UNIVERSITY OF ADELAIDE LIBRARY
21/8/05

CALCAREOUS EPIPHYTES ON MODERN SEAGRASSES AS CARBONATE SEDIMENT PRODUCERS IN SHALLOW COOL-WATER MARINE ENVIRONMENTS, SOUTH AUSTRALIA

Kirsty Margot Brown
Bsc(Hons), MSc

Geology and Geophysics
School of Earth and Environmental Sciences
The University of Adelaide

This thesis is submitted posthumously
in fulfillment of the requirements
for the degree of
Doctor of Philosophy in Geology
at The University of Adelaide

April, 2005

PREAMBLE

This is a posthumous dissertation. The author, Ms. Kirsty Brown, was tragically killed in Antarctica while the document was in the final stages of draft preparation. The manuscript herein has been prepared principally by her research supervisor, Assoc. Professor Yvonne Bone, with the help and approval of the other members of the Ph.D. committee, Professor Anthony Cheshire (University of Adelaide) and Professor Noel P. James (Queen's University, Kingston, Canada).

All field and laboratory research had been finished at the time of her death, completed drafts of the early chapters had been written, and partial drafts of the final chapters were in progress. The concluding chapter and the abstract had yet to be written.

This version of the dissertation adheres, as closely as possible, to the document that was found on her computer when she passed away. A deliberate and conscious effort has been made to not change the nature of the narrative, the flow of logic, the presentation style, or the conclusions reached. The only alterations have been to improve English grammar and expression, make sure the references and text correspond, include missing references, complete, modify, and to finish critical illustrations, so that altogether the whole document is both physically and intellectually of thesis quality. Where the text was vague or unclear it has been corrected, based on recalled discussions between Ms. Brown and her thesis supervisor, Dr. Bone.

In short, this is a clear, readable, and accessible document, but essentially unmodified from when Ms. Brown last worked on it. Ms Brown had a firm grasp of the problem being addressed, was fully aware of the current state of knowledge in the scientific literature, had completed the research she deemed necessary to solve the problem, and had formulated preliminary conclusions. Data that she had not yet incorporated into the text is presented on two CDs, as this material would have considerably enhanced the final document.

So, it is an unfinished work, but one that does, nevertheless, cover all the official requirements of a University of Adelaide PhD thesis, which are that it must:

(a) display original and critical thought
(b) be a significant contribution to knowledge
(c) relate the topic of research to the broader framework of the discipline within which it falls and
(d) be clearly, accurately and cogently written and be suitable illustrated and documented.

Dr. Yvonne Bone, Associate Professor, Supervisor
Dr. Anthony Cheshire, Professor, Co-supervisor
Dr. Noel P. James, FRSC, Professor, Co-supervisor

April, 2005

ve consent to this thesis copy of our daughter, Kirsty Brown, when deposited in the University Library, being made
ilable in all forms of media, now or hereafter known.

ned ....
Mr T Brown

6/8/05
Date

Mrs T Brown

6/8/05
Date

DEDICATION

To Friends

ACKNOWLEDGEMENTS

Directly off Kirsty's laptop computer:

"Acknowledgements
CEMMSA
To the many who assisted me with SCUBA work
Met Office - Greg House
Margareth and Anne for data, and constant companions on West Island
All my volunteer none divers helpers whilst at West and on other field trips
Parents and family
Supervisors
Friends in OZ, UK and spread over the world. - miles/rolf
Des Lord Ltd
BHP - Whyalla
Doug and Steve? - chinamens
Alex Wilks, Rob, miles rolf, Tim, has/linda/aaron/ian etc.
Doug Shearman

thanks:
To those who made it possible
To those who encouraged me to stay
To those who kept me sane
To those who urged me to finish

To all who supported me!"

From Dr Y Bone and Dr N James, to the following for their invaluable assistance with the assembling of this thesis:-

- from The University of Adelaide:
    Dr Liz Campbell, Hashim Carey, Linda Deer, Sally Edwards and Siobhan George

- from the UK:
    Dr David Barnes and the staff of the British Antarctic Survey,
    Brian Barrett (Leeds University, ex The University of Adelaide)

- and especially to Kirsty's family.

To The University of Adelaide for allowing this thesis to be submitted posthumously for examination for the degree of Doctor of Philosophy
(from Kirsty's supervisors - Ass. Prof Y Bone, Prof N James and Prof A Cheshire))

ABSTRACT

CALCAREOUS EPIPHYTES ON MODERN SEAGRASSES AS CARBONATE SEDIMENT PRODUCERS IN SHALLOW COOL-WATER MARINE ENVIRONMENTS, SOUTH AUSTRALIA.

The main aims of this research was:-

i) to assess whether the quantity of carbonate sediment produced by calcareous epiphytes contributes significantly to temperate carbonate sediments,

ii) to determine the controlling factors of the productivity of calcareous epiphytes,

iii) to assess wether calcareous epiphyte assemblages can indicate the health of modern seagrass environments, and

iv) to assess whether calcareous epiphyte assemblages can indicate palaeo-environments in the rock record.

The study was carried out along the coastline of South Australia. This area is important because it not only hosts the largest E-W trending temperate water carbonate platform in the world, but also because virtually no assessment of calcareous epiphyte productivity has been done in this region, although it hosts nearly 15,000 km^2 of seagrass.

The number of sites sampled and estimations of productivity over time, have limited previous estimations of calcareous epiphyte productivity. This study obtained samples from 20 locations, ranging from the north-west coast of Eyre Peninsula through to the region south of the Coorong, an area covering approximately 1300 km of coastline. A total of 429 quadrats (50x50 cm) were observed and sampled. The data thus obtained was used to address the aims.

A two-year data series from one site (West Island, near Victor Harbor) was used to determine the effect of seasonality. The other sites were selected to test the effect of other physical, chemical and biological parameters. Carbonate values were estimated using a separation process developed for this project, which allows the retainment of the carbonate particles. Faunal and floral assemblages information was determined by visually estimating their abundance and identity on 1600 individual blades and stems from the sites.

Positive answers were obtained for all the aims.

TABLE OF CONTENTS

Contents of the files of the CDs are listed as separate files on the CDs.

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 1

INTRODUCTION

1.1 AIMS

Modern carbonate sediments and ancient carbonate sedimentary rocks are in large part biogenic, formed by the calcareous hard parts of benthic and planktic marine organisms (Bathurst 1975, Tucker & Wright 1990). It has only recently been recognized that the calcareous benthos that grows on seagrasses in neritic marine environments contributes significantly to such deposits. There is, however, little information as to the nature and amount of sediment produced by this process. The aim of this research was to determine if the quantity of carbonate material produced by calcareous epiphytes on seagrass forms a significant proportion of the marine sediment in South Australia, a Southern Ocean-facing state of Australia (Fig. 1.1). The hypothesis that calcareous epiphytes (Fig. 1.2a, b) are an important source of sediment for temperate water carbonate provinces (Fig. 1.3), both in the present and the past, is also examined. Additionally, the project addressed whether the identification of epiphytic flora and fauna assemblages can be used to determine palaeo-environments.

1.2 RATIONALE

The hypothesis that calcareous epiphytes are important sediment producers is based on the high turnover rates of their hosts, in this case seagrass. Seagrasses (Fig. 4a, b) are aquatic monocotyledons that continuously produce new blades, whilst shedding the old blades. Calcareous epiphytes that encrust this renewable substrate are also continuously growing and being removed as the seagrass blades are shed, hence the turnover of epiphytes is greater than it would be if the host substrate were stable. To date studies of calcareous epiphyte abundances have usually been restricted by the number of localities sampled or by the number of seagrass species examined. In South Australia only one known study has taken place, at one site and on only one genus (Thomas & Clarke 1986).

The southern Australian margin has one of the largest extents of temperate seagrass anywhere in the world (den Hartog 1970, Larkum & den Hartog 1989, Kirkman & Kuo 1990, Kirkman 1997). South Australia alone is host to 9,612 km^2 of seagrass (Edyvane 1999a, b) and Western Australia is host to 22,000 km^2 (Kirkman 1997). The proximity to the largest E-W trending temperate water carbonate system in the world (James *et al.* 2001) makes southern Australia an ideal location to test whether epiphytic carbonate material can and does make a significant contribution to the sediment.

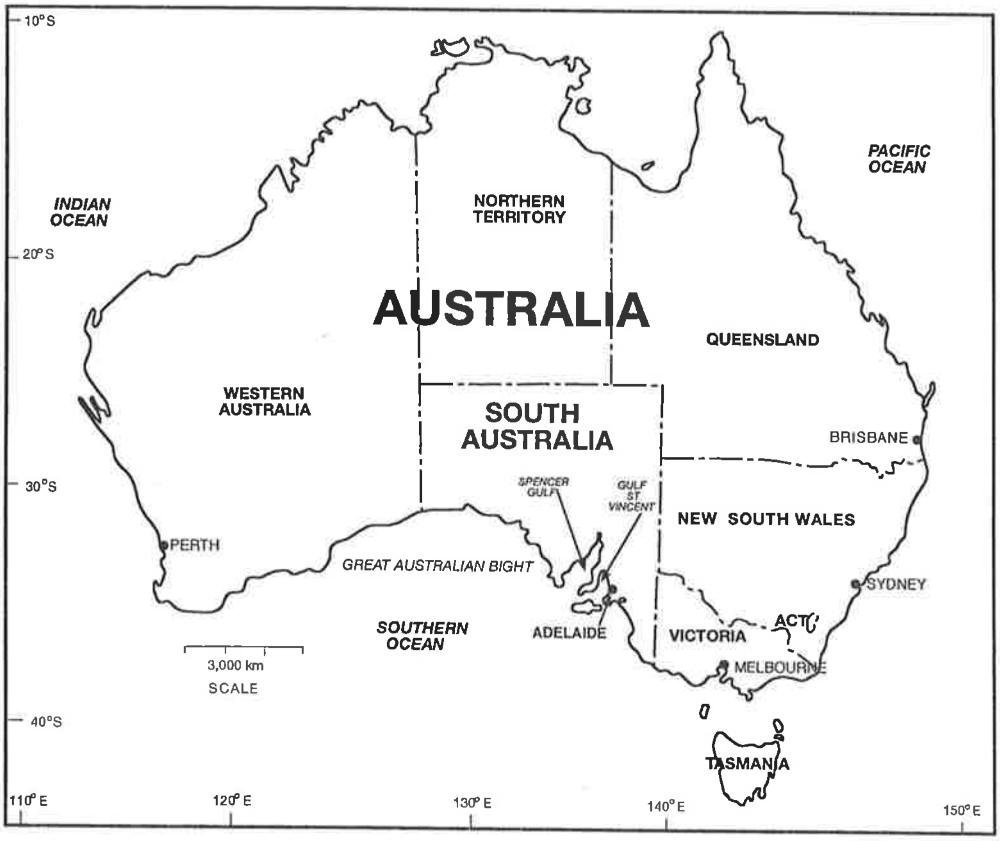


Fig. 1.1. Geographic map of Australia. The entire coastline of South Australia, apart from the two gulfs, faces the Southern Ocean. It lies between latitudes 30° S and 40° S.

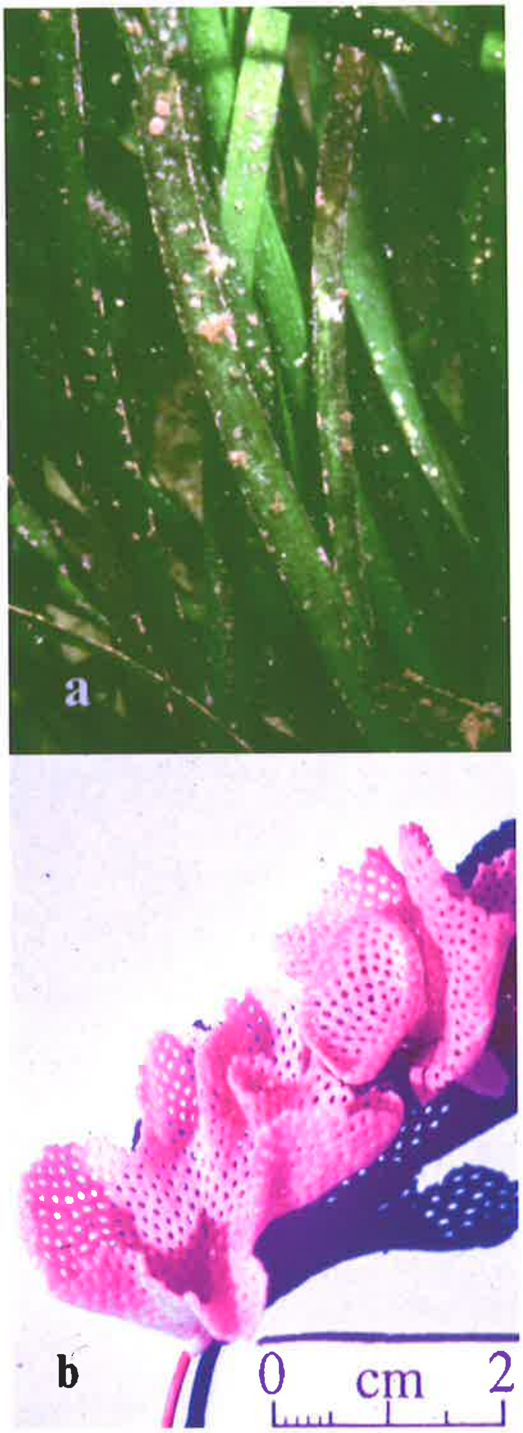


Fig. 1.2.

(a) This calcareous algae encrusting blades of *Posidonia* is an example of a calcareous epiphytic plant. All calcareous epiphytic plants belong to the Rhodophyta. Field of view is approx. 12 cm.

(b) A variety of calcareous-secreting animals, all marine invertebrates, can occur as epiphytes on seagrasses. The fenestrate bryozoan colony shown here is one example of the many bryozoan species that use seagrasses as their substrate. It is encrusting a stem of *Amphibolis*.

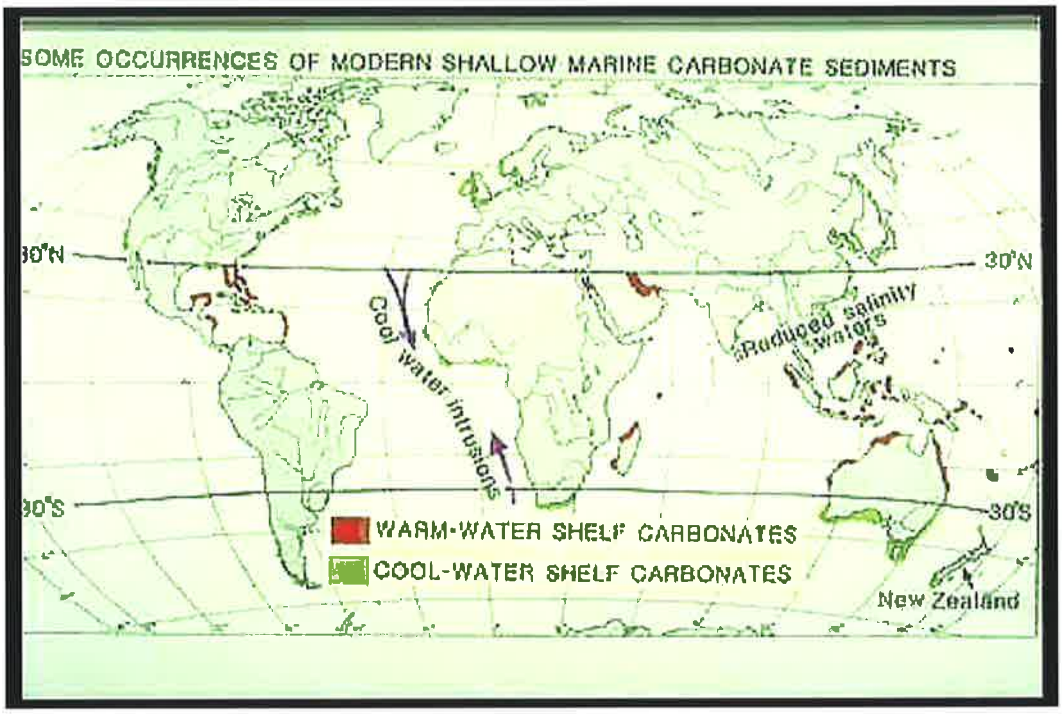


Fig. 1.3. Some of the major occurrences of warm-water and cool-water shelf carbonates are shown in the above map of the world. It can be seen that southern Australia has one of the largest provinces of modern cool-water shelf carbonates. This area is all higher than 30°S latitude. (adapted from Nelson et al. 1988)

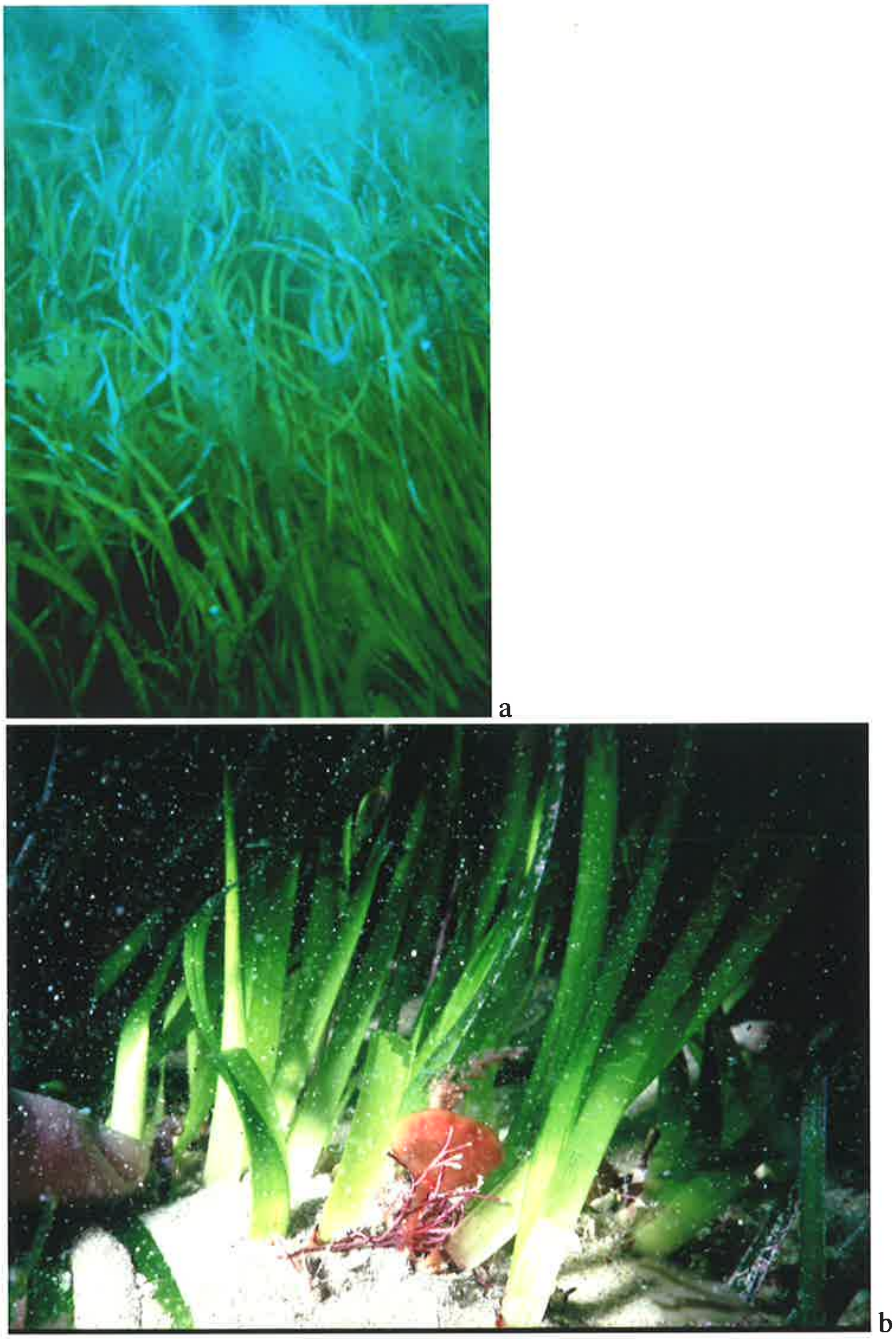


Fig. 4
Seagrasses are marine monocotyledons. They continuously produce new leaves whilst simultaneously shedding the old leaves. They are photosynthesisers, which constrains them to the photic zone. Their optimum depth is from the shoreface to ~40 m. The leaf tips of the leaves (straps) can withstand short-term exposure.

