizome biomass, **c)** root biomass and **d)** shoot density. Note different scales on the Y axis. Where no cross bar appears on top of the standard error line it means that the standard error was beyond the scale of the Y axis.

a).



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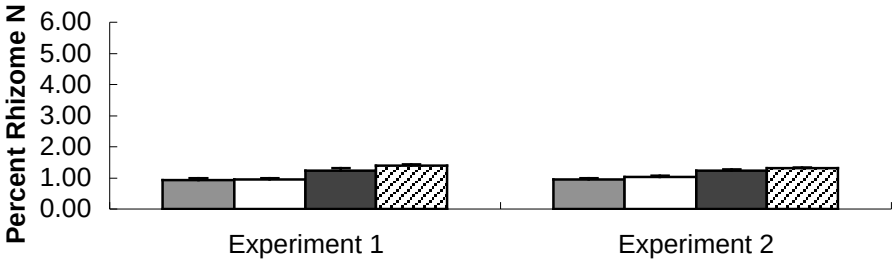

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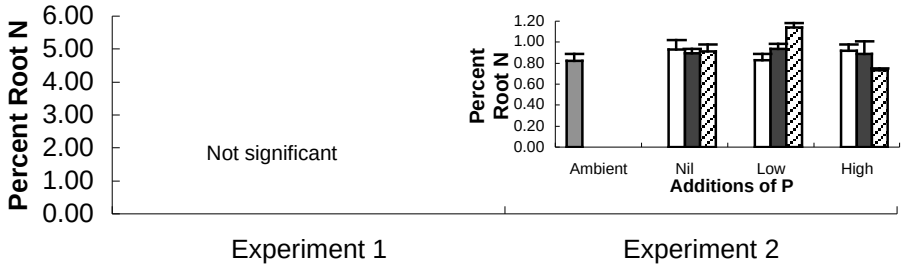

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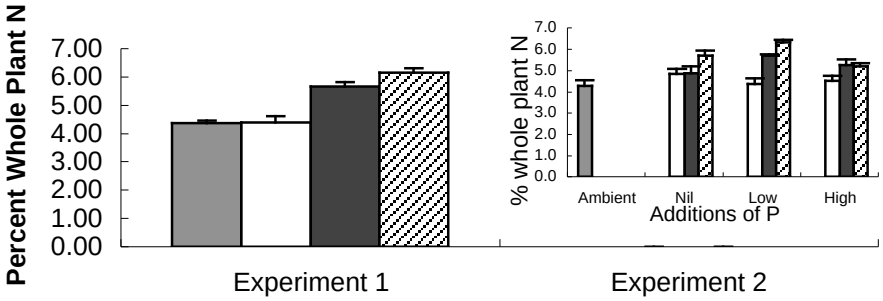

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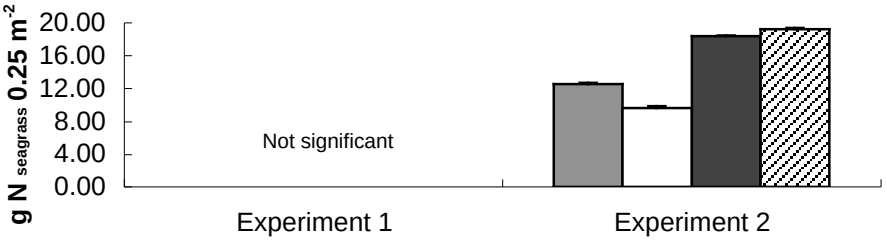
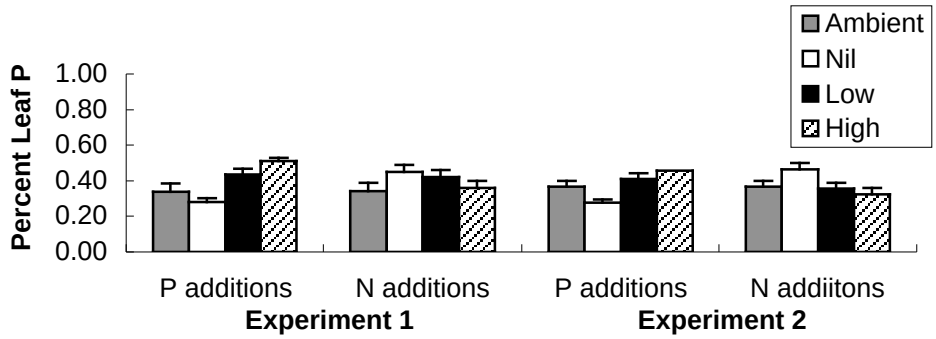


Figure 5.7 Significant plant tissue %N responses to additions of Osmocote® at Picnic Bay during Experiment 1 and Experiment 2 for: **a)** leaves, **b)** rhizomes, **c)** roots, **d)** whole plants, **e)** meadow nutrient status ($gN_{seagrass}$ 0.25 m^{-2}). Note different scales on the Y axis and inset graph.

a).



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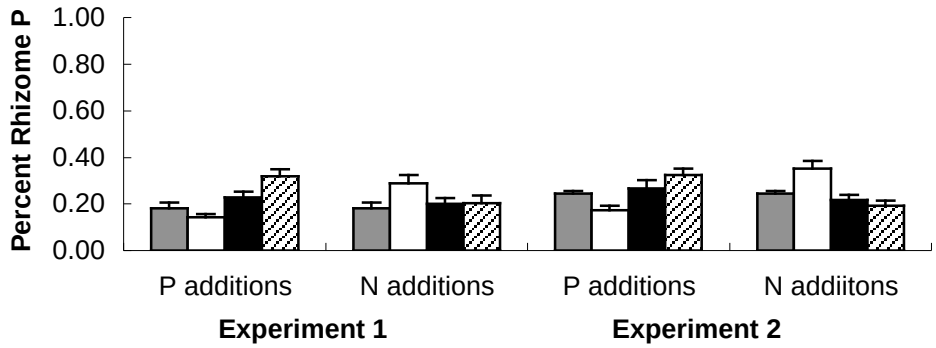

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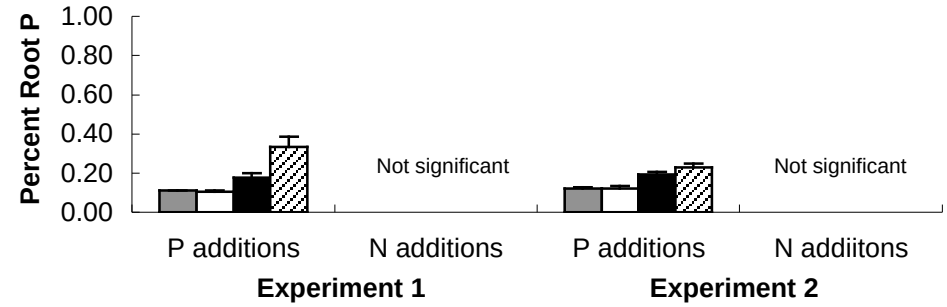

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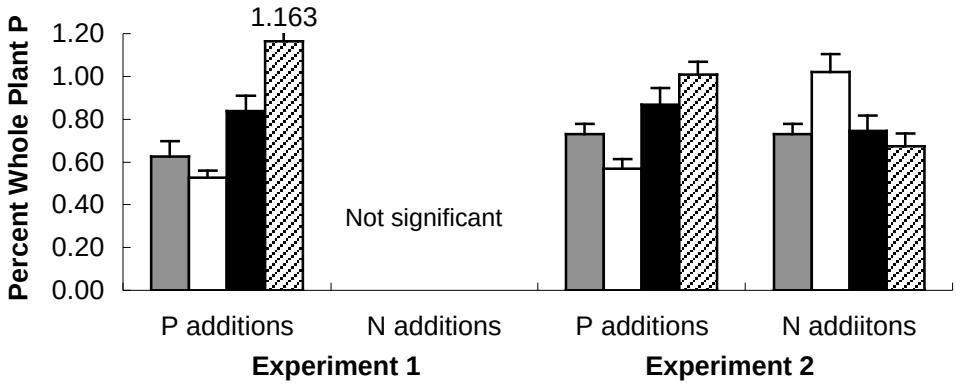

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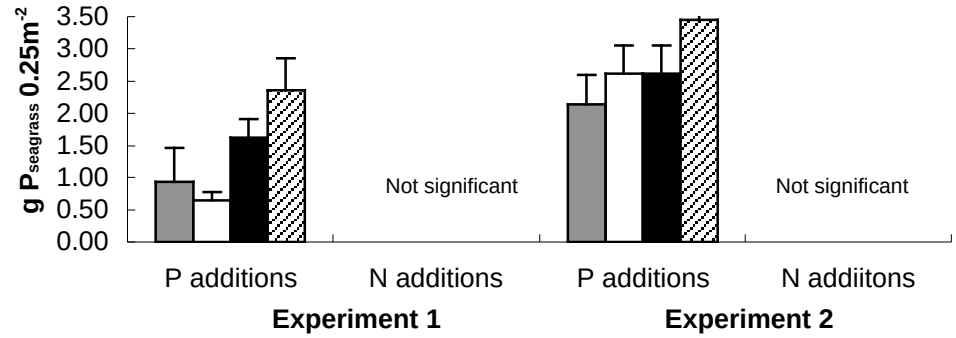


Figure 5.8 Significant plant tissue %P responses to additions of Osmocote® at Picnic Bay during Experiment 1 and Experiment 2 for: **a)** leaves, **b)** rhizomes, **c)** roots, **d)** whole plants, **e)** meadow nutrient status ($gN_{seagrass}$ 0.25 m^{-2}). Where a number is displayed above a bar this represents the mean nutrient value of that bar which is beyond the scale of the y axis. Where no cross bar appears on top of the standard error line it means that the standard error was beyond the scale of the Y axis.

Table 5.11 Summary of responses by plant abundance parameters to applications of fertilizer for each location during Experiment 1: seagrass senescing, May–August and Experiment 2: seagrass growing, August–November for Bolger Bay and Picnic Bay.

Bolger Bay

Parameter	Significant term	Experiment 1 (seagrass senescing, May–August) *post priori* outcomes	Significant term	Experiment 2 (seagrass growing, August–November) *post priori* outcomes
Leaf Biomass	Lifting*P	Biomass at high and no additions of P significantly greater than biomass in low additions. Ambient not significantly different from either group.	ns	
Rhizome Biomass	ns	Greatest average response was in quadrats fertilized with N_HP_H	ns	For the majority of these parameters the term Lifting*P though not significant explained the largest proportion of the data variability. For rhizome biomass and shoot density the largest proportion of variance was explained by Lifting*N*P. Greatest average response was in quadrats fertilized with N_HP_H for all parameters except root biomass when it occurred in quadrats fertilized with P_H
Root Biomass	Lifting *P	Root biomass increased with high P additions but not with low additions; Root biomass in nil addition quadrats was not significantly different from P_H. Ambient quadrats not significantly different from either group.	ns	
	Lifting*N	Root biomass associated with ambient and nil N additions were higher than that in quadrats dosed with N fertilizer.		
Total Biomass	ns	Greatest average response was in quadrats fertilized with P_H.	ns	
Shoot Density	Lifting*N*P	Shoot density increased with high loadings of P but not when the N:P for fertilizer combinations was in favour of N.	ns	

Table 5.11 continued.

Picnic Bay

Parameter	Significant term	Experiment 1 (seagrass senescing, May–August) *post priori* outcomes	Significant term	Experiment 2 (seagrass growing, August–November) *post priori* outcomes
Leaf Biomass	ns	For most of these parameters the term Lifting*P explained the largest proportion of the variability in the data. For leaf biomass and shoot density the largest proportion of variance was explained by Lifting*N*P. Greatest average response was in quadrats fertilized with N_HP_H for all parameters except leaf and total biomass when it occurred in quadrats fertilized with N_LP_H.	ns	Greatest average response was in quadrats fertilized with N_H.
Rhizome biomass	ns		Lifting*N	Additions N fertilizer increased rhizome biomass from N_N quadrats but not incrementally and not from N_A quadrats.
Root biomass	ns		ns	Greatest average response was in quadrats fertilized with N_H.
Total Biomass	ns		ns	Greatest average response was in quadrats fertilized with N_H.
Shoot Density	ns		Lifting*N	Additions of N fertilizer increased shoot density from N_N quadrats but not incrementally and not from N_A quadrats which did not differ from N_N quadrats.

Table 5.12 Summary table of plant tissue nutrient responses to applications of fertilizer at Picnic Bay during Experiment 1: seagrass senescing, May–August and Experiment 2: seagrass growing, August–November.

Parameter	Significant term	Experiment 1 (seagrass senescing, May–August) *post priori* outcomes	Significant term	Experiment 2 (seagrass growing, August–November) *post priori* outcomes
Nitrogen				
% leaf N	Lifting*N	Additions of N fertilizer increased %N but not incrementally	Lifting*N	Leaf %N significantly higher in quadrats with N additions in comparison to N_N quadrats, however whilst N_H quadrats are greater than N_A, N_L quadrats are not greater.
% rhizome N	Lifting*N	Additions of N fertilizer increased %N and incrementally.	Lifting*N	Additions of N fertilizer increased Rhizome %N from nil additions (N_N and N_A) but not incrementally.
% root N	ns	Highest average response was in quadrats fertilized with N_H.	Lifting*N*P	Root %N tended not differ with increase loadings of N fertilizer at nil and high loadings of P fertilizer but at low loadings of P root %N increased significantly with increased loadings of N fertilizer.
% whole plant N	Lifting*N	Additions of N fertilizer increased %N but not incrementally.	Lifting*N*P	Whole %N increased with loadings of N fertilizer at every level of P fertilizer and whole %N increased with loadings of P except at $N_NP_{L.}$.
			Lifting*N	Additions of N fertilizer significantly increased Whole Plant %N incrementally from the controls.
g $N_{seagrass}$ (0.25 m^{-2})	ns	Highest average response was in quadrats fertilized with $N_HP_{H.}$	Lifting*N	Additions N fertilizer increased $gN_{seagrass}$ 0.25 m^{-2} from N_N quadrats but not incrementally and not from N_A