(a) *Posidonia* often grows as a tightly-packed meadow, with the tips of the leaves growing to the surface. Field of view is approx. 30 cm.

(b) The *Posidonia* leaves emerge directly from a basal sheath, which is often buried by loose sediment. The basal sheath is frequently used as a substrate by calcareous epiphytes. Seen here are examples of coralline algae and a foliose bryozoan – *Parmularia reniformis.*

(cont. over page)

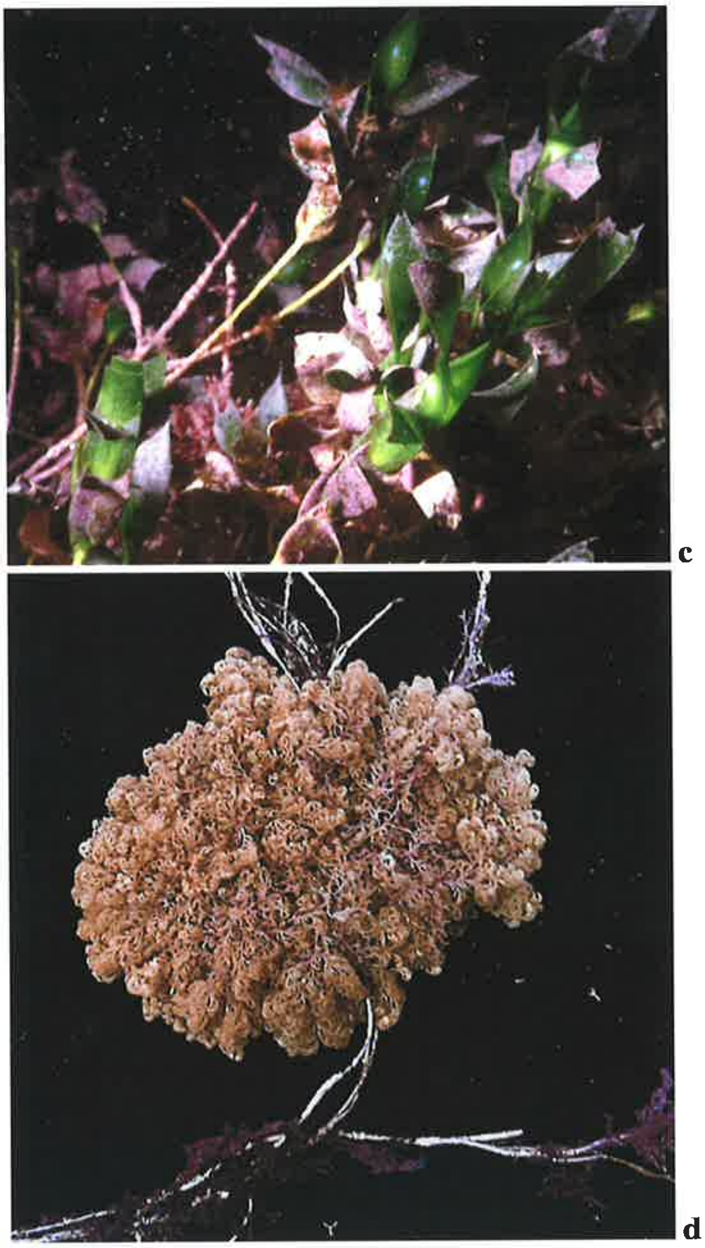


Fig. 1.4 (cont.)
(c) *Amphibolis* has wiry stems that grow from a root-mat. These stems have tufts of short leaves growing at the tips. The leaves in the example above are heavily encrusted with platy calcareous algae. Field of view is ~ 10 cm.
(d) This example of *Amphibolis* consists entirely of stems. One small section of a stem has been the settling site for a large articulated zooidal bryozoan colony – *Orthoscuticella ventricosa.* Other sections of the stems have been encrusted by calcareous algae (now white) and soft red algae.

1.3 IMPLICATIONS

Knowledge and understanding of sediment origin, rates of accumulation and seagrass species type have a number of implications, particularly for coastal management, identification of palaeoenvironments, basin development and the global carbon cycle.

1.3.1 Coastal management

It is necessary to manage a coastal system once anthropogenic changes to the coastline interfere with the natural processes. To minimise effects such as coastal erosion of cliffs and beaches it is not only important to know the wave and current patterns, but also to identify the source of the sediment. If the source of the sediment is lost, then sediment removed by natural processes cannot be replaced, i.e. the conveyor system breaks down. This can result in the overall net loss of sediment from an area and an increase in exposure to erosion. Major beach or cliff erosion is economically expensive because of the reduced numbers of tourists to beaches and the threat of property loss. An example of this process is currently occurring on the Adelaide metropolitan coastline. Sand is being displaced northward by longshore drift at a faster rate than it is being deposited. Replacement sediment is being artificially deposited on the beaches to sustain their width and aesthetic attractiveness. The cause of this net loss of sediment has been attributed to building on the adjacent coastline and seagrass loss. Reduction of seagrass reduces the stability of the sand and also potentially reduces the abundance of 'new' carbonate sediment produced from calcareous epiphytes.

Managing coastal systems also requires the ability to recognise the health of an ecosystem. Non-calcareous algal epiphytes are commonly used to monitor seagrass ecosystem health because of the apparent increase in biomass of these algae during times of increased eutrophication (Cambridge *et al.* 1986, Silberstein *et al.* 1986, Neverauskas 1987). The use of calcareous epiphytes has also been implicated. It has been speculated that high abundances of calcareous epiphytes is indicative of oligotrophic ecosystems, whereas eutrophic ecosystems have higher proportions of non-calcareous filamentous algal epiphytes (May *et al.* 1978). Current knowledge of the controls on carbonate epiphytic productivity is limited and hence the use of calcareous epiphytes to determine the state of a system is also limited. This study hopes to extend this knowledge by examining relationships between abiotic parameters and the abundance of floral and faunal assemblages of calcareous epiphytes.

1.3.2 Palaeogeography, palaeoclimatology, palaeoecology

Palaeo-environments are largely identified using analogies to similar present day environments. Recognising the origin of sediment components identifies the types of environment in which the deposition occurred. The origins of carbonate sediment components in temperate environments are varied. This project investigates the calcareous epiphyte contribution to temperate water carbonate systems.

In addition, the recognition of calcareous epiphytic species/assemblages and their sediment type in the rock record provides an excellent proxy for the presence of seagrass and their specific environment (0-40 m mean water depth - mwd). Specific calcareous epiphytes may contain further information about water temperature and salinity through their retained carbon and oxygen isotopic signatures, enabling the understanding, not just of the specific environment, but also of regional climatic processes. Species-specific calcareous epiphytes may enable the recognition of substrate seagrass genera or even species. As well as identification of environments and their changes with time, knowledge of the presence of seagrass in a particular area at a known time helps trace seagrass evolution and biogeographical distribution. Indeed, the norm is for no preservation of seagrass to occur.

1.3.3 Carbon cycle

Carbon dioxide (CO_2) is the most important greenhouse gas. It has been estimated that there has been a global increase of 30% CO_2 since the late 18th century contributing to global warming. Carbonate precipitation is important as a long-term sink for CO_2. Extending the knowledge about the origin and rate of carbonate sediment deposition in all environments increases the understanding of the global carbon cycle. It has been estimated that 48-55% of modern ocean-floor deposits and 18% of all continental sedimentary rocks are composed of calcium carbonate (defined as >30% carbonate; Lisitzin 1996, Ronov & Yaroshevskiy 1969). Oceans contain approximately 60 times more CO_2 than does the atmosphere; consequently processes in the oceans predominantly control the medium to long-term global carbon cycle (Chester 1990). It has been estimated that 5.7 billion tons of $CaCO_3$ are produced in the oceans each year (Milliman & Droxler 1996, Milliman *et al.* 1999). Carbonate flux to the ocean floor at a water depth of 1000 m has been estimated at 8 $g/m^2/yr$ (Milliman *et al.* 1999). The predominance of the carbonate production today occurs from pelagic microorganisms, i.e. foraminifers and coccolithophoroids, but benthic production is also important (Lisitzin 1996, Langer *et al.* 1997). Current estimations of global carbonate productivity do not include that from calcareous epiphytes.

1.4 EPIPHYTES

1.4.1 Definition

The term 'epiphyte' has many definitions (see CD:data). The following section describes these different uses of epiphyte and clarifies the definition that was adopted in this study. The term epiphyte is frequently used in conjunction with other terms, including epibionts, epibenthic, epiplanktonic, epifauna, epizoan and epilithic, the definitions of which will also be described.

Broadly speaking, the term epiphyte is not only a noun but also describes the relationship between an encrusting organism and its host. Confusion arises from whether the author was using the term to describe the marine or terrestrial realm, the encrusting organism or the host. The three most widely used descriptions of the term are outlined below.

- An animal or plant that lives attached to a plant (Harlin 1980, Borowitzka & Lethbridge 1989, Russel 1990, Frankovich & Zieman 1994, Hageman *et al.* 1996, Womersley 1984, 1987, 1994a, b, 1996).
- Plants that are attached to another substrate - animal, plant or a non-living object. This definition usually refers to terrestrial plants such as orchids, ferns, and members of the pineapple family. (Encyclopaedia Britannica Inc. 1998, Turner 1982).
- Plants that are attached to plants (Friday & Ingram 1985, Lawrence 1989, Taylor 1990, Keough & Jenkins 2000, Issacs *et al.* 1996, Jernakoff *et al.* 1996, English *et al.* 1997).

The latter is probably the most widely used, but incorrect, definition. If this definition is accepted in the marine realm then there are no true calcareous epiphytes because there are no true calcareous plants that attach themselves to other plants (coralline algae are members of the Protista Kingdom, not Plantae).

If the term is used to describe the attaching organism, then the well-established term epilithic becomes obsolete. The direct translation is epi- (επι) = on and –phyte (φυτον) = plant (Barkman 1958, Turner 1982). Bearing this in mind, it is more parsimonious to accept that the definition refers to the substrate upon which the organism or plant lives, i.e. the host plant. The host plant has been termed 'phorophyte' (Oschner 1928 cited in Barkman 1958), - or 'basiphyte' (Dawes 1998).

Other related terms have also had multiple definitions (Table 1.1), but using the above argument, the following definitions are recommended.

Table 1. 1 A range of definitions in the literature for organisms that can be epiphytic. i.e. live as epiphytes.

Epifauna	‘Organisms which live attached to another, larger organism’ (Whitten and Brooks, 1972).
	‘Living on seafloor or on rocks or seaweed’ (Clarkson, 1993).
	‘Animals living on the sea floor, soft sediment, rocks or vegetation’s (Mckerrow, 1986).
	‘A fauna of animal organisms that have grown upon the hard shell of a host animal ie brachiopods, molluscs, echinoids, bryozoans, serpulids, barnacles The organisms themselves are epizoans (epizoic organisms)’ (Challinor, 1986)
	‘Animals living on the surface of the mud at the base of the seagrass (sessile communities on the blades of the seagrass)’ (King *et al.*, 1991).
Epibionts	‘Growing on the extension of living organisms living on a surface the of sea bottom’ (Henderson’s dictionary of biological terms, Longman scientific and technical U.K. Lawrence 89).
	‘Attaching to the surface of substratum’ (Taylor, 1990).
Epibenthic	‘Larger mobile animals that are loosely associated with seagrass beds rather then individual shoots’ (Keough & Jenkins, 1995).
Periphyton	‘microalgae (diatoms and microscopic filamentous forms), algal propagules, bacterial, microfauna and particulate material found in the mucus-like layer that commonly coats seagrass leaves’ (Jernakoff *et al* ., (1996).

- Epifauna - organisms upon animals (also referred to as epizoan) (Sladeckova 1962, Thomas 1978, Taylor 1990, Womersley 1994a, b, Encyclopaedia Britannica Inc. 2000).
- Epibionts - organisms upon animals and/or plants.
- Epilithic - organisms upon rocks (Womersley 1994a, b).
- Epibenthic - organisms upon the seafloor.
- Epiplanktonic - organisms upon floating objects (e.g. driftwood).
- Epigenous – growing upon (but necessarily firmly attached to) a substrate (Womersley 1994a, b).
- Compound epiphytism – growth not directly on e.g. seagrass, but on an early epiphyte that is attached directly to the host (Ducker & Knox 1978, Ducker 1979 cited in Johansen 1981).

The following section gives a detailed description of the implications of epiphytes as they are used in this study.

1.4.2 Calcareous epiphyte species type

Epiphyte is a broad term; it therefore refers to all species that conform to that definition. Nevertheless, only those marine organisms that **precipitate calcareous hard skeletal parts** and fall under the definition of an epiphyte were considered for this project, i.e. coralline algae, bryozoans, foraminifers, serpulids, spirorbids, ostracods and bivalves. Phorophytes are not restricted to the phylum Plantae and also include Chlorophyta (green algae), Phaeophyta (brown algae) and Rhodophyta (red algae/seaweed). This project concentrated only on seagrasses.

1.4.3 Calcareous epiphyte mobility

The question as to whether epiphytes need to spend their entire lives attached or not in order to conform to the definition is unresolved. Frankovich & Zieman (1994) consider that complete production must occur whilst still attached, so mobile gastropods and benthic foraminiferas, which are able to move between plants, are excluded. Alternatively, it is possible to distinguish two types of epiphytes: holo-epiphytes, which remain attached for their whole life cycle and hemi-epiphytes, which are only attached for part of their life cycle. Organisms that remain on the plant long enough to produce a carbonate skeleton that is entirely produced whilst on that plant and is left behind after the organism moves on or the plant dies, were included in the study. This extends the study to include certain benthic foraminifer species and potentially some ostracod species. Due to the necessity for the extensive examination of the life cycles of species to determine whether they are holo- or hemi- epiphytes, some species may not be recognised as true epiphytes by other researchers.

1.4.4 Host and epiphyte relationship

Epiphytes are defined as being non-parasitic. Penetration into the dead outer tissue has been observed. For example, Ducker *et al.* (1977) showed that a non-algal epiphyte (species not identified) had thread like processes penetrating the cuticle of an *Amphibolis antarctica* stem. These processes may not only aid attachment, but also may be used to exchange nutrients (Ducker & Knox 1978). This relationship is termed alleloparasitic, as it is believed that nutrient exchange is mutualistic (Ducker *et al.* 1977). These organisms would be excluded with strict use of the definition. For this reason, Barkman (1958) added the phrase "living tissues" to the definition. Those that do penetrate the outer tissue have been termed amphiepiphyte (Dawes 1998). Dawes (1998) used the term holoepiphytes for those that do not penetrate the tissue, but for this study, this term will be used to define the epiphyte life cycle (see above). It is impossible to determine the true relationship without thin sectioning or other detailed studies of each species, which is outside the scope of this study. Hence this project assumed that the relationships were not parasitic.

1.4.5 Epibionts

Epiphytic organisms may also be found attached to other substrates, i.e. they may be epibionts and/or epilithic. Those epiphytes that are not restricted to plants are termed facultative epiphytes. This study assumes that the recruitment on to seagrass is purely opportunistic (Barkman 1958). Those organisms that are restricted to growing attached to plants are termed obligate (Barkman 1958). Facultative and obligate species were included in this study.

1.4.6 Encrustation after host death

Are organisms still epiphytic if they attach themselves after the host has died? Taylor (1990) states that the epiphytes should be living when the epiphyte attaches itself. This definition was adopted for this project and only living seagrass plants were collected for this reason.

1.4.7 Summary of the definition of an epiphyte

An epiphyte is an organism, (plant or animal) which, for most of its life (if not the entire), is attached to the living outer tissues of a plant. It does not draw water or food from the living tissue.

It is not always possible to know which organisms conform strictly to the above definition without detailed studies of each individual organism. Therefore, for practical purposes the following assumptions have been made:

- All calcareous organisms that are found living on, but which are not obviously motile (e.g. gastropods), and have spent the dominant part of their lives attached to the seagrass are included as epiphytes.
- None of the epiphytes utilise the seagrass for any other purpose than as a substrate.

1.4.8 Consequences of host and epiphyte relationship

The definition of an epiphyte includes the concept that it is non parasitic. Some epiphytes cause indirect damage to the plant by shading the photosynthetic surface. Light reduction results in lower primary productivity of the plant and may thus reduce the depth to which the plant can survive (see CD:data). Light reaching the blade surface can be reduced by up to 50-82%, depending on epiphyte abundance and species type (Silberstein 1985, Silberstein *et al.* 1986, SMCWS 1996, Masini *et al.* 1990, Gordon *et al.* 1994). These values are for non-calcareous epiphytes and may be different for calcareous epiphytes. Some invertebrates, e.g. the bryozoan *Membranipora* (Fig. 1.5) are translucent to transparent whilst alive and hence do not reduce the light availability to the same extent (Wing & Clendinning 1971).

Epiphytes can also be detrimental to growth simply by their abundance (Hayward 1974, Silberstein 1985). They reduce leaf flexibility and increase drag, which, during high wave action, may result in the premature shedding of the leaf. The surface area that the epiphytes occupy diminishes the surface area available for oxygen and phosphorous exchange (see discussion below). Patriquin (1972) noted that breakage of *Thalassia* blades encrusted by epiphytes appeared to be mainly as a result of the decay of the leaf tissue beneath the epiphytes.

The general consensus is that epiphytes utilise the host purely for substrate. There is some evidence, however, that is contradictory. Eacott (2000) indicates that there are significant differences in stable carbon and oxygen isotope ratios for specific epiphytes from different host types (seagrasses vs. inorganic objects). This suggests that there are chemical interactions between host and epiphyte. There is also evidence to suggest that organic carbon (nitrogen & phosphate) is exuded from the blade surface into the water column (Harlin 1971 cited in Mann 1982, Kirkman *et al.* 1979, Ogden 1970 cited in McRoy & Hellferich 1980, Ducker & Knox 1978, Lobban & Harrison 1994). These nutrients are an additional source for epiphytes to utilise, which would otherwise be absent. In some cases, algal epiphytes have

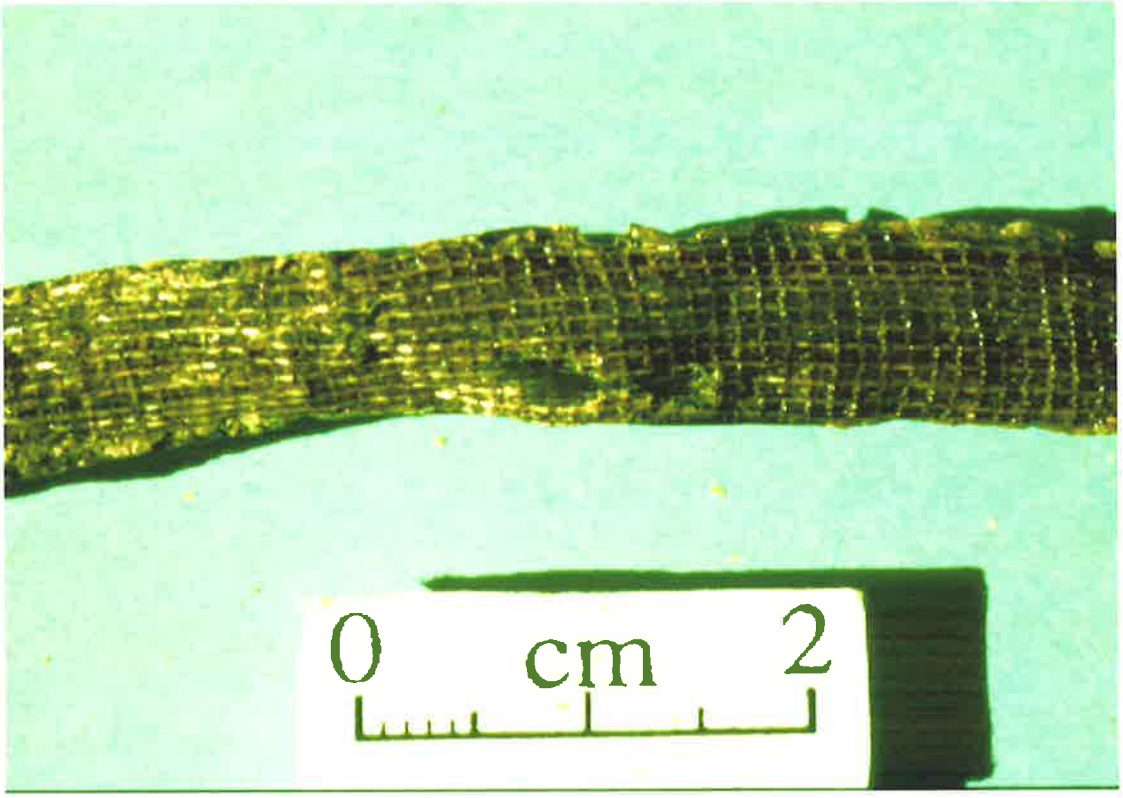


Fig. 1.5
A blade of *Posidonia* encrusting with a colony of the bryozoan, *Membranipora*. Adaptation of some members of the bryozoan family to which this species belongs, to an external skeleton that has little calcareous material has enabled the bryozoan to use the seagrass as its substrate without any detrimental effect on the seagrass, i.e. no reduction in photosynthesis. The frontal and basal walls of the bryozoan are transparent and composed of chitinous protein. The walls adjoining zooids are very thin sheets of translucent intermediate Mg calcite. Other genera with the same capabilities include *Thairopora* and *Conopeum.*

been shown to have connective tissue to the host plant to enable nutrient exchange (Ducker & Knox 1978). Brix & Lyngby (1985 cited in Jernakoff *et al.* 1996) have since shown that the studies measuring N & P exudation from leaf blades had experimental artefacts producing excessively high values. Also, experiments using artificial seagrass strips report that many of the encrusting flora are identical to those on neighbouring seagrass, indicating that they use seagrass only as an attachment surface (Silberstein 1985, Shepherd *et al.* 1989). Alternatively, it has been suggested that some epiphyte/host relationships have a mutualistic exchange of nutrients (Ducker & Knox 1984). One mechanism that might lead to an exchange in nutrients is by the reduction or disturbance of the micro-layer by the feeding action of the ciliates of bryozoans (McKinney & Jackson 1989). Further detailed study is clearly required to truly understand the biological processes operating in the epiphyte/host relationship.

1.4.9 Previous calcareous epiphyte studies

The first studies evaluating the quantity of carbonate from epiphytes were carried out by Land (1970), Patriquin (1972) and Smith (1972). Nelsen & Ginsburg (1986) concluded that epibionts (epiphytes) could account for the entire high magnesium calcite and aragonite mud-sized fraction within Eastern Florida Bay. There are only two other studies of epiphyte carbonate productivity in tropical waters (Bosence 1989, Frankovich & Zieman 1994).

The first study in temperate waters was carried out on the mainland shelf of Southern California (Smith 1972). The data on the quantity of epiphytic material found was, however, not published. A number of studies although mainly based in Western Australia, covered other areas as well (Table 1.2). Thomas & Clarke (2002) identified the sedimentology and morphology of seagrass beds in Holdfast Bay (Fig. 1.6), South Australia, and deduced that calcareous epiphyte carbonate was in the range of 0.41-150 g/m^2/yr. Since then only one other study of calcareous epiphytes has taken place in South Australia, but no quantitative data was included (Tang, unpublished data).

Values documented in these studies are difficult to compare because data was obtained by different methods (Chapter 2) and also used different definitions of an epiphyte (Table 1.1). All of these studies, despite this, indicate that calcareous epiphytes are important as sediment producers.

Other productivity studies of non-calcareous epiphytes have examined their importance as

Table 1.2. Summary of previous studies evaluating carbonate production by calcareous epiphytes.

Location	Plant type	Epiphytic taxa	Method	$CaCO_3$ g/m^2/yr	Author
		TROPICAL			
Discovery Bay, Jamaica	*Thalassia testudinum*	Coralline algae, serpulids	Biological	40-180	Land (1970)
Barbados	*T. testudinium*	Coralline algae, foraminifers, bryozoans	Biological	2800	Patriquin (1972)
	Seagrass			134	Webster & Parnankap (1977)
Papua New Guinea	*T. hemprichii*		Biological	14.2 – 71.6	Frankovich & Zieman (1994), adapted from Heijs (1984, 85)
Eastern Florida Bay	*T. testudinum*	Coralline algae, Spirorbids	Biological	118 ±44	Nelson & Ginsburg (1986)
Largo Sound, Florida	Seagrass	1 foraminifer species *Arcaias angulatis*		60	Hallock *et al* (1986)
Florida	*Thalassia*	Coralline algae, bivalves foraminiferas, spirorbids,	Biological.	55-1042	Bosence (1989)
San Salvador	*Thalassia* sp.			136-304	Armstrong (1989)
Florida Bay	*Thalassia testudinum*	Coralline algae, spirorbids, bivalves	Biological	1.9 to 282.7	Frankovich & Zieman (1994)
Bucanon & Russel Bank, Florida Bay	*Thalassia testudinum*	Epiphytes + other benthic fauna	Chemical	<219	Yates & Halley, 2001
		TEMPERATE : WESTERN AUSTRALIA			
Eastern Shark Bay,	Seagrass meadow	Total carbonate production of meadow	Chemical	120	Smith & Atkinson (1983)
Warnbro Sound	*Posidonia sp.*		Chemical	2,200	Searle (1984)
Shark Bay	Seagrass		Geological	1700	Searle (1984)
Marion Bay	*P. australis*			1420	Horner, 1987
Shark Bay	*P. australis*	Coralline algae, bryozoans, foraminiferas, gastropods, & non-calcareous algae	Biological	35-526 (Salinity dependant)	Walker & Woelkerling, 1988

Table 1.2 cont'd

Location	Plant type	Epiphytic taxa	Method	$CaCO_3$ g/m/yr	Author
Princess Royal Harbour	i)*A. antarctica,* ii)*P. australis* iii) *P. sinuosa*		Biological	i) 60 ii)70-117 iii)40-60	Walker *et al.* (1991)
Rottnest Island & Warnbro Sound	*A. antarctica*	Coralline algae	Biological	150-220	Sim (1991)
Owen anchorage	i)*A. griffithii* blade ii)*A. griffithii* stem	Coralline algae + others	Biological	i) 444.5 ii) 166.0	Sim (1998)
Owen anchorage	*P. coriacea*	Coralline algae + others		228.1	Sim (1998)
Owen anchorage	*Heterozostera tasmanica*	Coralline algae + others		347.8	Sim (1998)
Eastern Shark Bay,	General		Geological	400	Logan quoted in Lord, (1998)
Success Bank, Owen anchorage	*i) P. coriacea* ii) *H. tasmanica* iii) *A. griffithii*		Biological	i) 228 ii) 348 iii) 611	Lord (1998)
Success Bank, Owen anchorage	i)*A. griffithii* blade ii)*A. griffithii* stem iii) whole plant	Coralline algae	Biological	i) 872 ii) 142 iii) 90-224	Lavery (2000)
Warnbro Sound	i) *P. australis*	Not including foramanifers	Biological	Av. 151.8 (37-209.8) 2.56mwd	Cambridge pers. comm. (2002)
Warnbro Sound	*P. sinuosa*	Not including foramanifers	Biological i) 2.5mwd ii) 0.5mwd	i)20-277(av77.5) ii)65.8-408.8 (av. 317.7)	Cambridge pers. comm. (2002)
Shoalwater,	*P. sinuosa*	Not including foramanifers	Biological 4mwd	149.3 (32.8-255.6)	Cambridge pers. comm. (2002)
		TEMPERATE SOUTH AUSTRALIA			
Holdfast Bay,	*Posidonia* sp.	-	random collection.	0.41 - 150	Thomas & Clarke, (1986)

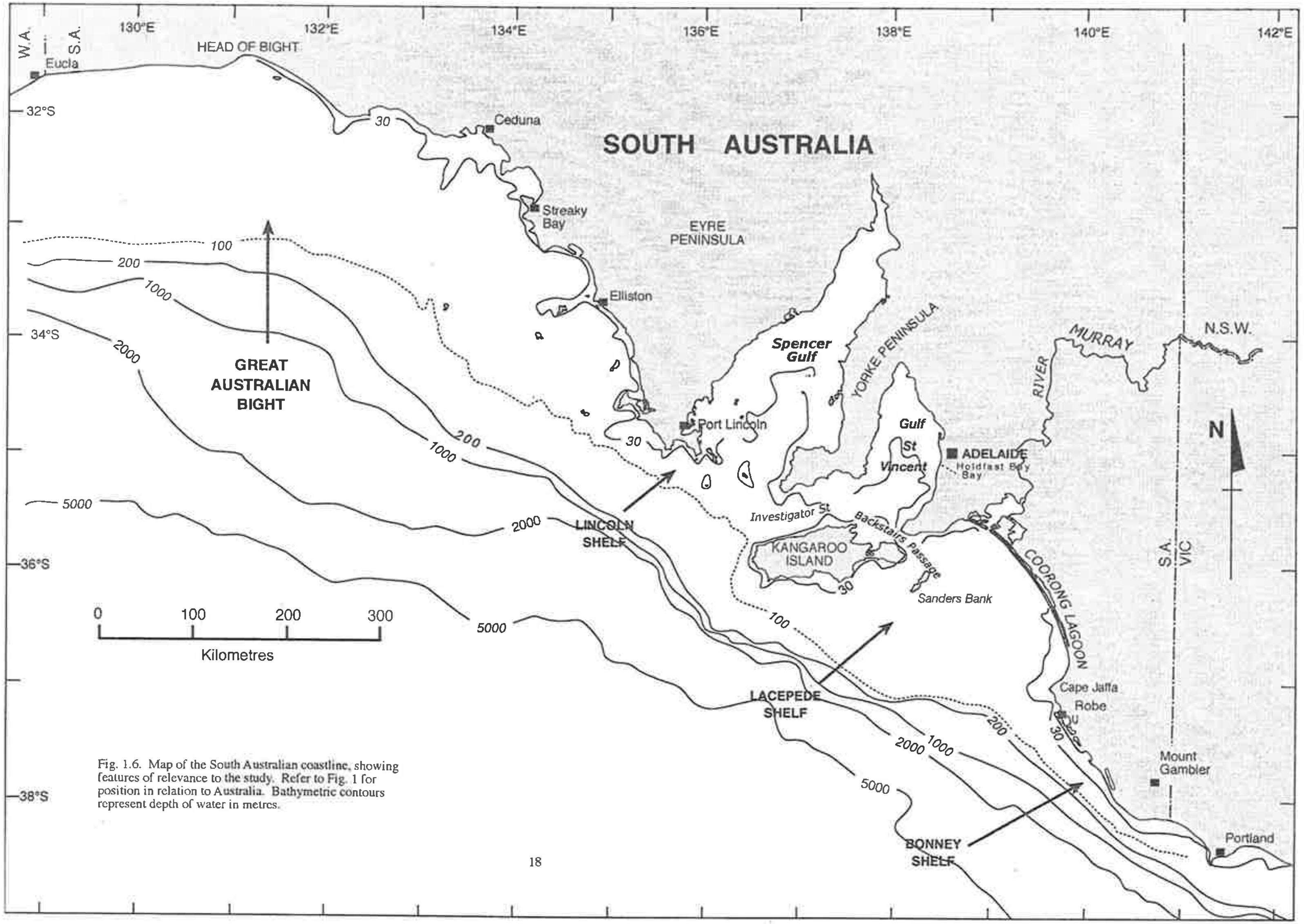


Fig. 1.6. Map of the South Australian coastline, showing features of relevance to the study. Refer to Fig. 1 for position in relation to Australia. Bathymetric contours represent depth of water in metres.

primary producers, (e.g. Penhale 1977, Kirkman *et al.* 1979, Heijs 1984, Brouns & Heijs 1986, Mazella & Alberte 1986, Masini *et al.* 1990, Silberstein *et al.* 1986, Kendrick *et al.* 1998a, b, Cebrián *et al.* 1999, Ralph & Gademann 1999, Bologna & Heck 1999, Reyes & Sanson 2001). Some of these studies found that primary productivity from algal epiphytes can be twice that of their host (e.g. Ralph & Gademann 1999, Masini *et al.* 1990) or up to 50% of the total seagrass system (Penhale 1977, Morgan & Kitting 1984, Mazzella & Alberte 1986) and all studies concluded that they were important.

Other research has involved the estimation of the role of epiphytes in seagrass dieback, (e.g. Bulthuis & Woelkerling 1983a, b, Neverauskas 1988a, b, Cambridge *et al.* 1986, Silberstein *et al.* 1986, Shepherd *et al.* 1989). Colmenero & Lizaso (1999) showed that the bryozoan *Calpensia nobilis* that grows attached to the rhizomes increased both rhizome and blade growth, presumably as a defence against encrustation. A similar mechanism was found by Dixon *et al.* (1981) who demonstrated that where *Macrocystis pyrifera* (Giant Kelp) was found encrusted with the bryozoan *Membranipora membranacea,* blade loss rates increased compared to clean plants, again thought to be a defence mechanism. Although studies of recruitment mechanisms are limited, it has been shown that both passive and active methods occur (Hunt & Scheibling 1997).

1.4.10 Calcareous epiphyte taxa

The following groups of organisms have known calcareous epiphytic species:

- coralline algae (Family Corallinaceae);
- bryozoans (Phylum Bryozoa);
- foraminifers (Order Foraminiferida);
- serpulids (Family Serpulidae);
- spirorbids (Family Spirorbidae);
- ostracods (sub-Class Ostracoda) and
- bivalves (Class Bivalvia).

The common name for each of these groups will be used throughout this thesis. Lists of calcareous and non-calcareous epiphyte species on different seagrass genera have been compiled by Ducker *et al.* (1977) (*Amphibolis* sp.), Ducker & Knox (1978, 1984), Harlin (1980), Humm (1964) (*Thalassia testudinum*) and Marsh (1970 cited in Ducker *et al.* 1977) (*Zostera*).