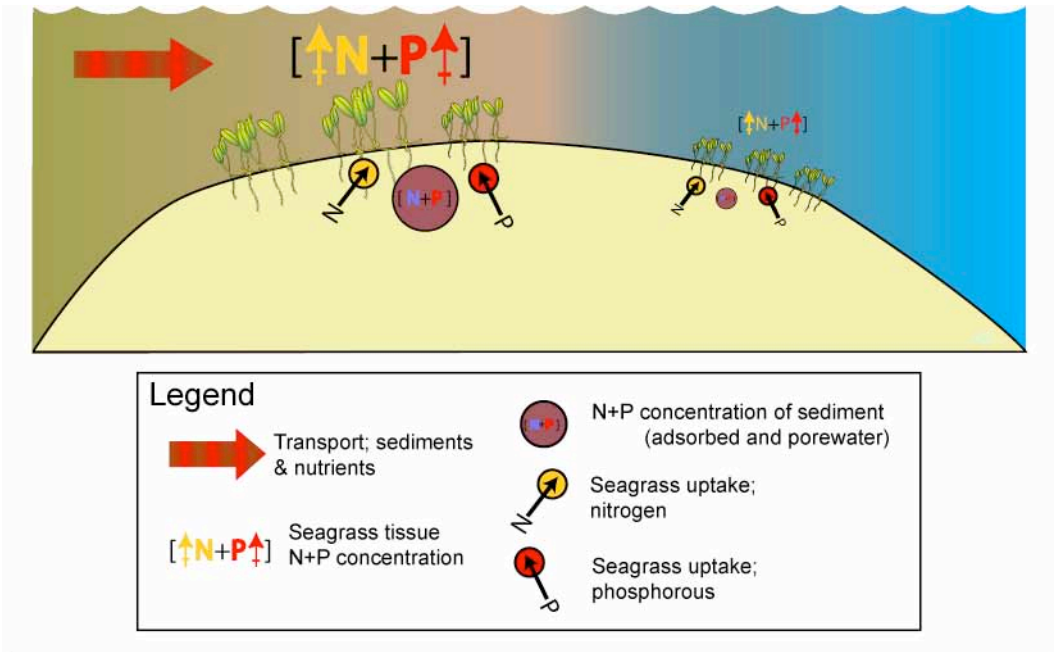
Table 5.12 continued.

Parameter	Significant term	Experiment 1 (seagrass senescing, May–August) *post priori* outcomes	Significant term	Experiment 2 (seagrass growing, August–November) *post priori* outcomes
Phosphorous				
% leaf P	Lifting*P	Additions of P fertilizer increased levels of %P and incrementally	Lifting*P	Additions of P fertilizer increased % leaf P incrementally in comparison with P_N quadrats but P_L quadrats and P_A quadrats did not differ from each other
	Lifting*N	Additions of N fertilizer and manipulation decreased %P but not incrementally	Lifting*N	% leaf P significantly lower in $N_{H,}$ N_L and N_A quadrats than in N_N quadrats
% rhizome P	Lifting*P	Additions of P fertilizer and manipulation increased %P and incrementally.	Lifting*P	Additions of P fertilizer increased % rhizome P incrementally in comparison with P_N but not P_A.
	Lifting*N	Additions of N fertilizer decreased %P but not incrementally.	Lifting*N	% rhizome P significantly lower in $N_{H,}$ N_L and N_A quadrats than in N_N quadrats.
% root P	Lifting*P	Additions of P fertilizer increased %P and incrementally.	Lifting*P	Additions of P fertilizer increased % rhizome P from nil additions (P_N and P_A) but not incrementally.
% whole plant P	Lifting*P	Additions of P fertilizer increased %P and incrementally.	Lifting*P	Additions of P fertilizer increased % leaf P incrementally in comparison with P_N quadrats but P_L quadrats and P_A quadrats did not differ from each other.
			Lifting*N	% leaf P significantly lower in $N_{H,}$ N_L and N_A quadrats than in N_N quadrats.
g $P_{seagrass}$ (0.25 m^{-2})	Lifting*P	Additions of P fertilizer increased %P but not incrementally.	Lifting*P	Additions of P fertilizer increased % rhizome P in comparison to P_N but not P_A and not incrementally.

Table 5.13 Summary of significant results for each experiment at each location for plant production and plant tissue nutrients.

	Experiment 1 seagrass senescing, May–August	Experiment 2 seagrass growing, August–November
Bolger Bay	***Plant production***	***Plant production***
	seagrass yield responded to large inputs of P fertilizer, (N:P small in favour of P), (Table 5.11, Fig.5.6)	no plant yield parameter was statistically significant.
	decreases in leaf biomass and shoot density were observed when the fertilizer N:P ratio was large (i.e. in favour of N).	a trend for increases in plant biomass when the P)proportion of the nutrient pool was large relative to N (i.e. sediment N:P is small). (Table 5.11, Fig. 5.6)
	Plant tissue nutrients	***Plant tissue nutrients***
	no data	no data
Picnic Bay	***Plant Production***	***Plant Production***
	no plant yield parameter statistically significant	yield parameters increased in response to additions of N fertilizer. (Table 5.11, Fig. 5.6)
	observations of the different treatment levels revealed a trend for plant biomass to increase when the P proportion of the nutrient pool was large relative to N (i.e. sediment N:P is small). (Table 5.11, Fig. 5.6)	
	Plant tissue nutrients	***Plant tissue nutrients***
	plant tissue % N increased with increases in N fertilizer (Fig. 5.7)	plant tissue %N increased with loadings of N fertilizer (Fig. 5.7)
	plant tissue %P increased with increases in P fertilizer (Fig. 5.8)	plant tissue %P increased with loadings of P fertilizer (Fig. 5.8)
	non-incremental decrease of leaf and rhizome %P with increases in N fertilizer. (Table 5.12 Fig. 5.8)	leaf, rhizome and whole plant % P decreased with increases in loads of N fertilizer. (Table 5.12, Fig. 5.8)

Chapter 6 General discussion



Conceptual diagram depicting luxury uptake in Halophila ovalis*—nutrient 'sponge'.*
Left of the model depicts coastal environments with high nutrient loads, right of the model represents enironments with low nutrient loads.

Rationale and objectives of this study

As explained in Chapter 1, the inshore coastal seagrass meadows of the Great Barrier Reef Lagoon are characterized by structurally small species that are low in biomass and spatially and temporally ephemeral. There has been little research on the dynamics of these meadows. In contrast, structurally large species from temperate and tropical regions of the Northern Hemisphere have been studied extensively (Duarte 1999). As a consequence, much of our knowledge on seagrass ecology is based on the dynamics and interactions of these Northern Hemisphere seagrass species.