Fig. 1.7a a
Coralline algae often encrust seagrasses. Seen here is a crustose example, almost completely covering the *Posidonia* blade it has used as its substrate. Scale bar is in cm. Articulated corallines also commonly use seagrasses as their substrate. Four spirorbid specimens are also seen in the photo: two are encrusting the *Posidonia* whereas the other two are encrusting the encrusting coralline algae!

1.4.10.1 Coralline algae

Coralline algae (Fig. 1.7a), (Division Rhodophyta) belong to the Kingdom Protista, rather than the Plantae and are the only phototropic calcareous epiphytes (except for occasional symbiotic larger foraminiferas). The thallus (plant body) is mostly calcified, although some contain genicula (uncalcified segments between calcified intergenicula). The presence/absence of genicula can be used to broadly separate corallines into two groups - erect and encrusting respectively. Corallinaceae species found in southern Australia are described in Womersley (1994a, b).

Full identification of non-geniculate (encrusting) coralline algae can only be achieved by cross sections through the conceptacles (reproductive organs) and not by external features alone. External features can broadly identify the common species of geniculate coralline algae.

Attachment to the substrate initially occurs with the aid of mucopolysaccharides that quickly form a halo around the spores. This is followed by the development of hypothallial filaments and hypobasal calcification that cements sporelings to substrata (Steneck 1986).
(see CD:data and CD:SEM)

1.4.10.2 Bryozoans

Bryozoans (Fig. 1.7b) are small colonial filter-feeding organisms, which are mostly marine and predominantly sessile. The individual organism is known as a zooid and collectively they are known as a colony. Individual zooids are connected by skeletal tissue usually composed of calcium carbonate. Bryozoans are known to have existed since the Upper Cambrian and at particular times have been significant components of the fossil record (Clarkson 1998). A good general introduction to bryozoans is Clarkson (1998) and Bock (2001). Bock in Shepherd & Thomas (1982) provides descriptions of many common modern bryozoans from southern Australia.

Calcareous epiphytic bryozoans occur in two general morphologies; encrusting (e.g. *Membranipora membranacea*) or erect (e.g. *Triphyllozoon moniliferum*). A Mediterranean study identified 36 epiphytic bryozoans on *P. oceanica* (seagrass) blades (Hayward 1974) of which 32 were cheilostomes, one of which was host specific and 3 only which grew on plants (i.e. most were facultative). Other authors have identified 90 and 72 epiphytic bryozoan species (Harmelin 1972 & Gautier 1962 respectively cited in Hayward 1974).

Fig. 1.7b

Many different morphological forms of bryozoans are able to use seagrasses as their substrate, from flat encrusting forms to delicate erect to robust foliose et al.

The upper photo shows two colonies of articulated zooidal bryozoans encrusting a stem of *Amphibolis*. An articulated coralline alga is encrusting the end of the stem. $A1 for scale. (Photo: Y. Bone)

The lower photo shows two fenestrate bryozoans colonies encrusting *Amphibolis* stems, with the one on the left showing the section of the colony that is cemented around the stem. Scale bar is in cm. (Photo: N. James)

Encrusting bryozoans attach themselves to a substrate by secreting a bioadhesive cement on to the surface from the epithelial tip (Soule & Soule 1977). This occurs shortly after attachment and metamorphosis of the ancestrula zooid. The cement flows over the substrate and hardens quickly; this is rapidly followed by the deposition of the skeletal walls by the basal epithelium. Collectively, this area of the colony is known as the growing edge. Erect bryozoans may attach at one pinpoint location, multiple pinpoint locations or have a large surface area.

Taxonomic identification is carried out using morphological variations between bryozoan colonies at the zooid level. The most useful features include growing edge zooids, ancestral zooids and ovicells and operculum shape. (see CD:data and CD:SEM)

1.4.10.3 Foraminifers

Foraminifers (Fig. 1.7c) are single-celled protists that have external tests composed of secreted organic matter, or calcium carbonate, or agglutinated sediment grains. Benthic and planktonic foraminifers are abundant throughout the world's oceans (Brasier 1996).

Epiphytic foraminifers have been documented worldwide, although predominantly in tropical waters (Semenuik 2001) (Table 1.3). A study by Semeniuk (2001) includes tropical, subtropical and temperate epiphytic foramanifer species on *Posidonia australis*.

Three forms of attachment process have been recognised; i) "clinging" with the use of a pseudopodium, which still allows movement along the blade, ii) "adhesive" which use an organic membrane that is easily severed, and iii) "encrusting" which cement their tests via an inorganic lamina that is often calcitic (Poag 1982). Species identification is predominantly carried out using morphological features including wall structure and composition, chamber shape and arrangement, apertures and ornamentation. (see CD:data and CD:SEM)

1.4.10.4 Serpulids & spirorbids

Serpulids (Fig. 1.7d) and spirorbids (Fig. 1.7e) belong to the Class Polychaeta and are segmented coelomate worms. Serpulids and spirorbids are commonly confused taxonomically. The main taxonomic differences are the lower number of thoracic setigers (3-4) (a setiger is a segment with setae) and an asymmetrical thorax of the spirorbids, compared to 5-12 thoracic setigers and a symmetrical thorax of the serpulids. Both families produce

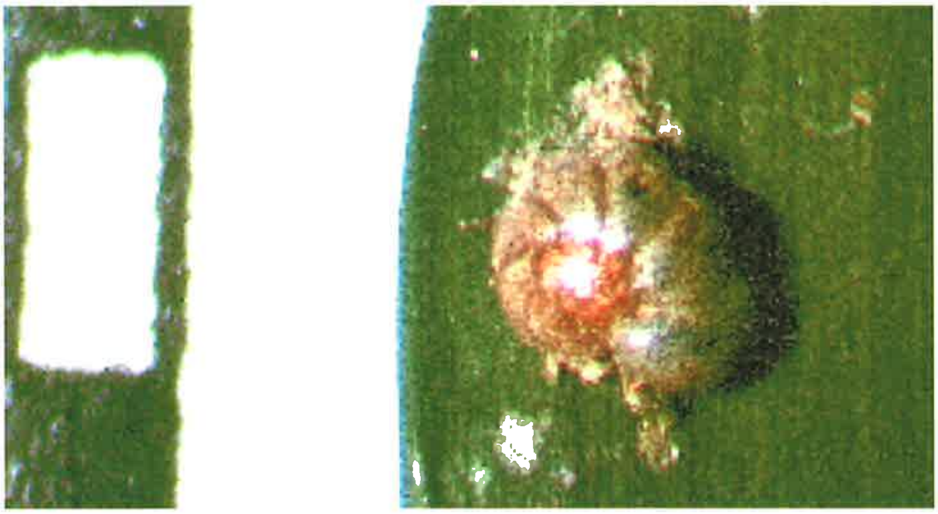


Fig. 1.7c
Foraminfers are only loosely attached to their substrate. Seen here is a living specimen of the species *Discorbi,s* on a blade of *Posidonia*. The *Discorbis* will spend its entire life on the blade, but will fall off immediately if it dies, becoming part of the underlying sediment accumulation. Alternatively, it may remain attached if the blade is shed, and passively move shorewards. Scale bar on LHS is 1 cm.

Table 1.3. Summary of previous studies examining epiphytic Foraminifera studies (**cited in* Semeniuk, 2001).

Location	**Author**	**Host**
Gulf of Naples	*Schmidt, 1953	*Posidonia*
Shark Bay, W.A.	*Davies, 1970	*P.australis* & *Cymodocea antarctica*
Abu Dhabi, Persian Gulf	*Murray, 1970	Seagrass
Barbuda, West Indies	Brasier, 1975	*Thalassia testudinum*
Jewfish Bay, Bahamas	*Steinker & Steinker, 1976	*Thalassia*
West Indian region	*Bock, 1969	*Thalassia*
Gulf of Elat, Israel	*Frenkel, 1974	
Caribbean	*Brasier, 1975	
Bermuda	Spindler, M., 1980	*Sargassum natans*
Vulcano Island, Eolian Archipel	Langer, 1993	*P. oceanica* and algal species
Medes Islands, NW Mediterranean	Ribes, 2000	*P. oceanica* & artificial substrate
Western Aus.	Semeniuk, 2001	*P. australis*

Fig. 1.7d
Serpulids are worms that live in "free-form" calcareous tubes. There are only three genera of Serpulids in South Australia, each containing one species. They can only be identified by dissection of the soft body parts. They are encrusting an oyster shell in this photo. Scale is an $A1. (Photo. from Y Bone)

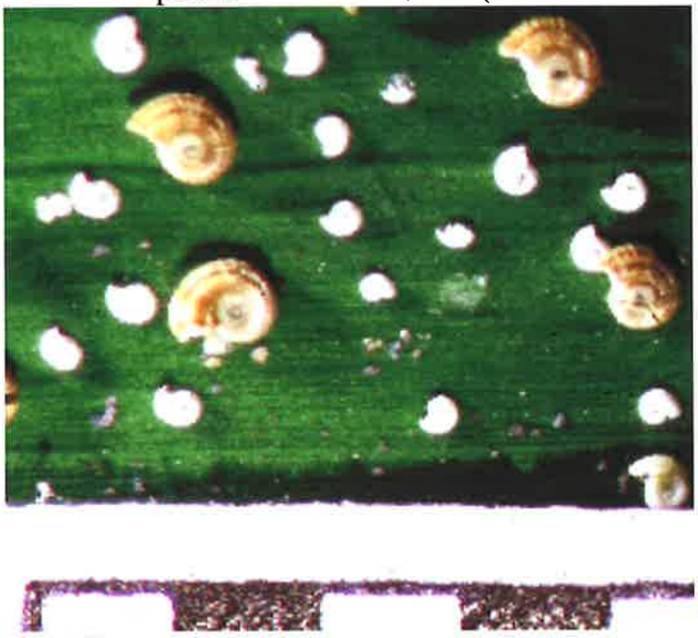


Fig. 1.7e
Various sized spirorbids encrusting a *Posidonia* blade. The scale is in cm. There are only three genera of Spirorbids in South Australia, each containing one species. They can only be identified by dissection of the soft body parts. The calcareous tube is always tightly coiled. See also Fig. 1.7a.

calcareous tubes, although spirorbids tend to be smaller and coiled and serpulids tend to be larger and uncoiled. Identification can, to a certain extent, be carried out using the morphology of the calcareous tubes although tube shape can change due to different substrate types and environmental effects. For accurate identification soft body parts are required. A good introduction to polychaetes of southern Australia can be found in Shepherd & Thomas (1982) and Knight-Jones & Knight-Jones (1973). (see CD:data and CD:SEM)

1.4.10.5 Ostracods

Ostracods, (Fig. 1.7f) from the Phylum Crustacea, are described as laterally compressed crustaceans enclosed within a protective shell (Brasier 1996). Ostracods occupy numerous niches, both marine and freshwater and even in humid forest soils (Brasier 1996), however, they are not common as epiphytes. They can be identified by their valves alone, but more accurate identification should be made using soft-body parts. Whether there are any true epiphytic ostracods is inconclusive, as no studies contain much level of detail to this end.
Many ostracod species are closely associated with seagrass, but because of their small size they are not considered to be significant sediment contributors. (see CD:data and CD:SEM)

1.4.10.6 Bivalves

Bivalves (Fig. 1.7g) usually have inequilateral calcareous shells united by a dorsal hinge (Clarkson 1998). Some bivalve species have the ability to permanently attach themselves to substrates, e.g. oysters, but few are known to attach themselves to seagrasses. The only known calcareous epiphytic bivalve is *Electroma georgina*, a member of the oyster family (Edgar 1997). The other significant class of Mollusca, gastropods are common amongst seagrass, but there are no recorded epiphytic species. (see CD:data and CD:SEM)

1.4.11 Calcareous epiphyte summary

The definition of a calcareous epiphyte is broad but for the purposes of this project an epiphyte is:

an organism, (plant or animal) that secretes a calcareous skeleton and that, for most of its life (if not its entire life), is attached to the living outer tissues of a plant: it is assumed, until proven otherwise, that it does not derive food or nutrients from the host.

There have been 10 previous studies of calcareous epiphytes in tropical environments and 15 studies in temperate regions. All but one of the temperate studies has taken place in Western Australia or New South Wales, Australia (Table 1.2). Results of previous studies indicate that productivity from calcareous epiphytes is high and so the potential importance to carbonate

Fig. 1.7f.
The external and internal views of an ostracod valve. Scale is the same for each SEM photograph. Ostracods are also only loosely attached to their substrate. An ostracod may spend its entire life on the blade/leaf of seagrass, but will fall off immediately it dies, becoming part of the underlying sediment. Occasionally, it may remain attached when the leaf is shed, and passively be carried shorewards.

Fig. 1.7g
Electroma georgiana is the only mollusc in South Australia that uses seagrass as its substrate. The common name of the bivalve is "Butterfly Shell", because of the shape, transparency and light weight of the valves. It attaches to the distal part of the blade of *Posidonia.*

sediment production is profound. This in turn, has implications for coastal management, palaeo-environmental analysis, and the global carbon cycle.

1.5 SEAGRASSES

1.5.1 Introduction

Kingdom: Plantae
Division: Magnoliophyta
Class: Liliopsida
Subclass: Alismatidae Takhtajan

Seagrasses are flowering plants (monocotyledons) that are adapted to living completely submerged in the marine environment. Seagrasses have turnover rates that are high enough to provide a constant new substrate for epiphytes to colonise. Such rapid turnover rates and the sheer abundance of seagrasses are the basis for the hypothesis that epiphytes attached to seagrass produce significant quantities of sediment particles. Macrophytes also have high rapid turnover rates, but do not usually occur in such abundance.

1.5.2 Origin and evolution

1.5.2.1 General

Seagrasses are the only higher plants that have re-adapted to live fully submerged in the marine realm (Larkum & den Hartog 1989, Dawes 1998). There are two schools of thought about the evolutionary pathway of seagrass:

- they evolved from freshwater hydrophytes, or
- they evolved from intertidal saltmarsh-type plants (Aridis *et al.* 1993, Larkum *et al.* 1989, Arber 1920, Sculthorpe 1967, den Hartog 1970).

The arguments are derived from the biological similarity/dissimilarity between seagrass species and their terrestrial counterparts (Ducker *et al.* 1977).

It is generally accepted that the origin was from saltmarsh plants due to the following evidence:

- *Thalassodendron* and *Amphibolis* (Fig 1.2b) are the only current genera that show viviparous reproduction (a seed which germinates while still attached to the parent plant) which is a feature also shown by intertidal mangroves (Aridis *et al.* 1993, den Hartog 1970 cited in Ducker *et al.* 1977). Mangroves, however, are dicotyledons and the evolutionary pathway separating monocotyledons from dicotyledons occurred long before seagrasses evolved.

- The presence of a leaf sheath (Fig. 1.2a), which saltmarsh plants also have, but freshwater hydrophytes do not (Aridis *et al.* 1993, Larkum *et al.* 1989).
- Seagrasses have fairly complex physiology in order to cope with their environment. Present day freshwater hydrophytes exhibit reduced complexity. Hence, it is considered unlikely that seagrasses could have developed the complex physiology even in the Cretaceous.
- Several seagrass species have subcuticular cavities similar to terrestrial monocotyledonous halophytes (Barnabas 1982).

There are only a few confirmed fossil seagrass occurrences (Larkum & den Hartog 1989). The use of epiphytes as proxies for seagrass beds has been limited due to a lack of detailed studies of modern environments (Larkum & den Hartog 1989). Nevertheless, attempts have been made to use foraminifers (Brasier 1975, Wright & Murray 1972), general invertebrate assemblages (Petta & Gerhard 1977, Bretsky 1978, Baluk & Radwanski 1977, Hoffmann 1977), the remains of sirenians (dugongs) (Domning 1977, 1991, 1999), the effect of seagrass roots on neighbouring shells (Cottrell 1974) and specific fining-upward sedimentary sequences (Wanless 1981) to identify the presence of seagrass.

The oldest confirmed specimens known are Cretaceous *Thalassocharis* from the Netherlands and Germany (Voigt & Domke 1955 cited in Larkum & den Hartog 1989). *Archeozostera*, previously identified as a seagrass, has been re-identified as a terrestrial plant (Bridges & Philips 1995). It is argued that the origin of seagrass was around the margins of the ancient tropical Tethys and Paratethys Seas, bounded by Africa, Gondwana and Asia during the mid-late Cretaceous (van Keulen 1995, Larkum *et al.* 1989, Dawes 1998). By the Eocene seagrass fossil samples increase in number and diversity (*Posidonia*, *Cymodocea*, *Thalassodendron* and *Thalassia*) indicating a wider distribution (variance hypothesis), especially in the Asian-Pacific and neo-tropic region (van Keulen 1995, Larkum & den Hartog 1989).

Genetic sequencing offers an alternative method for identifying evolutionary pathways, with preliminary, phylogenetic analysis of chloroplast genomes indicating that modern seagrasses are derived from 3 separate evolutionary events (Waycott & Les 1996).

1.5.2.2 Australia

The period at which seagrass arrived in Australia is debatable. It has generally been considered that the collision of Australia with Asia in the Miocene and the overall lower sea levels during the Pliocene allowed extensive interchange of biota in the tropics, correlating with the arrival of seagrass in Australia (Larkum *et al.* 1989). There is some evidence, however, to indicate the presence of seagrass in the Eocene of South Australia (James & Bone 2000). Today Australia hosts the highest species diversity of seagrass on any continental shelf in the world and a high proportion of the population is endemic (Aridis *et al.* 1993, Johnstone 1982, Walker & Prince 1987 cited in Larkum & den Hartog 1989). There are two endemic genera (*Amphibolis* and *Heterozostera*) and 18 endemic species, 16 of which are restricted to temperate regions (Aridis *et al.* 1993, Kirkman 1997, Larkum & den Hartog 1989). The cause of this endemism is believed to be higher sea-levels during the Quaternary, isolating the Australian fauna and flora from the rest of the world. Whether the endemism is a result of species evolution in Australia, or represents relict species, is uncertain due to the lack of fossil specimens.