This thesis investigated the interactions between sediments and nutrients among these structurally small, intertidal seagrasses along the coastline of the central region of the Great Barrier Reef World Heritage Area, under ambient and enhanced nutrient conditions. To achieve this, I created an inventory of sediment structure, nutrient levels, and associated chemical parameters along with seagrass abundances for eleven intertidal seagrass meadows within this region (Chapter 3). I then examined whether the sediment structure and nutrient environment was regulated by the presence of different seagrass species (*Halophila ovalis*, *Halodule uninervis* and *Zostera capricorni*) and seagrass densities (Subchapters 4.1, 4.2). Realizing that this assessment was made at a time of year when seagrasses in this region have limited growth (i.e. are senescent), I then examined the ambient intra-annual sediment structure and nutrient interaction with *Halophila ovalis* at two locations (Subchapter 4.3). Finally, I investigated the response of rhizosphere nutrients and seagrasses of these two *Halophila ovalis* meadows to additions of Osmocote® fertilizer (Chapter 5). This analysis was conducted in locations with differing mineralogy and at two times of the year (senescent and growing).

In this chapter, I discuss the major findings of my thesis and the implications of these findings for our understanding of the dynamics of the intertidal seagrass meadows, future research and management in the central region of the GBRWHA.

Location (geography and environmental history of the site) as the most important influence on the presence, distribution and abundance of intertidal seagrasses in the central region of the GBRWHA

Within the GBR region, four seagrass habitat types have been recognized: 'River estuaries' 'Coastal', 'Reef' and 'Deepwater' (Carruthers *et al.* 2002). Whilst all these habitats are influenced by disturbance, they are both spatially and temporally variable. Each of these habitats is moderated by different processes and therefore possesses different ecological functions. This thesis concentrated on a subset of coastal seagrass habitats; the intertidal meadows of the central region of the GBRWHA.

From a global perspective, I recorded relatively low porewater values for these meadows (Table 3.2). In addition, I observed comparatively high levels of adsorbed N combined with low levels of adsorbed PO_4^{3-} (cf. Udy and Dennison 1997a, b, Udy *et al.* 1999). Biomass measures were low for all species (Chapter 3), but tissue nutrient content was high for *Halodule uninervis* and *Halophila ovalis* (Chapter 3, Table 3.4). These observations, combined with the low suspended and particulate nutrients recorded along this coastline (Furnas and Mitchell 1995), suggest that the nutrients in the coastal shallow seagrass environments of this region are bound up in the sediments and biome rather than free in the water column. This accords with the conclusions of another detailed study of a structurally small seagrass, *Halophila ovalis* (Hillman *et al.* 1995), and indicates that such seagrass meadows represent a significant bio-sink for nutrients. Despite these generic conclusions, variability between locations was the most significant statistical outcome throughout the thesis.

The importance of location indicates the significance of local site history. The geographic setting of a location dictates its sediment regime, while the frequency of disturbance dictates the structure of the meadow. The factors that affect the sediment regime at each location are: a) distance from major rivers, b) protection from south-easterly trades winds, c) frequency and magnitude of resuspension, and d) sediment particle sorting. Differences in sediment mineralogy and grain size, in turn, influence the nutrient regime at specific locations. For example, across the 11 locations surveyed in Chapter 3, sediments with a high clay content tended to have a high adsorbed nutrient

pool compared with locations with coarser sediments (Fig. 3.1). This importance of location is further supported by most of my statistical analyses with differences in sediment structure and sediment nutrient pools being driven by differences in 'location' regardless of the presence or abundance of seagrass (Subchapters 4.1 and 4.2: Concept 1).

However, a comparison of total nutrient pools across a range of locations revealed an interaction between meadow biomass and total sediment nutrient concentrations. This result was evident where I compared vegetated (combined plant and sediment nutrient pool) and unvegetated (sediment nutrient pool where no plants were growing) areas. The two locations that supported relatively higher seagrass biomasses had a greater total nutrient pool than adjacent unvegetated areas (e.g. Ellie Point and Windy Point; Subchapter 4.1, Table 4.4). Even those meadows that support smaller biomasses of seagrass (e.g. Bolger Bay, Horseshoe Bay, Subchapter 4.1, Table 4.4) recorded ratios of total nutrient pools greater than one indicating larger total nutrient pools present in the vegetated sites as opposed to the unvegetated sites. However, between meadow comparisons indicate, it is only in those meadows supporting large seagrass biomass where a majority of the total nutrient pool is in the biome (Subchapter 4.1, Table 4.4). Although this result is intuitive, it highlights the differences between locations and species in meadows of relatively high biomass with those of low biomass. The uniqueness of location and species-specific interactions with the local environment is one of the most significant findings of this study.

Recognizing the importance of species-specific functions and forms

In the past, seagrass meadows have been assumed to be functionally uniform. My study indicates that this as an oversimplification. *Zostera capricorni*, a congener of one of the species best studied globally (*Z. marina*), approximated some of the commonly held views supporting this idea. The seagrass form and function model (Walker *et al.* 1999) places all seagrass genera on a continuum of structural, distributional, physiological and ecological characteristics (see Figure 1.1). The seagrasses that occur in the Great Barrier Reef Region are from all genera listed as tropical plus *Zostera*. In general, genera to the left of the model are ephemeral, colonizing, high food value seagrasses, while those to

the right are persistent, stabilizing and low food value seagrasses. In this context, *Zostera capricorni* is further to the right on the continuum than the species of *Halophila* and *Halodule* studied here (Subchapter 4.2).

It is important to not only consider the location in which a seagrass grows, but its place on the seagrass form and function model continuum to understand how a particular seagrass ecosystem operates. An obvious extension of this approach is that the 'broad-brush' management strategy often applied to coastal marine ecosystems is inappropriate in regions where a variety of seagrass 'forms' co-exist. A caveat to this conclusion is that my study was conducted in the Southern Hemisphere winter. The response of seagrasses may differ throughout the year. Studies into the way seagrasses respond to their environment at different times of the year are crucial to developing an adequate management strategy for seagrass in this region.

Revisiting the importance of seasonality to seagrasses

Seasonality in the tropics is often underemphasized, not only in seagrass ecology but also in mainstream ecology. Traditional models of seasonality are driven by photoperiod and temperature, which do not vary much in the tropics. This has led many researchers to conclude that seasonal changes in standing crop of tropical seagrasses are less pronounced than those of temperate seagrasses (Duarte 1989, Hillman *et al.* 1989). However a new model for seasonality in the tropics is finally receiving acceptance. This model is based on rainfall and differentiates between 'wet' and 'dry' seasons (Wright *et al.* 1999). Earlier studies on seagrass indicated a seasonal growth cycle for seagrasses of the central GBR by assessing changes in biomass (Mellors *et al.* 1993, McKenzie 1994, Lanyon and Marsh 1995, Rasheed 1999). In addition to investigating changes in biomass, I also analysed the nutrient status of the sediment environment, the seagrass itself and changes in all these parameters with season (Subchapter 4.3). I showed that intra-annual variation (between winter and spring) in sediment (adsorbed and porewater) and plant tissue nutrients and biomass occurred at two *Halophila ovalis* meadows.

These differences occurred concurrently at the two meadows sampled despite their differences in sediment structure, nutrient status and biomass (Subchapter 4.3). Levels of adsorbed $PO_4^{3-}{}_{(Bray)}$ and porewater NH_4^+ were significantly lower during the growing

season than during the senescent season (Table 4.17, Table 4.19, Table 4.20). At Bolger Bay, only levels of porewater PO_4^{3-} were also significantly lower during the growing season than during the senescent season. Biomass increased significantly within both meadows during the growing season (Table 4.22, Table 4.23, Table 4.24). There was also a non-significant increase in plant tissue nutrients at this time of year at both locations (Table 4.22, Table 4.23, Table 4.24). The increase in plant tissue nutrients combined with the significant increase in biomass resulted in the plant nutrient status of the meadow at both locations being significantly greater during the growing season than during the senescent season.

Whilst growth was more rapid during the warmer months (as evident by the increase in biomass), the strategies observed for increasing the biomass of *Halophila ovalis* differed between these two locations. In the Bolger Bay meadow, biomass increase resulted from significant increases in all growth parameters: shoot production, rhizome extension and number of new meristems (Table 4.23). In contrast at nearby Picnic Bay, all parameters increased and therefore contributed to the significant increase in biomass during the growing season, however only the increases in the number of new meristems was significant (Table 4.24). As these meadows differed with respect to their stages of development, these results provide evidence that *Halophila ovalis* can modify its growth strategy under different meadow conditions and development. Greater rhizome elongation was associated with the colonising meadow (Bolger Bay), while the established meadow (Picnic Bay) increased meristem production and hence branching as a strategy for filling gaps within the meadow.

A comparison of seasonality within *Halophila ovalis* meadows in this region with that of a meadow on the opposite side of the continent shows a similar response where *Halophila ovalis* responds to seasonal cues although at different times of the year (Hillman *et al.* 1995). As discussed previously, I observed large increases in growth and biomass accumulation associated with a decrease in sediment nutrients at both locations from winter (June) to spring (October) (Subchapter 4.3, Table 4.16). These contrasted with no significant change in tissue nutrient concentrations over the same period (Subchapter 4.3, Table 4.21). This result differs from that of Connell and Walker (2001), who observed at this time of year, very little increase in biomass during winter and spring but a large increase in plant tissue content at this time of year. They

attributed this increase in tissue nutrient content to N increases in the water column, suggesting that *Halophila ovalis* was capable of opportunistic nutrient uptake similar to *Zostera marina* (Short and McRoy 1984). The increase in water column N is a product of the wetter winter weather in Western Australia dictated by its Mediterranean type climate (wet winters, dry summers). In contrast, north Queensland weather is monsoonal (wet summers, dry winters) with large variations between years. An influx in nutrients to north Queensland habitats caused by monsoon rain could be bound up in the plants via luxury uptake during early autumn and utilized later when warmer temperatures and less turbid conditions initiate rapid growth for *Halophila ovalis* during spring (this study) and for summer for the Swan River system (Hillman *et al.* 1995, Connell and Walker 2001). What all these studies show, is that *Halophila ovalis* responds to similar cues (nutrients, light and temperature), but at different times of the year as determined by the local climate.

Halophila ovalis—nutrient sponge!

Nutrient limitation of a plant occurs when its growth ceases because the nutrients necessary for growth are at levels that make further growth impossible. If a plant is nutrient limited, it does not necessarily mean that there is not enough nitrogen or phosphorus available. It may also mean that these nutrients are not available in appropriate proportions required by the plant (i.e. nutrient ratios). A detailed discussion of the evidence for nutrient limitation of seagrasses within the Great Barrier Reef region was presented in Chapter 3 (Table 3.7). I collected my empirical data at a time when seagrasses were not actively growing. As discussed above plant-nutrient interactions differ between seasons. Thus the only true test of nutrient limitation is to test a plant's response to nutrient enhancement in different seasons.

During the course of the experiment outlined in Chapter 5, the meadow at Bolger Bay declined. As a result of this decline, no data on the physiological response to nutrient enhancement is available for this meadow. During the period of these experiments at Bolger Bay, I observed an influx of very fine silt that settled on the leaves and I suggest that this may have caused seagrass decline at this site. There was no such dieback at Picnic Bay. Thus the combination of the physiological and growth response of *Halophila ovalis* at that location allows for an informed (although inferred) interpretation of the consequences of nutrient enhancement.

The seagrasses displayed a physiological response to nutrient addition during the seagrass senescing season (winter), but this was not reflected by increases in biomass. Despite this lack of biomass increase, tissue nutrient increased with the additions of fertilizer. This ability of plants to increase their tissue nutrient content while not increasing in biomass is known as luxury uptake. During the seagrass growing season (spring), the seagrasses responded by increasing biomass with additions of N fertilizer and increasing in tissue nutrients with the addition of both N and P fertilizer. Nitrogen limitation occurs when there is proportionally less nitrogen than phosphorus, i.e. there is excess phosphorus. It is not surprising that nitrogen limitation occurred late in spring (November) as the nitrogen in the sediments would have been used up by seagrass growth during the earlier months of spring. During both experiments, % leaf P increased with inputs of P fertilizer and decreased with inputs of N fertilizer, suggesting that the plants were secondarily limited by the nutrient P or that the experimental dosages failed to supply the nutrient in the proportions required by this species for the synergistic uptake of N.

These results suggest that during winter (Experiment1), the growth of *Halophila ovalis* achieved ‘maximum growth rate’ but the plants continued to store the excess nutrients via ‘luxury uptake’ (Fig. 6.1). Other factor(s) must have been limiting growth at this time, possibly low light levels (resulting from the frequency of re-suspension events caused by strong winds in the Bay) or low water temperatures. As these other factor(s) became less limiting, the rate of plant growth increased using up the N within the sediment nutrient pool. This caused an imbalance between the N:P nutrient pool, consequently the plants responded to inputs of N. As the plants did not respond to the incremental increase in N fertilizer and assuming that the seagrasses as opposed to the other flora present in the system are the major uses of this nutrient, I suggest that at this stage, N would have been at the luxury uptake stage (Fig. 6.1). During this time, tissue nutrient content continued to increase with increases in fertilizer additions. The observations of nutrient tissue concentration highlight the complexity of the interaction between nutrient supply, plant growth rate and tissue nutrient content in these seagrasses.

These various interactions may be summarized in a simplistic way if we assume a single nutrient is the factor limiting growth. Such a model is presented in Figure 6.1 as a way

of visualising these interactions. In this model, three main phases of nutrient supply are identified, first where nutrients limit growth (nutrient limitation), the second where nutrients are not limiting to growth but where they are still being taken into the plant tissue at a greater rate than plant growth, so are accumulating (luxury uptake) finally, the nutrients become toxic and as a result the plants die (toxicity). The critical level of nutrient availability then is where nutrient supply allows for maximum growth under those particular conditions. Within the range of 'nutrient limitation' there are at least two phases, the early phase were nutrient limitation is visually obvious by signs such as yellowing leaves with N limitation, this is followed by a so called 'hidden hunger' where all nutrients being taken up into the plant immediately become utilized in additional growth.