1.5.3 Current distribution

1.5.3.1 Global distribution

Today there are 12 genera and less than 70 known species that are distributed globally, except for Antarctica (Butler & Jernakoff 1999, Larkum & den Hartog 1989). Seven of these genera are found predominantly in the tropics: *Halodule, Cymodocea, Syringodium, Thalassodendron, Enhalus, Thalassia* and *Halophila*. Exceptions to this environmental constraint are *Halophila ovalis* which is eurythermic; *H. australis* which is restricted to temperate waters; *Cymodoceea nodosa*, *C angustifolia* and *Thalassodendron pachyrhizum which* are restricted to subtropical or warm temperate waters. The other five genera are confined to temperate waters: *Zostera, Phyllospadix, Heterozostera, Posidonia* and *Amphibolis* (Larkum & den Hartog 1989). Four species of the predominantly temperate genus *Zostera* also extend into tropical waters (Larkum & den Hartog 1989).

1.5.3.2 Australia

The species distribution is predominantly temperature dependent and the cut-off of tropical (>20°C) to temperate (<20°C) species being approximately 30°S near Geraldton on the west coast and 25°S on the east coast near Hervey Bay (Fig. 1.8; Larkum & den Hartog 1989, Butler & Jernakoff 1999). The difference in latitude on the east and west coasts is almost certainly to do with the presence of the Leeuwin Current (Fig. 1.9). The Leeuwin Current is derived in the Indonesian through-flow region and transports warm water down the west coast (Fig. 1.9, 1.1; Rochford 1984, 1986). The East Australian Current, derived from the Coral

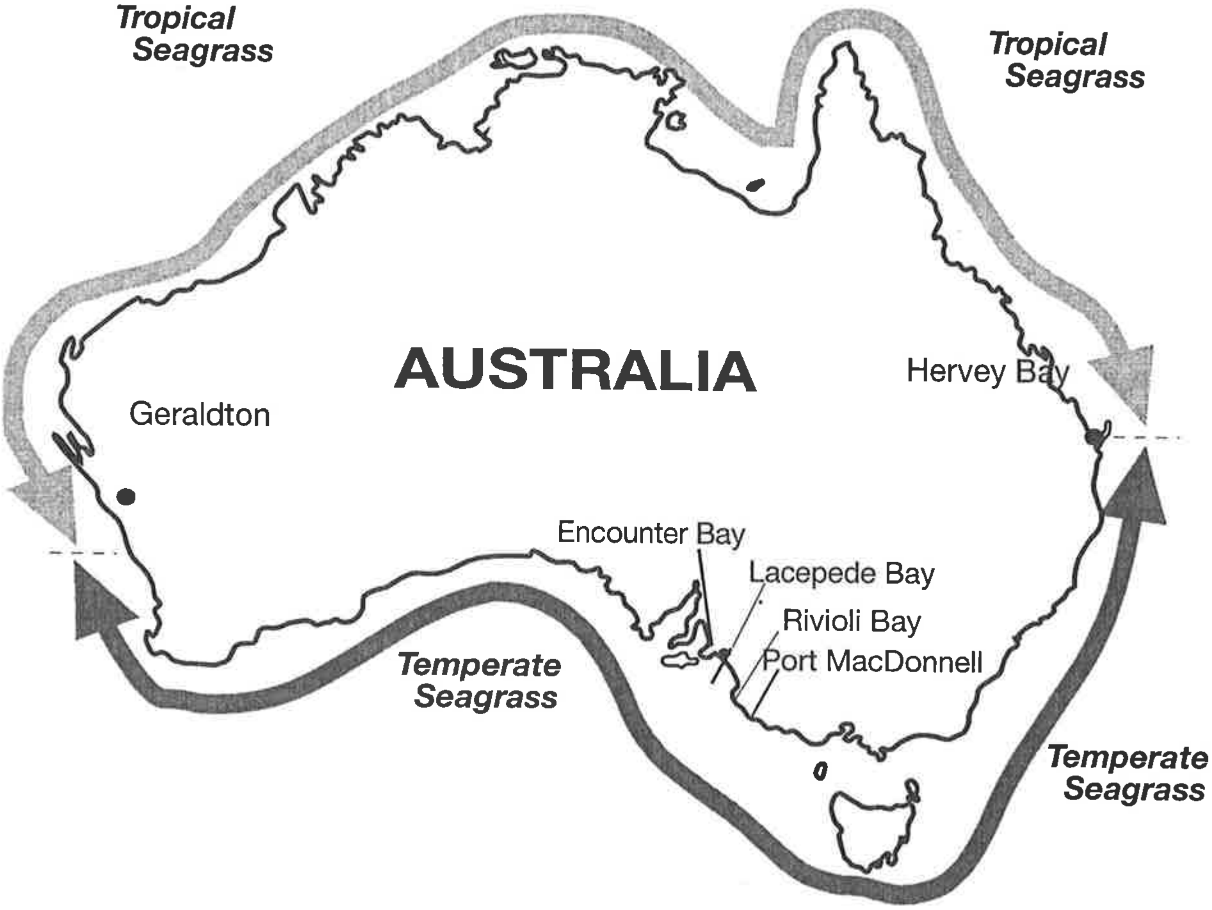
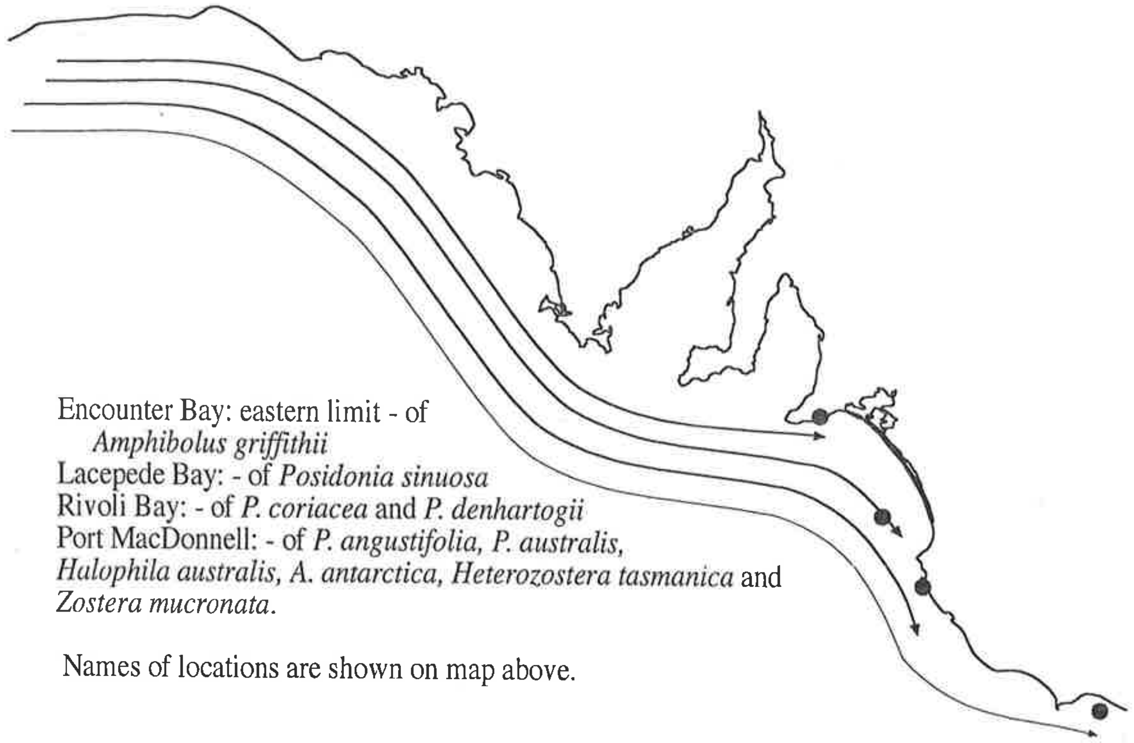


Fig. 1.8. Australian coastline, showing distribution of tropical and temperate seagrass above (adapted from Butler and Jernikoff 1999) and eastern limits of common South Australian seagrasses, sourced from the west, below.



Encounter Bay: eastern limit - of
Amphibolus griffithii
Lacepede Bay: - of *Posidonia sinuosa*
Rivoli Bay: - of *P. coriacea* and *P. denhartogii*
Port MacDonnell: - of *P. angustifolia, P. australis, Halophila australis, A. antarctica, Heterozostera tasmanica* and *Zostera mucronata*.

Names of locations are shown on map above.

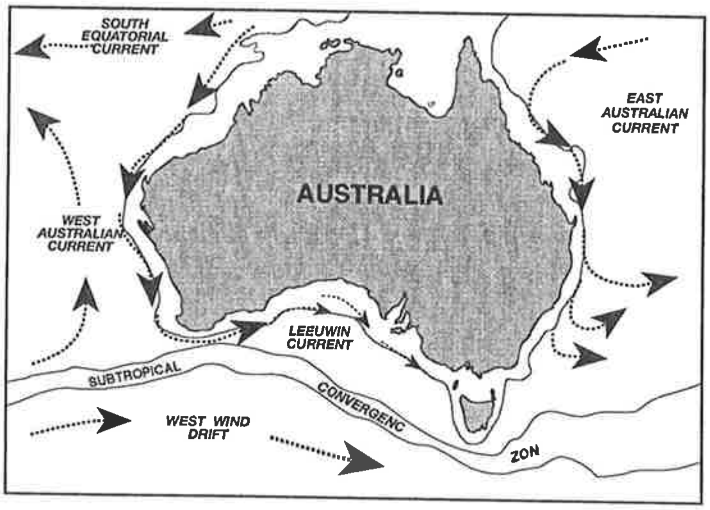


Fig. 1.9. Map of Australia with the main currents shown (adapted from James et al. 1992)

Sea, also brings warm waters down the east coast (Fig. 1.9, 1.1; Zann 2000), but does not seem to have such a pronounced effect on seagrass distribution (Fig. 1.8). The tropical seagrasses that occur in Australia belong generally to the Indo-Pacific tropical group.

Larkum and den Hartog (1989) divided the temperate seagrass species into 5 groups:

- restricted to the west coast and not reaching the Great Australian Bight (GAB; Fig. 1.1): *Cymodocea angustata*;
- restricted to the west coast and the GAB (and in some cases, Victoria; Fig. 1.1) (*Amphibolis antarctica, A. griffithii, Posidonia sinuosa, P. angustifolia, P. coriacea, P. denhartogii, P. kirkmanii, P. ostenfeldii, P. robertsoniae, Thalassodendron pachyrihizum, Zostera muccronata*);
- present in all temperate regions including the east coast (*Heterozostera tasmanica, Posidonia australis*);
- very restricted distribution on the southern coast, mainly in Victoria and Tasmania but sometimes extending to South Australia and southern New South Wales (Fig. 1.1). (*Halophila australis, Zostera muelleri*);
- present only on the east coast (*Zostera capricorni*) with records as far south as eastern-most Victoria and one record for Kangaroo Island (Fig. 1.1, 1.6).

1.5.3.3 South Australia

Western Australia and southern Australia have one of the world's most extensive known areas of temperate seagrass (Kirkman & Kuo 1990). South Australia (Fig. 1.6) alone has 9,612 km^2 (Edyvane 1999a, b). The most extensive seagrass meadows (dominated by *Posidonia* sp.) occur in the clear shallow sheltered gulf waters of the Spencer Gulf (5520 km^2) and Gulf St. Vincent (1530 km^2; Fig. 1.6; Edyvane 1999a, b, Lewis *et al.* 1997).

Twelve species of seagrass have been recorded in South Australian coastal waters (Edyvane 1999a, b). *Posidonia* sp. and *Amphibolis* sp. generally decline in abundance to the east (Fig. 1.8). This has been attributed to their affinity with warm temperate waters that decrease eastward coincident with reduced effects of the Leeuwin Current (Kirkman 1997). Encounter Bay (Fig. 1.8) is the eastern limit of *A. griffithii*, Lacepede Bay (Fig. 1.8) of *P. sinuosa*; Rivoli Bay (Fig. 1.8) of *P. coriacea* and *P. denhartogii*; and Port Macdonnell (Fig. 1.8) of *P. angustifolia* (Robertson 1984, 1986, Shepherd & Roberston 1989, Kirkman 1997). *Halophilia australis*, *A. antarctica*, *Heterozostera tasmanica, Zostera muelleri* and *Z. mucronata* are distributed throughout the region (Kirkman 1997, Lewis *et al.* 1997; Fig. 1.8).

1.5.4 The importance of seagrasses

High primary productivity, habitat and sediment stabilisers are the three most important features of seagrass ecosystems. This does not include the role that is the focus of this study, i.e. as a substrate for calcareous epiphytes.

1.5.4.1 Productivity

Petersen (1918 cited in Zieman & Wetzel 1980) first documented the importance of seagrass beds for shallow coastal ecosystem primary productivity. In the last 30 years, seagrass ecosystems have been recognised as one of the most productive ecosystems in the world (Bittaker & Iverson 1976 and references therein, Zieman & Wetzel 1980). Productivity is dependent on species type as well as environmental parameters, particularly temperature and light. Few organisms feed directly on the seagrass blades themselves because of their low nitrogen, high cellulose content and the presence of phenolics. Many non-calcareous epiphytes and other organisms that inhabit the seagrass are, however, important food sources (Robertson 1980, Pollard 1984, Howard *et al.* 1989, Bell & Pollard 1989 cited in Hutchings *et al.* 1991, Jernakoff & Nielsen 1998, 1997, Klumpp *et al.* 1992).

Primary productivity of Australian seagrasses was reviewed by West & Larkum (1982), Larkum *et al.* (1989) and King *et al.* (1991). Productivity is defined as the rate at which a given quantity of organic material (biomass) is produced over a given time (Zieman & Wetzel 1980, Lalli & Parsons 1997). Biomass is defined as the weight of all living material in a unit area at a given instant and includes the entire plant with rooting structures (Zieman & Wetzel 1980). Most productivity estimates are of above-ground structures only and then the term biomass is synonymous with standing stock. A number of methods are used to estimate productivity (Table 1.4). The most widely used and accepted technique for obtaining biomass productivity values is leaf-marking (Dennison 1990). This is carried out by marking, with a syringe needle, (or other device), the base of the blades. After a set time, usually no longer then 100 days, the blades are collected, the blade elongation is measured and the carbon content assessed. The method was first devised by Zieman (1968) and has been reviewed several times since (e.g. Kirkman & Reid 1979, Zieman 1974, Dennison 1990). *Amphibolis* sp. requires a slightly different marking method to that of *Posidonia* sp. because of the short length and clustering of blades (Walker 1985).

Lepidochronology examines the changes in thickness of seagrass sheaths through a one year cycle (Boudouresque *et al.* 1983, Pergent & Pergent-Martini 1999). The different thicknesses

Table 1.4. Summary of seagrass productivity available for the species relevant to this study. Values are for aboveground productivity and biomass only.

Location	Method	Productivity/biomass	Turnover	Reference
Posidonia australis				
W.A.		400^{bdw} 5.3*	4.3^	Cambridge (1979) *cited in* West & Larkum (1982)
Port Hacking, N.S.W.		140^{bdw} 0.57-1.44*		Kirkman *et al.* (1979)
		400^{bdw} 5.3*	2.3^	Kirkman & Reid (1979)
Bonna Point, N.S.W.	Leaf-marking	1-3.2* 189-286^{bdw} 215^{sd}	3.1^ 8.4$^{\pounds}$ 117.7$^{\checkmark}$	West & Larkum (1979)
Quibray Bay N.S.W.	Leaf-marking	1.0-1.9* 101-137^{bdw} 80^{sd}	3.9^ 10.6$^{\pounds}$ 93.6$^{\checkmark}$	West & Larkum (1979)
Jervis Bay N.S.W.	Leaf-marking	0.9-5.2* 294-453^{bdw} 199^{sd}	3.3^ 9.0$^{\pounds}$ 110.6$^{\checkmark}$	West & Larkum (1979)
Port Hacking N.S.W.	Leaf-marking	1.2-3.6* 190-198^{bdw} 121^{sd}	4.5^ 12.3$^{\pounds}$ 81.1$^{\checkmark}$	West & Larkum (1979)
Chinamans Creek, Spencer Gulf S.A.	Leaf-marking	2.7-5.5* 444-616^{bdw} 240^{sd}	2.8^ 7.7$^{\pounds}$ 130	West & Larkum (1979)
Carnac Is., W.A.	Leaf-marking	2.7 ± 0.3* 149-356^{bdw} 520^{sd}	5.3^ 75$^{\checkmark}$	Silberstein (1985); Silberstein *et al* (1986)
Woodman Point, W.A.	Leaf-Marking	1.4± 0.3* 59-221^{bdw} 380^{sd}	6.4^ 65$^{\checkmark}$	Silberstein (1985); Silberstein *et al* (1986)
Princess Royal Harbour, W.A.		324 ± 160^{bdw} 590 ± 270^{sd}		Hillman *et al* (1990)
Oyster Harbour, W.A.		232 ± 179^{bdw} 790 ± 510^{sd}		Hillman *et al* (1990)
King George Sound, W.A.		436 ± 150^{bdw} 1200 ± 390^{sd}		Hillman *et al* (1990)
Shoalwater, Warnbro Sound, W.A.	Leaf-marking	241.2^{bdw}	2.6^	Marbà & Walker (1999)
Rottnest Is.	lepidochronology		7$^{\#}$	Pergent & Pergent-Masini (1999)
Rottnest Is., W.A.	diving-PAM		2.92-5.6^ 65-125$^{\checkmark}$	Ralph & Gademann (1999)
Nancy Cove, Rottnest Is., W.A.	Leaf-marking	2.2* 152^{bdw} 13.4^{+}		Udy & Dennison, (1999)
Cockburn Sound, W.A.	Leaf-marking	2-7.4* ~140-200^{bdw}	5.2-6.4^ 57-70$^{\checkmark}$	Cambridge & Hocking, (1997)
Fisherman Bay, Spencer Gulf, S.A.	Leaf-marking	8-13.5^{+}		Seddon, (2000)
9 sites Spencer Gulf, S.A.	Leaf-marking	4 – 676 (av. 198)^{sd}		Seddon, (2000)
Shark Bay, W.A	Leaf-marking		3.97^ 92$^{\checkmark}$	Walker pers comm. (2002)