Seagrass tissue nutrients (%N and %P) represent an integration of nutrient availability and uptake at a site (Mengel and Kirkby 1987, Fourqurean *et al.* 1992). I have compared my tissue nutrient results, collected in 1994 and 1995 with values from published data collected 10 and 25 years previous to this. This comparison shows that the ambient levels of tissue %N and %P have increased over this time (Fig. 6.2). This temporal increase in seagrass tissue nutrients corresponds with increases of fertilizer usage in the adjacent Burdekin River catchment over the same period (Fig. 6.2). Brodie (2002) states that at present we essentially have no indications of the effects of terrestrial runoff on seagrasses of the Great Barrier Reef region. I present here, preliminary evidence of a relationship between increasing fertilizer usage and increased tissue nutrient content in *Halophila ovalis*, growing adjacent to the catchment (Fig. 6.2). This observation of increased nutrients over a 25 year period indicates that the seagrass *Halophila ovalis* in coastal environments is a potential bio-indicator of nutrient increases in the marine environment.

Some seagrasses have been identified as being able to absorb excess nutrients, through luxury uptake and store these nutrients in their tissues. With fertilisation of sediments in my experiments, the tissue nutrient content of *Halophila ovalis* increased without increases in biomass during the senescent season. My enhancement experiments provide evidence that *Halophila ovalis* is capable of further luxury uptake (Fig. 6.2). Consequently, I suggest that the ability of *Halophila ovalis* to act as a nutrient sponge

qualifies this species as a useful indicator of nutrient levels in the inshore region of the Great Barrier Reef Lagoon.

Controls and key processes of intertidal meadows of structurally small seagrasses in this region

As explained earlier, the structurally small species that comprise intertidal seagrass meadows in the central region of the GBRWHA are low in biomass, ephemeral, short lived, and generally recruit from seed banks (Inglis 2000). They are also adapted to low light conditions (Pollard and Greenway 1993), having recruited, grown and evolved in an area characterized by high turbidity as a result of seasonally high terrestrial freshwater, nutrient, and sediment inputs which differ inter-annually (Blake 1996, Brodie 1996). Based on the evidence presented in this thesis for *Halophila ovalis*, I suggest that structurally small seagrasses in this region are not primarily nutrient limited but are limited by one or more of the other factors that affect their growth. In understanding these other potential growth limiting interactions, as I have already noted in Chapter 1, that seasonality in temperature, light availability and meteorological events have an impact upon the ability of plants to grow. In understanding these factors, I have developed a simple conceptual diagram to depict the interaction between plant growth, nutrient uptake and different disturbances as they change between seasons (Fig. 6.3).

Thus, I suggest that in this region, the disturbance regime of a location, that is, the localized aspects of exposure to predominate winds, tidal exposure, turbidity and hence light availability, and to a lesser degree the frequency and intensity of herbivory, particularly that of dugong grazing (Preen 1995) dictates the species present and to some level, their abundance. The extent and intensity of these localized disturbances on an intra-annual scale will vary between seasons, with light availability determined by the extent of turbidity, as driven by the seasonal wind regimes, and in a smaller capacity seasonal differences in temperature (i.e. Fig. 6.3).

The between year (inter-annual) differences in disturbance regime of a seagrass meadow will also vary depending on the prevailing climatic conditions as caused by the Southern Ocean Oscillation. Over longer temporal scales, larger scale disturbances such as cyclones (intensity and frequency) affect seagrasses either directly (removal) or

indirectly (extended periods of high turbidity and hence changes in light regime). In the periods between these major disturbances I believe that established meadows act as nutrient sinks, with the sediments providing net retention of nutrients, while the seagrasses absorb the nutrients either by increasing in biomass (*Zostera capricorni*) or increasing tissue nutrient contents (*Halophila ovalis* and *Halodule uninervis*). However these habitats have the capacity to become nutrient sources to the Great Barrier Reef Lagoon during cyclones as the sediments are turned over and seagrass meadows are removed.

Future directions for management and research of intertidal seagrasses in the central region of the GBRWHA

It is recognized that seagrasses provide habitat and food for organisms and that the architecturally large seagrass species that maintain high biomass meadows have the ability to modulate sedimentary and biogeochemical processes. This has led to seagrass meadows being considered as one of the most valuable marine ecosystem in terms of the value added benefits of their ecosystem services (Costanza *et al.* 1997). Duarte (1999) has called for knowledge produced locally to be scaled up so that assessments of the value of seagrass resources can be made at the regional and global scales. Whilst a global seagrass model may be desirable, caution is required, as currently this model would be skewed towards systems that are characterized by persistent meadows of structurally large seagrass species. Consequently, any approach to the management of seagrass habitat based on views generated from research on structurally large (temperate) species would be inappropriate for the inshore intertidal meadows that I studied and that predominate within this region of the Great Barrier Reef World Heritage Area.

The current legislative tool for the protection of seagrasses in Queensland is the *Fisheries Act 1994* (Qld). The policy of the management agency, the Queensland Fisheries Service, is one of no net loss of seagrass. The difficulty in maintaining this level of protection will only increase as the *Fisheries Act 1994* (Qld) becomes rolled into the *Integrated Planning Act 1998* (Qld). The *Intergrated Planning Act* (Qld) (IPA) commenced in 1998 with the aim of achieving ecologically sustainable development at the local, regional and state levels. The State Coastal Plan is a statutory instrument under section 29 of the *Coastal Protection and Management Act 1995* (Qld) (Coastal

Act) and has the effect of a State Planning Policy. As a State Planning Policy, local governments must appropriately reflect the Coastal Plan in the preparation of their planning scheme, through IPA. Seagrasses, particularly those from intertidal habitats, run the risk of being vulnerable or even escaping legislative awareness as the legislation involved in the management of seagrasses is complex and responsibility for intertidal habitats is obscure. There may be a need for an integrated seagrass management system to be proactively developed in Queensland, perhaps alongside similar systems for mangroves and saltmarshes that occupy similar transitionary (intertidal) environments.

I suggest that the first step towards an integrated seagrass management system should be to encompass the variability inherent in the different seagrass habitat types that occur in Northeast Australia (Carruthers *et al.* 2002). Within each habitat type it is important to recognize the different species and their relative form and function; for example, coastal seagrass habitats should be recognized as intertidal, or subtidal. Whether these meadows are made up of structurally small or large seagrass species is also important. Environmental management plans for each seagrass habitat type should be formulated under the regional planning schemes as per the IPA requirement for each municipality responsible for the implementation of such plans under the relevant regional Coastal Management Plan. These plans could be formulated within a common conceptual framework for each seagrass habitat type and could be proactively updated as new local information is acquired. This type of approach would foster community understanding that not all seagrass meadows are the same, and that differences exist between meadows due to their geographical setting, species composition and abundance, sediment mineralogy, stage of meadow development and past nutrient history. As the understanding of the natural dynamics of these structurally small seagrass meadows increases, more informed decisions can be made about the magnitude of impacts on these environments from anthropogenic sources.

For these plans to be realistic, I suggest more detailed information on temporal change and the processes that maintain seagrass meadows as a resource is required. Included in this should be an assessment of the nutrient state of each major meadow type across a broad spatial scale. Within this evaluation, seagrass can be classified along the nutrient continuum as having hidden hunger, (increasing), partaking in luxury uptake (maintenance) or suffering from toxicity (decreasing) (Figure 6.1) To be able to achieve

this, results from my study indicate that information needs to be collected from a variety of locations over a long temporal scale. These data could then form a part of an iterative approach to management as described above, and the data implemented into the revised regional and local management plans. With the advent of global climate change, the frequency of episodic events such as cyclones is expected to increase. These changes will be accompanied by increases in precipitation and temperatures which will intensify seasonality in the tropics. Many of these attributes are already being experienced with El Niño/La Niña events. Consequently there is a need for long term studies (>10 yr) to establish the degree of stability of seagrass communities in these dynamic systems and to develop nutrient monitoring protocols for seagrass meadows.

One approach to developing longer term, broadscale monitoring programmes would be to utilize the activities of ongoing monitoring such as the Seagrass Watch programme, a community based monitoring programme of intertidal seagrass meadows across Queensland. Whilst gathering the information on the state of these seagrass meadows, this community based programme needs to be integrated with other studies. That is, studies that look closely at processes that affect the stability and persistence of seagrass beds within this region, such as ongoing assessment of the nutrient state of these meadows. Monitoring plant nutrients at regular intervals including pre-wet, post-wet and dry seasons would be ideal. However monitoring during the winter months, when structurally small seagrasses of this region are in senescent growth mode is the next best option. During this time plants are assimilating excess nutrients as luxury uptake reflecting the longer term total net nutrient pool available, and when the system is unaffected by seasonal pulsed inputs. In addition, the plants have a slower growth rate at this time, and thus excess nutrients are not being used to generate new plant tissue. From the collection of habitat and plant tissue nutrients, a spatial and temporal nutrient map could be established. Comparing this map with baseline inventory information established by this thesis, managers will be able to determine whether nutrients are increasing in coastal habitats where seagrasses occur in this region. Thus, this study will allow an ongoing and proactive management of catchments with respect to the downstream effects of nutrients in coastal marine seagrass ecosystems of north eastern Australia.

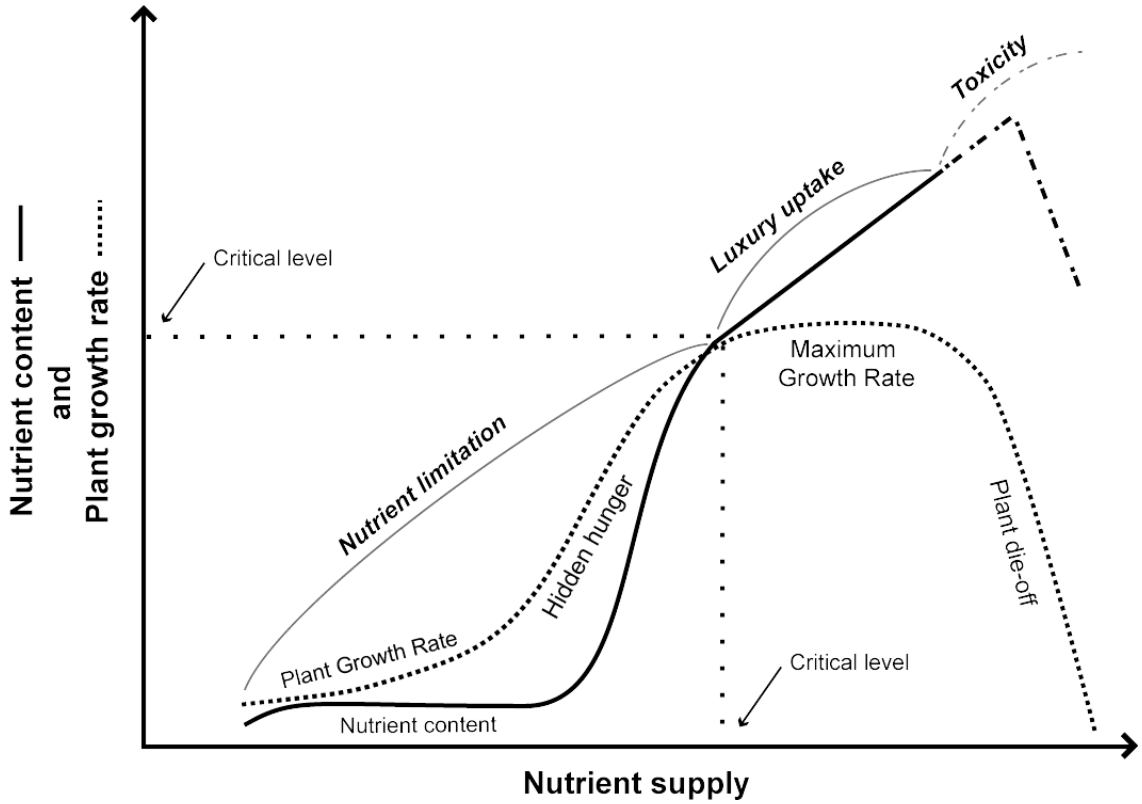


Figure 6.1: A graphical model representing the different phases of nutrient uptake and plant growth with increasing nutrient supply (loosely based on Smith and Loneragan 1997). Two measures are presented, the tissue nutrient content and the plant growth rate.