P. sinuosa				
W.A.		3.9* 660^{bdw}	2.1	Cambridge (1979) *cited in* West & Larkum (1982)
Princess Royal Harbour, Albany, W.A.	Leaf-marking	1.07-1.25* 1784^{sd} $0.73\text{-}0.97^{-}$		Gordon, *et al* (1990)
Princess Royal Harbour, W.A.		165 ± 131^{bdw} 910 ± 590^{sd}		Hillman *et al* (1990)
Oyster Harbour, W.A.		188 ± 154^{bdw} 1200 ± 790^{sd}		Hillman *et al* (1990)
King George Sound, W.A.		309 ± 136^{bdw} 2060 ± 136^{sd}		Hillman *et al* (1990)
Cockburn Sound, W.A.	Leaf-marking	1-3* $\sim 140\text{-}190^{bdw}$ $142\text{-}2000^{sd}$	3.65-5.2^ $70\text{-}100^{\checkmark}$	Cambridge & Hocking, (1997)
Penguin Is., Geographe Bay, W.A.	Leaf-marking	$96.2\text{-}321.4^{dbw}$	1.6^	Marbà & Walker, (1999)
Rottnest Is.	lepidochronology	$4.3^{\#}$		Pergent & Pergent-Masini (1999)
4 sites Spencer Gulf, S.A.	Leaf-marking	$11\text{-}738\ (\text{av.} = 240)^{sd}$		Seddon, (2000)
Nancy Cove, Rottnest Is., W.A.	Leaf-marking	3.2* 349^{bdw} 5.9^{+}		Udy & Dennison, (1999)
P. angustifolia				
Marmion Lagoon,W.A.	Leaf-marking	254.6^{bdw}	1.9^	Marbà & Walker, (1999)
Rottnest Is., W.A.	lepidochronology		$4.2^{\#}$	Pergent & Pergent-Masini (1999)
2 sites Spencer Gulf, S.A.	Leaf-marking	$2\text{-}145\ (\text{av.} = 76)^{sd}$		Seddon, (2000)
P. coriacea				
Success Bank, W.A.	Leaf-marking	~1-9* $<250^{bdw}$ $975\text{-}1925^{sd}$		Kendrick *et al* (1998)
***Amphibolis griffithii* blades**				
Success Bank, W.A.	Leaf-marking	*~2-22 $>250^{bdw}$		Kendrick *et al* (1998)
Success Bank, Owen anchorage, W.A.	Leaf-marking		5.4^ $68^{\checkmark}$	Sim (1998)
Shoalwater Bay, Warnbro Sound, W.A.	Leaf-marking	531.7^{bdw}	4.0^	Marbà & Walker, (1999)
Rottnest Is., W.A.	Leaf-marking	$0.038 \pm 0.004^{@}$	~3.5^ $104.3^{\checkmark}$	Carruthers, (1999)
Nancy Cove, Rottnest Is., W.A.	Leaf-marking	2.9* 97^{bdw}		Udy & Dennison, (1999)
***A. griffithii* stem**				
Success Bank, W.A.		$475\text{-}1025^{sd}$		Kendrick *et al* (1998)
Nancy Cove, Rottnest Is., W.A.	Leaf-marking	165^{bdw}		Udy & Dennison, (1999)

***A. antarctica* blades**				
Shark Bay, W.A	Leaf-marking	2-17* 600-2000^{bdw}		Walker, (1985)
Shark Bay, W.A.		1600^{bdw}		Walker & McComb, (1988)
Rottnest Is., W.A.	Leaf-marking	0.086±0.007$^{@}$	~5.2^ 70.2✓	Carruthers, (1999)
Parker Point, Rottnest Is. W.A.	Leaf-marking	214.2^{bdw}	4.2	Marbà & Walker, (1999)
Fisherman Bay, Spencer Gulf	Leaf-marking	0.09-0.11$^{@}$	~5.5^ 66.4✓	Seddon, (2000)
Nancy Cove, Rottnest Is., W.A.	Leaf-marking	2.4* 71^{bdw}		Udy & Dennison, (1999)
Shark Bay, W.A	Leaf-marking		5.6^ 65.2✓	Walker pers comm. (2002)
***A. antarctica* stem**				
Shark Bay, W.A		~280-1100^{bdw}		Walker, (1985)
Nancy Cove, Rottnest Is., W.A.		109^{bdw}		Udy & Dennison, (1999)
***A. antarctica* whole plant**				
Shark Bay, W.A	Leaf-marking	~270-1250^{sd}		Walker, (1985)
9 sites Spencer Gulf, S.A.		2-715 (av.218)^{sd}		Seddon, (2000)

* g dw m^{-2} d^{-1} (productivity)
$^{+}$mm shoot^{-1} d^{-1}
$^{@}$leaves cluster^{-1} d^{-1}
^ crops yr^{-1} (turnover rate)
^{sd} shoots m-^{2} (shoot density)

$^{-}$ mg shoot^{-1} d^{-1}
^{bdw} g^{-1} dw m^{-2} (biomass)
^{r} mm blade d^{-1}
✓ days for complete replacement of canopy
$^{\#}$ blades yr^{-1} shoot^{-1}

are caused by seasonal changes and are retained along the rhizomes after the blades have shed. However, this method can only give numbers of blades produced per year, rather than biomass figures. Biomass productivity is not a true measure of primary production (photosynthesis & respiration) as it does not account for losses by exudation, herbivory and respiration. *In situ* measurements of productivity can be calculated from measuring photokinetic properties using a diving-PAM (Pulse Amplitude Modulated) fluorescence instrument) (Ralph & Gademann 1999) or from using sealed incubation chambers (Masini 1990).

It should be noted that there are no productivity values available for *Amphibolis* stems, although they are generally believed to live for up to 2 years (Womersley 1984, Walker 1985, Coupland 1997). Table 1.4 summarizes the productivity values obtained from previous studies using a range of methods, for the seagrass species relevant to this study.

1.5.4.2 Habitat providers

Seagrass beds provide increased surface area for attachment, are a source of constant food, and give shelter from predation, current velocity and excessive light (Kikuchi 1980). Space for recruitment is generally regarded as a limited resource in many marine environments (Holmes *et al.* 1997 and references therein). The constant turnover of seagrass blades provides a constant source of new recruitment space for benthic colonisers that would otherwise be absent. Combined with the importance of available recruitment space, the food source and sheltering aspect of seagrass beds make them ideal locations for nurseries. Some species that use seagrass beds as nurseries are commercially important (Bell & Pollard 1989, Howard *et al.* 1989). These include King George Whiting (*Sillaginodes punctata*), the abalone *Haliotis cyclobates* (Péron 1816 cited in Stevenson & Meville 1999), blue-swimmer crabs (Seddon *et al.* 2000) and penaeid prawns (Coles *et al.* 1993, Young 1987). Many other species present in seagrass beds are ecologically important and it is likely that the full extent of the importance of the seagrass ecosystem is not fully appreciated or understood at this time.

1.5.4.3 Sediment stabilisers

Studies have shown that seagrass canopies deflect water flow, diverting the flow above the seagrass canopy (Kikuchi 1980, Fonseca *et al.* 1982, Fonseca & Kenworthy 1987, Gambi *et al.* 1990 cited in Terrados & Duarte 2000). The bed surface acts as a buffer zone helping prevent the erosion of coastal environments (Scoffin 1971). Terrados and Duarte (2000) found that reduced current flow reduces particle re-suspension. These sediment particles become entrapped amongst the roots and rhizomes, resulting in the build-up of sediment (Ball *et al.* 1967 cited in Wanless 1981, Kikuchi 1980). It has been shown that the build-up of sediment occurs at different rates according to the root structure. *Posidonia* spp. for example, has hairy sheaths that quickly entrap sediment (Fig. 1.4a), whereas *Amphibolis* has a fine mesh of lignified roots that tightly binds sediment. Both *Posidonia* and *Amphibolis* have rhizomes that grow upward in order to avoid burial. This contrasts with *Zostera marina* where rhizomes grow horizontally and the sediment-trapping action of its root system is apparently less efficient (Kikuchi 1980).

The build-up of sediment can be important over time, e.g. 1 m in 1000 years (pers. comm. Wiltshire 1998). This is clearly seen in an area where seagrass no longer exits. The most common feature of sediment removal from an area where seagrass was present or is dying is a 'blow out'. These consist of a sharp erosional scarp facing seaward with seagrass present on the landward side and bare sand on the seaward side. The height of the scarp varies from 0.3 to 1.5 m and can expand relatively quickly. Natural processes usually cause blowouts, although anthropogenic activities increase their frequency and the rate at which they develop. The profile across a blow-out scarp from seawards to landwards tends to show a fining upward sequence. This has been described in detail and has been used to interpret similar sequences in the fossil record (Wanless 1981). Alternatively, where no scarp develops, erosion of sediment may occur more slowly. The sediment is still bound together by the roots and rhizomes of the plants and sediment is removed in a planar manner, slowly exposing the root systems and the sediment, a layer at a time.

1.5.5 Dieback, causes and consequences

1.5.5.1 General

A minimum value of 2000 km^2 seagrass loss (not including dieback caused by the wasting disease in Europe and North America) has been reported since 1935 (Seddon *et al.* 2000). Causes of seagrass decline can be natural or anthropogenic. Kirkman (1997) reviews the dieback in Australia and Seddon *et al.* (2000) reviews reported major diebacks globally. Both describe the various causes. Natural causes include cyclone and storm damage, burial by moving sands, high temperatures/salinities, low tides, algal blooms, reduced light, exposure and disease. Anthropogenic sources include thermal effluent from power stations, sewage outfalls, stormwater runoff, agricultural runoff, sediment dredging and boat propellers and moorings. The main consequence of anthropogenic influence is a decrease in light availability to the seagrass by increased turbidity or increased algal epiphyte growth (Cambridge *et al.* 1986, Silberstein *et al.* 1986, Shepherd *et al.* 1989, Masini & Manning 1997). Finally, global warming and ozone depletion also threaten the health of seagrass beds (Seddon *et al.* 2000). The exact nature of all these effects on seagrass is uncertain although recent studies have begun to address the impact (Seddon *et al.* 2000).

1.5.5.2 South Australia

A seagrass loss of 217 km^2 has been recorded in South Australia, predominantly from the Spencer Gulf region and Adelaide metropolitan coastal area (Seddon *et al.* 2000). This loss has been attributed to both anthropogenic (Adelaide region) and natural causes (Spencer Gulf) (Hart 1997, Neverauskas 1988a, Thomas & Clarke 2002, Shepherd *et al.* 1989, Seddon *et al.* 2000). Seddon *et al.* (2000) identified that the 127 km^2 seagrass dieback in 1993 in eastern Spencer Gulf occurred as a result of a combination of excessive air temperatures, low tides and low barometric pressure (the latter enhancing and prolonging high temperatures and low tides), i.e. the seagrasses became desiccated. In the Adelaide metropolitan coastal area (Fig. 9) the loss of 41 km^2 of seagrass is attributed to stormwater/sewage outfalls that increase nutrients and turbidity in the region. Nutrient increase is believed to cause a decline by i) algal blooms increasing turbidity, ii) increased algal epiphytes effectively smothering the seagrass (Lapointe *et al.* 1994), and iii) additional nutrients having a toxic effect on the seagrass. (Increased sediment loads in the water column, caused by the changing sedimentological regime, further add to the turbidity reducing the light penetration and ability of the seagrass to photosynthesise).

1.5.6 Seagrass summary

The evolutionary history of seagrass is not fully known due to the poor preservation potential of seagrass. Those specimens that have been found plus evidence from other sources indicate that they evolved around the edges of the Tethys Sea in the early Cretaceous. The time at which seagrass reached the Australian continental margin is not established due to limited evidence, but was no earlier than the Eocene. Seagrasses, since the Miocene has become relatively isolated from the rest of the world resulting in high endemism. In South Australia there are 12 species from 5 genera that cover an area of 9,612 km^2. Seagrass is important for a number of reasons including high productivity, habitat and sediment stabilisation. The dieback of seagrass has potential economic impacts such as the reduction in abundance of certain commercially important fish and loss of beaches important for tourism. The latter is caused by increased sediment transport, increased onshore and/or near shore wave activity and decreased sediment production.

1.6 SUMMARY

This study aimed to address some of the issues raised above to determine the relative and/or potential role of epiphytes in the present environment and to relate the findings to the past. Are calcareous epiphytes an important source of sediment at both the local and global scale? Can their presence in the rock record be identified from examination of the assemblages in today's environment? If so, can they be used as a palaeo-tool, to not only trace the evolution of seagrass, but also to identify their specific environment? Research on seagrass so far indicates their importance at a regional scale in terms of productivity, habitat providers and sediment stability. There is little, so far, to suggest how important their role has been in the past. Do calcareous epiphytes hold the key to their story? Will the impact of anthropogenic activities significantly affect seagrass and the calcareous epiphytic assemblages?

CHAPTER 2
METHODS

2.1 INTRODUCTION

This chapter outlines all methods used for all areas of this project including field, laboratory, and analytical procedures. Since previous studies have used a number of different methods, these techniques are also described and compared with those used in this study.

2.2 FIELD METHODS

Samples collected in the manner described below are applicable to all chapters. The aims of the fieldwork were to:

- select sites that represented a number of different environments to improve estimations of carbonate quantities throughout the region;
- select different sites that have parameters that are in common with one another, so as to compare and contrast controls on calcareous epiphyte carbonate production;
- use a sampling method that obtained representative samples of that area, yet at the same time retained information at various spatial scales.

2.2.1 Site selection

Twenty sites along the South Australian coastline were chosen because of the wide variety of environments in which seagrass is found (Fig. 2.1). These environments vary from the head of reverse estuaries (Gulf St. Vincent and Spencer Gulf - Fig. 1.1) to those exposed to the Southern Ocean, from water depths ranging from 0.4 to 15.5 m depth, across a salinity range of 32.2 to 43.7‰ and with surface water temperature ranging from 14.1 to 25.8°C. The aim was to evaluate the variation in calcareous epiphytic carbonate productivity and help determine the parameters effecting that variation.

A bioregionalisation project was completed by SARDI (South Australian Research and Development Institute) (Edyvane 1999a, b). The project identified 8 bioregions and 35 biounits (Table 2.1) using the IMCRA (Interim Marine and Coastal Regionalisation of Australia) 1995-1996 project and further field studies. Twenty seven of the 35 biounits have significant areas of seagrass. These biounits were considered when selecting the sites for this study. Twelve of these were sampled using the transect method described below (Table 2.2). The seagrass quantities were significant enough in some biounits to warrant more than one sample location and hence a total of 20 sites were sampled (Table 2.2). In addition, Chinaman Creek was sampled at three sub-sites (within one km^2) and West Island was

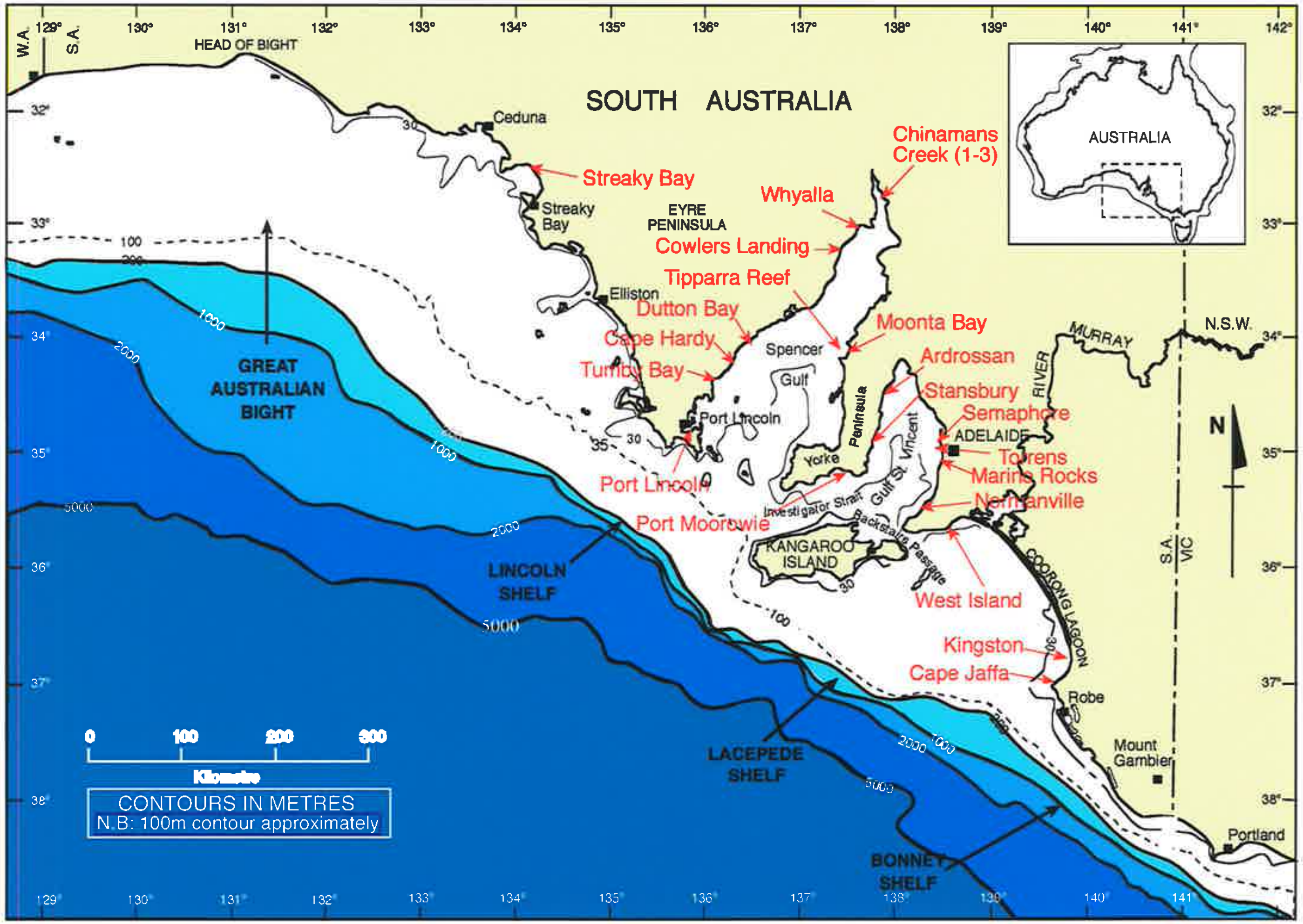


Figure 2.1 Location map of the South Australian coastal region and sample sites for this study