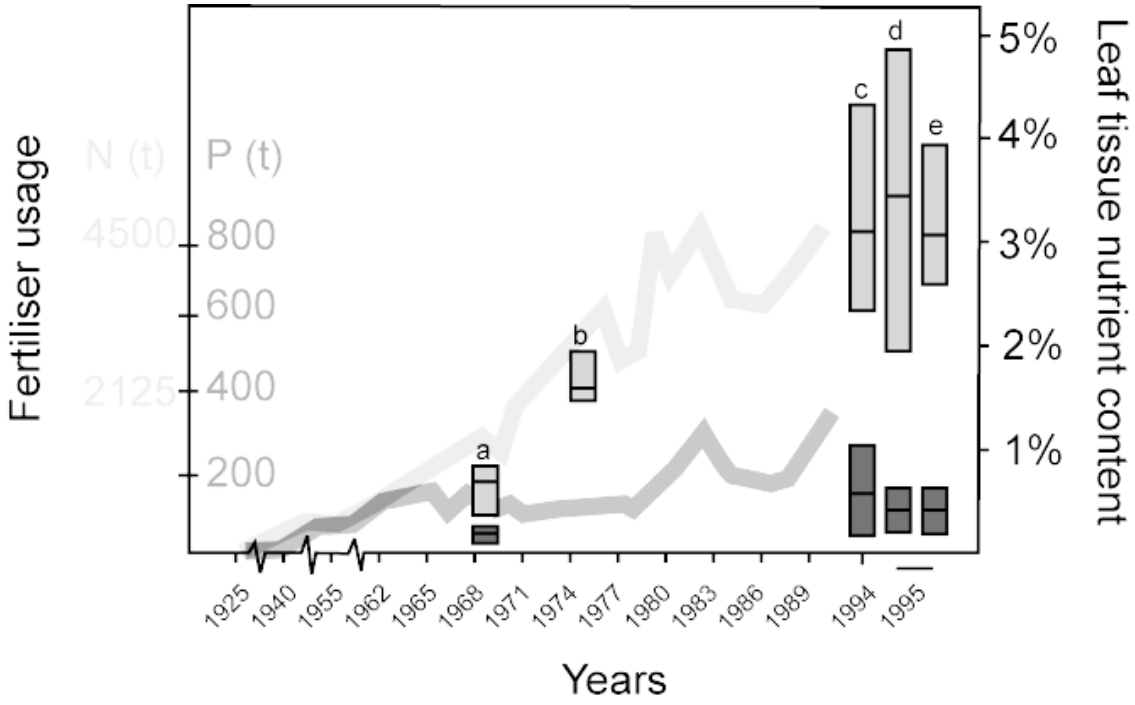
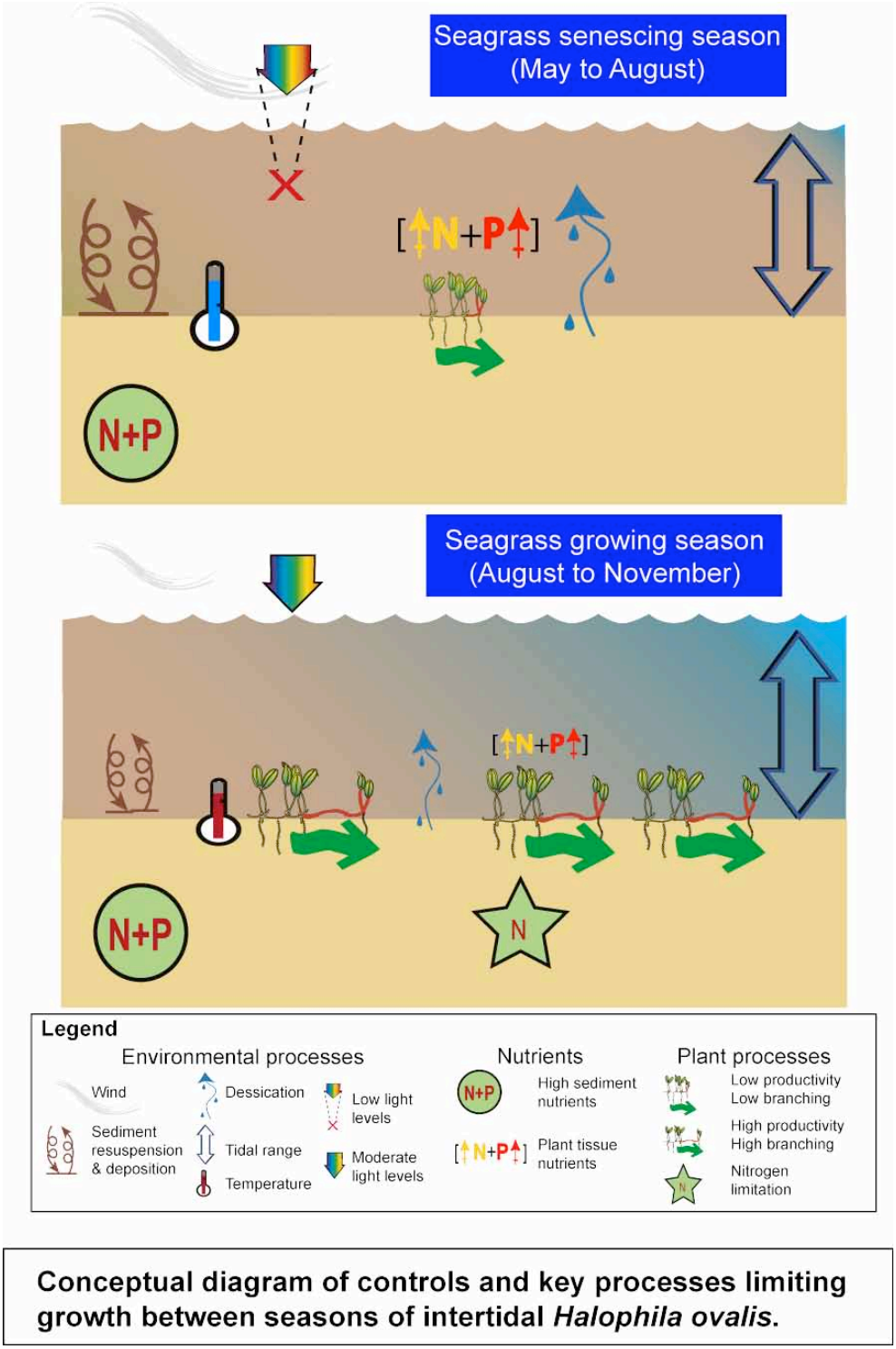


Figure 6.2 Values of % leaf N and % leaf P for plants of *Halophila ovalis* from Cleveland Bay North Queensland, spanning 26 years from a variety of literature sources and this thesis. a) was sampled in 1969 (Birch 1975); b) was sampled in 1984 (Lanyon 1991); c) this thesis, survey data for *Halophila ovalis* locations sampled in 1994 (Chapter 3); d) this thesis, experimental nutrient enhancement data including samples subjected to fertiliser additions during the senescent season sampled in 1995 (Chapter 5); and e) this thesis experimental nutrient enhancement data including sampled subjected to fertiliser additions during the growing season sampled in 1995 (Chapter 5). Each box represents the range of leaf tissue nutrient concentrations obtained from the literature or in this thesis from the minimum value to the maximum value recorded, with the cross bar representing the average of all values. Background lines represent the trends in fertiliser application in the Burdekin River catchment since 1925 (adapted from data in Pulsford 1996), for both nitrogen (N, pale) and phosphorous fertilizer (P, dark).



Conceptual diagram of controls and key processes limiting growth between seasons of intertidal *Halophila ovalis*.

Figure 6.3 A conceptual diagram of the processes that form and limit growth of intertidal seagrass meadows of structurally small species in the central region of the Great Barrier Reef World Heritage Area based on the results of this thesis. During the growing season (lower panel) plants grow faster and become nutrient limited (N limitation) but have warmer temperatures and few days exposed at low tide during the day. During the senescent season, temperature is lower, there are more frequent and stronger winds causing increased turbidity and the plants are exposed at low tide during the day and may become light stressed.