Table 2.1: Summary of the presence of seagrass in South Australia's Coastal Bioregional Framework.
Edited from [Edyvanne, 1999b]

Bioregions	Biounits	Geology & Physical description	Oceanography	Main marine Habitats	Total area (ha)	Area seagrass (ha)	Seagrass species found
Eucla	Nullabor	90m high Tertiary limestone (Nullabor) cliffs, Pleistocene calcarenite ramp at Merdayerrah Holocene dunes.	High wave energy, moderating at Head of Bight	Reef, sand	842,642		
	Wahgunyah	Extensive dune transgression system, on Nullabor Cliffs	Moderate to high energy,	Reef, Sand	195,381		
Murat	Fowlers	Pleistocene calcarenite cliffs interspersed with Holocene sediements. Precambrian basment exposed at major peninsulas.	Low in bays to high on offshore islands & cliffs	Reef, sand, seagrass	146,486	1,639	*P. sinuosa, P. angustifolia, A. antarctica, A. griffithii*
	Nutys	Offshore islands,		Reefs, sand, seagrass	283,165	144	*P. australis, P. sinuosa, Heterozostera tasmanica, Halophila australis, Caulerpa Cactoides.*
	Streaky	Sheltered embayments, rocky headland		Reefs, sand, seagrass, mangroves	190,949	86,163	
Eyre	Yanerbie	Pleistocene dune calcarenites & Holocene ses. Precambrian basement exposed occasionally. Two large coastal embayments – Venus & Baird Bay.	Low to high energy. Temp 14-18°C. Seasonal upwelling	Reefs, sand, Seagrass	82,854	6,602	Only within embayments; *Heterozostera tasmanica, Amphibolis antarctica, Zostera muelleria, P. australis, Ruppia*
	Newland	Holocene dune calcarenites forming barrier system. Offshore Islands present	High to low wave energy depending on geography	Reef, sand,	45,238	0	

Bioregionalisation framework cont'd

Bioregions	Biounits	Geology & Physical description	Oceanography	Main marine Habitats	Total area (ha)	Area seagrass (ha)	Seagrass species found
Eyre cont'd	Flinders	Pleistocene calcarenite dunes 50-100m high. Shore platforms, offshore islands, seamounts	High to low wave energy depending on geography. Temps 14-18°C. Upwelling seasonally.	Reef	125,957	0	
	Sheringa	Pleistocene dunes. A number of Islands are present, composed of basment, grante, or calcarenite.	High to low wave energy depending on geography. Temps 14-18°C. Upwelling seasonally.	Reef, sand, seagrass	51,156	65	Off islands, deepwater *Heterozostera tasmanica, Halophila, Amphibolis and Posidonia australis*
	Douglas	Variable coastline, sheltered embayments, rocky headland	High energy coastline, low energy bays.. Temps 14-18°C. Upwelling seasonally.	Reef, sand, seagrass	67,645	8,567	*P. angustifolia, Heterozostera tasmanica, Halophila australis, Caulerpa cactoides*
	Whidbey	Pleistocne calcarenite dunes, overcapped by Holocene dunes. Rocky coast, offshore islands, seamounts,	Extremely high energy coastline, low energy bays.. Temps 14-18°C. Upwelling seasonally.	Reef, sand	132,689	0	
	Jussieu	Southwestern arm of Spencer Gulf. Highly variable morphology. Minor Holocene barrier areas. Large sheltered embayment, rocky headlands, offshore islands	Low wave energy with prevailing offshore winds.	Reef, sand, seagrass	240,439	56,956	*P. australis, P. sinuosa, P. angustifolia, Halophila australis*
	Pondalowie	Limestone cliffs, with wide dune belts.	High energy	Reef, sand, seagrass	22,130	25	*A. antarctica, P. sinuosa, Heterozostera tasmanica,*

Halophila australis, Caulerpa scapelliformis

Bioregionalisation framework cont'd

Bioregions	Biounits	Geology & Physical description	Oceanography	Main marine Habitats	Total area (ha)	Area seagrass (ha)	Seagrass species found
Eyre cont'd	Gambier	Numerous islands consisting of crystalline basement, some with a cover of calcareous aeolinite. Deeper habitats	Low wave energy with prevailing offshore winds.	Sand, reef, seagrass	536.544	5,123	*Posidonia, Heterozostera*
	Gantheume	Calcarenite headlands, cliffs and shore platforms. Some Holocene beach deposits.	High energy, waves up to 2m.	Reef, sand, seagrass	167,363	1,263	*P. sinuosa, P. angustifolia, A. antarctica P. robertsoniae, Caulerpa*
Spencer	Dutton	Central Western part of Spencer Gulf hence sheltered. Dunes and shingle ridge development	Low wave energy with prevailing offshore winds.	Reef, sand, seagrass	255,443	25,706	*A. antarctica, P. sinuosa.*
	Franklin	Dominated by low wenergy freflective beaches.	Moderate wave energy	Reef, sand, seagrass, mangroves	198,588	15,447	*P. sinuosa, A. antarctica*
	Tiparra	Long sandy beaches and shore platforms. Some Limestone and clay cliffs	Low to moderately high energy	Reef, sand, seagrass	243,228	83,912	*P. sinuosa, A. antarctica, Heterozostera tasmanica*
	Wardang	Large embayments, rocky headlands composed of limestone cliffs. Some dune systems.	Low to moderately high energy	Sand, reef, seagrass	285,583	26,458	*P. sinuosa, P. angustifolia, A. antarctica*
Northern Spencer Gulf	Yonga	Low gradient Pleistocene calcareous surface. Beach ridge plains, ~730m in width fronted by wide inter- to subtidal sand flats.	Predominantly low energy. High tidal of 3.1m range at Port Pirie	Reefs, sand, seagrass	55,267	248,596	*P. sinuosa, P. angustifolia, A. antarctica.*
	Winninowie	Hinge zone between the Adelaide Geosyncline and Stuart Shelf. Wide intertidal and supratidal areas.	Very low wave energy. Tidal range 2.7m. Salinities in excess of 40. Temp 10-20°C.	Sand, seagrass	423,557	16,484	*P australis, P. sinuosa, Heterozostera tasmanica, A. antarctica, Halophila ovalis.*

Bioregionalisation framework cont'd

Bioregions	Biounits	Geology & Physical description	Oceanography	Main marine Habitats	Total area (ha)	Area seagrass (ha)	Seagrass species found
Gulf St. Vincent	Sturt	Dunes and limestone cliffs dominate. Large bays, rocky headlands present	Moderate-high energy	Reefs, sand, seagrass	183,058	25,611	*P. sinuosa, P. angustifolia, A. antarctica, Halophila australis*
	Investigator	Dunes and limestone cliffs. Deepwater habitat	Moderate-high	Sand	280,063		
	Orontes	Limestone cliff slopes, with occasional sandy beaches.	Low wave energies	Reef, sand seagrass	183,762	51,713	*P. sinuosa, P. angustifolia, Halophila australis*
	Clinton	Long beach areas and small dunes, to muddy flats	Low wave energy	Reef, sand, seagrass, mangroves	249,136	132,576	
	Yankalilla	Rocky headlands of Precambrian aged rocks. Sandy beaches, river outlets.	Moderate energy	Reef, sand, seagrass	51,562	7,645	*P. sinuosa, P. angustifolia, A. antarctica, Halophila australis.*
	Encounter	Steep cliffs to long beaches and dunes.	High energy	Reef, sand, seagrass	39,389	505	*P. sinuosa, P. angustifolia, A. antarctica, Haolphila australis*
	Sprigg	Holocene beach ridges, samphire flats and sandflats. Headlands and cliffs.	Low energy, deep water		160,548		*Zostera muelleri, P. australis, P. sinuosa, A. antarctica, Heterozostera tasmanica, Halophila australis*
	Backstairs	Holocene beach ridges, samphire flats and sandflats. Headlands and cliffs.	Strong tidal, deepwater, moderate energy	Reef, sand, seagrass	35,911	668	*Zostera muelleri, P. australis, P. sinuosa, A. antarctica, Heterozostera tasmanica, Halophila australis*

Bioregionalisation framework cont'd

Bioregions	Biounits	Geology & Physical description	Oceanography	Main marine Habitats	Total area (ha)	Area seagrass (ha)	Seagrass species found
Gulf St. Vincent cont'd	Nepean	Sheltered embayments		Reef, sand, seagrass	102,304	23,229	
	Cassini	Sea cliffs, single and boulder beaches.	Moderate to low wave energy	Sand, seagrass	45,760	662	*P. sinuosa, P. angustifolia, Heterozostera tasmanica, A. antarctica, Halophila australis, Caulerapa*
Coorong	Coorong	Extensive lagoon system, dune barrier.	High energy	Reef, sand, seagrass	1290,715	25,062	*P. australis, A. antarctica, P. angustifolia, P. coriacea, Heterozostera*
Otway	Canunda	Irregular topography,	Low – high energy. Temp 14-18°C.	Reef, sand	233,897	2	
	Nene	Rocky coast, offshore reefs	High energy	Reef, sand	32,543	0	
	Piccaninnie	Rocky coast, offshore reefs	High energy	Reef, sand, seagrass	44,923	44	*P. coriacea, p. australis, A. antarctica, Heterozostera tasmanica, Caulerpa*

Table 2.2. South Australian Coastal Bioregional Framework Biounits, relevant to selection of r Field Sites. (Biounits information from Edyvanne (1999b)).

Location	Biounit	Seagrass cover (Hectares)	Seagrass in biounit
Ardrossan jetty (Ard04/1999)	Orontes	51713	*Hal. australis* *P. angustifolia,* *P. sinuosa,*
Cape Hardy (CaHa10/1999)	Dutton	25706	*A. antarctica,* *P. sinuosa.*
Cape Jaffa jetty (CaJa11/1999)	Coorong	25062	*A. antarctica,* *Het. tasmanica* *P. angustifolia,* *P. australis,* *P. coriacea,*
Chinamans Creek 1 (ChCk 1 11/2000)	Winninowie	16484	*A. antarctica ,* *Hal. ovalis.* *Het. tasmanica,* *P australis,* *P. sinuosa,*
Chinamans Creek 2 (ChCk 2 11/2000)	Winninowie	16484	As for ChCk1
Chinamans Creek 3 (ChCk 3 11/2000)	Winninowie	16484	As for ChCk1
Cowlers Landing (Cow06/1999)	Yonga	248596	*A. antarctica.* *P. angustifolia,* *P. sinuosa,*
Dutton Bay (Dut10/1999)	Dutton	25706	*A. antarctica,* *P. sinuosa.*
Long Beach, Kingston (King11/1999)	Coorong	25062	*A. antarctica,* *Het. tasmanica* *P. angustifolia,* *P. australis,* *P. coriacea,*
Marino Rocks (Mar01/1999)	Yankalilla	7645	*A. antarctica,* *Hal. australis.* *P. angustifolia,* *P. sinuosa,*
Moonta Bay (Moo04/1999)	Tiparra	83912	*A. antarctica,* *Het. tasmanica* *P. sinuosa,*
Normanville jetty (Norm05/1999)	Yankalilla	7645	*A. antarctica,* *Hal. australis.* *P. angustifolia,* *P. sinuosa,*

Port Lincoln (PtLi03/1999)	Jussieu	56956	*Hal. australis* *P. angustifolia,* *P. australis,* *P. sinuosa,*
West Island shallow (WI shallow)	Encounter	505	*A. antarctica,* *Hal. australis* *P. angustifolia,* *P. sinuosa,*
West Island deep (WI deep)	Encounter	505	As for WI shallow
False Bay, Whyalla (Why03/1999)	Yonga	248596	*A. antarctica.* *P. angustifolia,* *P. sinuosa,*
Port Morrowie (PtMo04/1999)	Sturt	25611	A. antarctica, Hal. australis P. angustifolia, P. sinuosa,
Semaphore (Sem05/2000)	Clinton	132576	-
Stansbury jetty (Stan04/1999)	Orontes	51713	Hal. Australis P. sinuosa, P. angustifolia,
Streaky Bay (StBy03/1999)	Streaky	86163	-
Tiparra Reef (Tip10/1999)	Yonga	248596	A. antarctica. P. angustifolia, P. sinuosa,
Torrens outlet (Tor05/2000)	Clinton	132576	-
Tumby Bay (Tum03/1999)	Jussieu	56956	Hal. australis P. angustifolia, P. australis, P. sinuosa,

Table 2.3. Field site parameters. The wording in brackets under the location name is the designated code for each site. Coordinates of sampling locations were measured using a GPS300 set on WGS84, Lat/Lon (DEGMIN). The sampling method indicates whether it was necessary to use a boat to get to the locations. Date refers to the sampling date (West Island samples were collected at ~3 month intervals). Average monthly air temperatures were obtained from Bureau Meteorology. Water temperatures and salinity were measured 30 cm below the surface.

Location	Date	Latitude	Longitude	Biounit Name	Sampling method	Quadrats sampled	Air temp (°C)	Water temp. (°C)	Salinity (‰)	Water depth (m)
Ardrossan jetty (Ard04/1999)	12/4/99	34° 25.36'	137° 55.26'	Orontes	Shore	14	22.3	18.8	36.2	0.8
Cape Hardy (CaHa10/1999)	7/10/99	34° 12.11'	136° 18.17'	Dutton	Boat	7	20.1		36.5	10.0
Cape Jaffa jetty (CaJa11/1999)	27/11/99	36° 56.55'	139° 41.00'	Coorong	Shore	14	19.7			2.2
Chinamans Creek 1 (ChCk 1 11/2000)	25/11/00	32° 43.08'	137° 49.88'	Winninowie	Boat	14	25.8	24.4	43.6	4.9
Chinamans Creek 2 (ChCk 2 11/2000)	25/11/00	32° 42.87'	137° 50.10'	Winninowie	Boat	12	25.8	26.9	43.7	1.1
Chinamans Creek 3 (ChCk 3 11/2000)	26/11/00	32° 40.62'	137° 49.63'	Winninowie	Boat	12	25.8	25.4	43.7	2.56
Cowlers Landing (Cow06/1999)	14/6/99	33° 11.39'	137° 28.17'	Yonga	Boat	13	17.6		37.1	5.7
Dutton Bay (Dut10/1999)	7/10/99	34° 03.06'	137° 27.50'	Dutton	Boat	6	20.1		36.5	3.2
Long Beach, Kingston (King11/1999)	27/11/99	36° 49.00'	139° 51.50'	Coorong	Shore	14	19.7			3.1
Marino Rocks (Mar01/1999)	12/1/99	135° 02.70'	138° 32.70'	Yankalilla	Shore	4	27.9	22		2.4

Moonta Bay (Moo04/1999)	11/4/99	34° 03.20’	137° 33.23’	Tiparra	Shore	12	23.4	18	35.3	4.2
Normanville jetty (Norm05/1999)	22/5/99	35° 44.67’	138°30.61’	Yankalilla	Shore	14	16.1		33.7	3.1
Port Lincoln (PtLi03/1999)	19/3/99	34° 48.29’	135° 51.41’	Jussieu	Shore	14	23.9	20.2	32.2	0.9
West Island shallow (WI shallow)	02/99 - 03/01	35° 36.28’	138° 35.27’	Encounter	Shore	7- 14	15.9 -24.5	14.1 -23.2	36.0 -39.4	4 - 6
West Island deep (WI deep)	05/99 – 06/00	35° 36.28’	138° 35.27’	Encounter	Boat	6 - 14	15.9 -24.5	14.1 -23.2	36.0 -39.4	10.7
False Bay, Whyalla (Why03/1999)	17/3/99	30° 59.07’	137° 37.54’	Yonga	Boat	14	29.1			1.9
Port Morrowie (PtMo04/1999)	10/4/99	35° 06.52’	137° 31.18’	Sturt	Shore	13	21.2	18.6	34.4	1.3
Semaphore (Sem05/2000)	17/5/00	34° 49.30’	138° 27.28’	Clinton	Boat	7	18.4	15.9	39.4	8.4
Stansbury jetty (Stan04/1999)	10/4/99	34° 54.16’	137° 42.44’	Orontes	Shore	14	22.3	18.3	34.8	1.5
Streaky Bay (StBy03/1999)	22/3/99	32° 27.50’	134° 56.20’	Streaky	Shore	7	27.2			1.8
Tiparra Reef (Tip10/1999)	6/10/99	34° 02.25’	137° 22.14'	Yonga	Boat	10	22.9		36.6	10.7
Torrens outlet (Tor05/2000)	18/5/00	34° 56.53’	138° 27.58’	Clinton	Boat	14	18.4	16.4	39.1	
Tumby Bay (Tum03/1999)	20/3/99	34° 22.43’	136° 06.11’	Jussieu	Shore	14	23.9			

357
54
70
413
@ 24 [illegible]

sampled at two depths. Some biounits were inaccessible for various reasons, including occupational health and safety, limited facilities, time availability and financial constraints.

2.2.2 Sample collection

The following method was adapted from standard baseline seagrass surveys (English *et al.* 1997). The area covered was reduced from three transects, 30 m in length, and 10 m apart as described in English *et al.* (1997) to two transects, due to dive time limitations. The scale used was designed to obtain representative samples of the area as a whole by averaging out effects such as patchiness, but still allowing evaluation at different spatial scales.

Two transects, 30 m in length, 10 m apart were deployed perpendicular to the coastline (Fig. 2.2). A 50 x 50 cm quadrat was placed to one side of the transect, starting at the distal and deepest end. All plant matter rooted within the quadrat was removed at the sediment/water interface, using a knife or scissors. It was generally found that the sediment/water interface coincided with the junction of the blade & sheath (Fig. 1.4b). If, as on occasion, the *Posidonia* sheaths were exposed above the sediment water interface, the blades were cut just above the sheaths. The seagrass was placed in previously labelled bags made up of shade-cloth. Shade cloth was used to allow easy drainage and reduce the amount of decay. The bag number and water depth (measured using a calibrated Aladdin pro dive computer, then corrected to chart datum) were noted at each site. A sediment grab sample (to 5 cm depth) was also collected from within the quadrat site. The relative difficulty in collecting the sediment was noted, giving an indication of the sediment stability. Water samples were collected from just above the seagrass canopy and at the sea surface for analysis post diving. This procedure was repeated at intervals of 5 m along both transects, giving 7 stations per transect. If no seagrass was found at any particular quadrat, it was noted as such and included as part of the local regime. Each transect took approximately 40 minutes to complete. After collection, the samples were rinsed carefully with fresh water and allowed to air dry.

To reduce the chances of re-sampling quadrat sites at West Island (Fig. 2.1) where multiple sampling was carried out, the transect locations were repositioned 10 m further south each season for the 1st year and then returned close to the original site for the 2nd year sampling.

Because of predicted changes due to seasonality the aim was to collect samples at a similar time (summer/autumn) of year. This was not always possible and often opportunity over-rode necessity to go at a similar time. However, because seasonal variation was evaluated at one

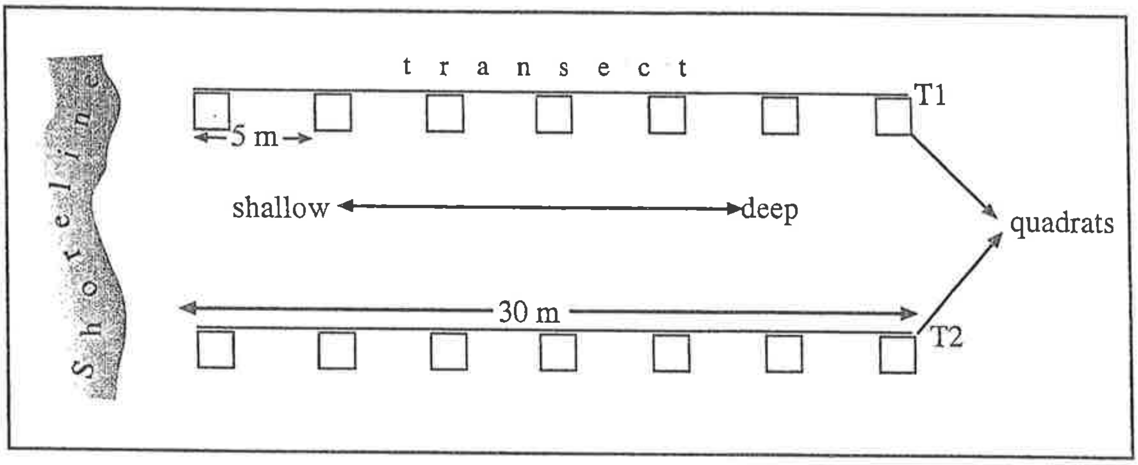


Fig. 2.2 Diagram of transect dimensions and orientation

site (West Island), it could be extrapolated to the other areas. The fieldwork at West Island was carried out between February 1999 and March 2001.

2.2.3 Parameters

The following parameters were measured quantitatively at each site:

- Temperature, salinity and conductivity; this was carried out using a calibrated TPS WP84. Surface measurements recorded 30 cm below the surface were more accurate due to changes in conditions when bringing samples up from the transect depth.
- Water samples were frozen as soon as possible for nutrient analysis (West Island samples were filtered prior to freezing). Analysis was carried out by the "Australian Centre for Tropical Freshwater Research", James Cook University.
- Depth measurements were obtained using a calibrated Aladdin Pro dive computer.
- Meteorological parameters, e.g. air temperature, humidity, wind speed, etc. were obtained for the two weeks either side of the collection day, from the Australian Meteorological Office.

The following parameters were observed and noted;

- Turbidity
- Visibility
- Cloud cover
- Sea state
- Wind speed
- Tide state
- Light intensity

Routine details such as date, dive time, time of day, method of data collection and dive buddy were noted (see CD).

2.2.4 Limitations and potential errors of field methods

The main limitation of this method is the uncertainty as to how representative the area sampled is to the environment in general. This is unanswerable without more detailed and intensive studies at each area, which was beyond the scope of this project. Table 2.4 outlines the limitations, the potential errors and the percentage estimation of those errors. The error percentage is estimated from observations throughout the practice of collection and sample processing. Some of the errors that occurred in the field were possible to correct during laboratory processes, e.g. sediment, sponges, roots collected during the fieldwork were

Table 2.4. Summary of potential errors incurred during fieldwork and the qualitative assessment of % error. Positive/negative errors are those that will produce higher/lower quantities of carbonate than the true values. M – measurable errors, A – avoidable errors, X = error was **not** measurable or avoidable ✓ = error was measurable or avoidable.

Positive errors	M	A	Estimated % error	**Negative errors,**	M	A	Estimated % error
Incorporation of seagrass external of the quadrat	X	✓	0.5	Blades rooted at inside edge quadrat missed	X	✓	0.5
Incorporation of plant material other than that found growing above the sed/water interface	X	✓	1	loss of grass when placing in bag (particularly v. young blades)	X	✓	1
Incorporation of sediment (including sponges)	X	X	5→2	Loose epiphytic material washing off	X	X	2
Incorporation of other calcareous organisms that are not epiphytic	X	✓	5→0.5	Incorporation of roots	X	✓	10 → 0.5
Total			11.5				13.5
Final error % after laboratory correction.			1.5				3

separated from the seagrass in the laboratory. Field errors, after correction during laboratory processing, are estimated at ~ ±3% error.

2.3 LABORATORY METHODS

2.3.1 Separation of calcareous epiphytes from seagrasses

These methods are applicable to Chapters 4-6.

Aims:

- to obtain quantitative values of the carbonate epiphytes;
- to retain the calcareous epiphytic material for later examination, i.e. it must be relatively whole and their skeletal chemistry not affected;
- to obtain values of the biomass on the epiphyte host.

Most methods for evaluating the amount of epiphytes estimate the carbon productivity by algal epiphytes, ignoring the carbonate secreted by the calcareous epiphytes. Even so, over the years a number of methods have been used to obtain estimations on $CaCO_3$ productivity. These can be grouped into biological, geological and chemical approaches (Hegge 1998, Lavery *et al.* 2000). Hegge (1998) summarised these:

- biological – involves direct measurements of the calcimass ($CaCO_3$ mass of live organisms per unit map area (Smith 1972)) and organic turnover rates;
- geological – involves examination of accumulation rates determined from stratigraphic and petrographic evidence together with dating of the deposit;
- chemical – involves the determination of the mass balance of calcium carbonate precipitated from seawater by examining changes in the total alkalinity and pH of the water and an estimate of the flushing rate of the water through the system (e.g. Yates & Halley 1999).

Each has been used to estimate epiphyte $CaCO_3$ productivity and all results fall into the range of zero to 2800 $g/m^2/yr$.

The predominant method used is biological and this was adopted for this project. There are a number of methods used to determine the biological estimation of epiphyte $CaCO_3$ productivity, including:

- CO_2 evolution;
    i. measurement of the CO_2 evolved after reacting with HCl (e.g. Land 1970);
    ii. dry samples, ash samples at 550°C for two hours (Ash 1 (g)), ash samples again at 990°C to liberate CO_2 (Ash 2 (g)). $CaCO_3$ = Ash 2– Ash 1 * $CaCO_3$ molecular weight, i.e. 100.1/ molecular weight of CO_2, i.e. 44.0. (e.g. Hegge 1998);

- Gravimetry – change in weight of blade after acidified with HCl (e.g. Nelsen & Ginsburg 1986);
- EDTA titration – titration of the solution obtained from acidifying the blade (Patriquin 1972, Frankovich & Zieman 1994);
- Scraping and titration – initial removal of epiphytes by scraping lyophilised (freeze-drying) blades, then acidifying separated epiphytes and titrating the solution (e.g. Patriquin 1972, Penhale 1977).

Frankovich & Zieman (1995) compared the different experimental methods (except for CO_2 evolution "ii"). They determined that the use of acid, whilst the epiphytes were still attached to the blades resulted in overestimations of the epiphytic carbonate. This was due to additional leaching of organic matter from the seagrass blades. All of the above methods have one thing in common – they destroy the epiphytic carbonate, rendering it useless for any further, more detailed analysis. For the purposes of this study, the calcareous epiphytes needed to be retained and hence none of these methods was suitable.

There were two possible ways of retaining the epiphytic carbonate:

- destroy the organic matter, or
- separate the plants from the epiphytes.

Sodium hypochlorite (commercial Chlorex® bleach - NaCl) and hydrogen peroxide (H_2O_2) have been used to remove organic matter (Gaffey & Bronnimann 1993), Hence, simple experiments were formulated to find the effectiveness of bleach and hydrogen peroxide on the removal of seagrass and non-calcareous epiphytes.

Similar abundances (20 g) of newly collected and air dried *Posidonia sinuosa* blades and *Amphibolis antarctica* plants were subjected to the following treatments, using bleach and H_2O_2:

- soaking plants in solutions of 35%, 10% & 5% w/w H_2O_2, and ~10% w/w NaOCl;
- at room temperature for 10, 20, 40, minutes and 1, 2, 5, 24 hours;
- at 70°C for 10, 20, 40, minutes and 1, 2, 5, 24 hours;
- as for 1, but plants cut into 1 cm^2 pieces;
- as for 1, but plants previously scrapped using a razor blade;
- as for 1, but plants vigorously rubbed together and rinsed with water over filters;
- as for 1, but samples placed in ultrasonic bath (Transtek 500T) for 1, 3, 5 hours after initial treatment;
- as for 1, but samples placed in sonifier (Model B-12) for 3, 6, 9, 20 minutes.

The results from these experiments showed that neither Chlorex® nor H_2O_2 are efficient at removing all the organic material. Hence, a separation method was sought. Chlorex® was more efficient at breaking down the organic material, but produced a 'mush' of organic material, making it nearly impossible to separate the epiphytes from the organic matter. The use of H_2O_2 allowed enough break down of organic material to sufficiently loosen the material easily by physical mechanisms.

Gaffey & Bronnimann (1993) warn against using H_2O_2 where preparing samples for mineralogical, petrographic and geochemical experiments. However, the primary reason to retain the epiphytes was to identify them to generic level and to use them for stable isotopic work. In order to test for mineralogical changes caused by the use of H_2O_2 a further simple experiment was carried out. This involved subjecting an aragonitic gastropod, inorganic calcite and dolomite to H_2O_2 at 35% w/w for 72 hours. The samples were analysed before the treatment for mineralogical composition using x-ray diffraction (XRD), and both before and after the treatment, for stable isotopic composition (using stable isotope mass spectrometry). No significant changes in stable isotopic composition occurred (Table 2.5).

Soaking the plants in 10% H_2O_2 for 24 hours did not break down the plants, but did loosen the bond between the calcareous epiphytes and the seagrass blade. To aid separation, placement in an ultrasonic bath for three hours loosened the calcareous epiphytes without damage. The solution was also warmed (<40°C) by the sonic vibration, which helped the reaction. Additionally, vigorously rubbing the blades together removed nearly all (>90%) of the carbonate. Sonification destroyed the carbonate too quickly and it was necessary to heat the samples or cut them into small fragments.

What section of the plant to use in the evaluation of the carbonate produced from calcareous epiphytes has been a further cause of variation in previous studies. Some studies used only the oldest blades (outer blades) (e.g. Nelsen & Ginsburg 1986). Data was then extrapolated by multiplying up to the density (number of blades/m^2) of the seagrass. Other studies have used selected whole shoots (e.g. Frankovich & Zieman 1995, Hegge 1998) and yet others have used whole quadrats (e.g. Walker *et al.* 1991). This study adopted the last method of using the whole quadrat sampled or where biomass was too great for practical purposes, half that obtained. Using half the seagrass obtained has the added advantages of being able to repeat the experiment if needed. It also allows identification of pristine calcareous epiphytes.

Table 2.5 Results of experiment examining the effects of H_2O_2 on the isotopic composition of the carbonate minerals.

Sample	Treatment	C^{13}	O^{18}
Calcite	No treat	-3.58	-6.64
Calcite	No treat	-3.87	-6.58
Calcite	72hr_H_2O_2	-3.62	-6.64
Calcite	72hr_H_2O_2	-3.52	-6.51
Aragonite	No treat	1.01	1.71
Aragonite	No treat	1.03	1.95
Aragonite	24hr_H_2O_2	1.13	1.83
Aragonite	24hr_H_2O_2	1.11	1.73
Dolomite	No treat	1.23	-21.23
Dolomite	No treat	1.26	-21.26
Dolomite	72hr_H_2O_2	1.22	-21.33
Dolomite	72hr_H_2O_2	1.24	-21.09

2.3.2 Summary of methods used to separate calcareous epiphytes

The following process was selected as the best method to separate and retain the epiphytic carbonate.

i) Rinse the samples carefully in fresh water to remove salt and loosen the sediment.

ii) Dry the specimens at room temperature (preferably aided by a fume hood) until totally dry (can take up to one week). Separate any roots and rhizomes that accidentally got incorporated, as well as fauna that is obviously not epiphytic, e.g. starfish, echinoids, gastropods. Weigh the sample.

iii) Divide the sample into a manageable quantity (less than 100 g). Retain the rest of the sample for later use.

iv) Separate the sample into the individual seagrass species. Additionally separate the blades and stems of *Amphibolis* sp. Reweigh each sub-sample.

v) In a fume cupboard, slowly pour 100 ml of 10% H_2O_2 over the samples and allow to stand for 1/2 hour. Top up with more 10% H_2O_2, until the seagrass is totally covered. Place in a dark cupboard, in a fumigated area and leave to stand for 24 hours.

vi) Place each sample in the ultrasonic bath for three hours.

vii) Pour the sample through two sieves (3.5 mm and 65 μm), and then using water, at moderately high pressure rub the seagrass together until the epiphytic carbonate falls off the seagrass. The majority of the carbonate then passes through the 3.5 mm sieve to be retained on the 65μm sieve, whilst the majority of the plant material is left behind on the 3.5 mm sieve.

viii) Retain the residual solution and allow it to stand for 5 minutes. Any carbonate that passed through the 65 μm sinks to the bottom. All but the last 500 ml is poured out, the remaining solution agitated and then sub-sampled (100ml). A further 30 ml of 35% H_2O_2 is added (resulting in a 10% H_2O_2 solution) removing any remaining organic material. The solution is then filtered dried and weighed to obtain an approximate evaluation of the epiphytic carbonate that has a diameter <65 μm.

ix) Air-dry the remaining plant material and the separated calcareous epiphytic material.

x) Once dry, the remaining plant material can then be checked for any remaining calcareous epiphytes. Scraping, picking and rubbing can then remove the last few calcareous epiphytes. The separated material is added to the previously separated material. The remaining plant material is weighed.

xi) The separated epiphytic carbonate is subjected to 10% H_2O_2 for a further 24 hours, to remove remaining organic matter. Remove the excess solution and top up with distilled water, allow to stand for 12 hours, then repeat. Allow to dry on a low heat.

xii) Finally, carefully pick through the remaining carbonate, removing any residual organic material. Re-weigh.

2.3.3 Limitations and estimations of error

The main drawback to this method is that it is time consuming. It takes approximately 10 hours laboratory time and 1.5 weeks waiting time to complete one transect. The process includes the assumption that when there is more than 1 plant species in a quadrat and a sub-sample size is required (stage iii) the sub-sample will retain the same ratio of plant species as that which was in the original quadrat. It was not possible to separate any sand grains that were adhered to the glutinous epiphytes. At stage ii, iii & iv of the process, looser epiphytes may fall off. These are retained and treated as before, but if they came from a mixed seagrass bed, it was not possible to determine which plant type they originated from, hence the data could only be added to the carbonate of the quadrat as a whole.

Table 2.4 gives a summary of the possible errors and the estimated % error incurred by each. In total, values could be up to 10% more than calculated, or 5% less than calculated. In reality, some samples will have higher inaccuracies than others. The main cause of error is terrigenous sediment contamination. The percentage estimations are qualitative only.

2.3.4 Sediment analysis

Descriptive composition and quantitative analysis of the carbonate/non-carbonate ratio was determined for every site. All samples were rinsed with fresh water and dried to remove inorganic salts. Grain size was determined by sieving 10 g of each sample, through 500 μm, 250 μm and 150 μm sieves. Each fraction was weighed and the dominant fraction was considered to represent the typical grain size. Assessment of the quantity of carbonate contained within each sample was carried out using acid digestion of the carbonate using 10% HCl. Using a known weight (wt 1) of sediment (10 g), the organic content was destroyed using 10% H_2O_2.. The sample was allowed to dry, reweighed (wt 2) and then the carbonate was digested using 10% HCl. After thorough rinsing, the sediment was allowed to dry and was reweighed again (wt 3). The difference between wt 3 and wt 2 is the carbonate content.

2.4 DATA ANALYSIS FOR CHAPTERS 3-5

2.4.1 Standing stock calculations

Carbonate values have been calculated as the amount of carbonate per area ($CaCO_3$ g/m^2) and per kilogram weight of seagrass ($CaCO_3$ g/kg of seagrass). The implications of using these two methods of calculating carbonate values are described below.

2.4.1.1 Carbonate production per square metre

This is calculated for each quadrat or plant species using the following equation:

$$C\ gm^2 = \left[\left(\frac{C}{\sum P_i}\right) \times P\right] \times 4 \qquad \text{Eq. 1}$$

where:
C $CaCO_3$ (g)
P Total dry seagrass (includes the carbonate) (g)
P_i Weight of individual seagrass groups used (weight includes the carbonate) (g).

The result is multiplied by 4 to give a one m^2 value, as the quadrat size is 50 cm X 50 cm.

2.4.1.2 Carbonate production per kilogram of seagrass

A disadvantage of the carbonate g/m^2 values is that they are dependent on the density of the seagrass and not on the amount of carbonate that is actually found on each plant. It is necessary to calculate the carbonate quantity independent of the various seagrass densities from site to site to compare carbonate values. The amount of carbonate found upon a known weight of seagrass is calculated, i.e. $CaCO_3$ g/kg of seagrass. This is calculated by;

$$\left(\frac{C}{P_i}\right) \times 1000 \qquad \text{Eq.2}$$

The relationship between $CaCO_3$ g/kg of seagrass and the seagrass sample size is a matter of ratio. The greater the ratio, the lower the $CaCO_3$ g/kg of seagrass value and vice versa.
For example, 10 g of $CaCO_3$ in 60 g of seagrass, a ratio of 1:6, results in 166.6 g of $CaCO_3$ g/kg of seagrass and 40 g of $CaCO_3$ in 60 g seagrass, a ratio of 1:1.5, results in 666.6 g of $CaCO_3$/kg of seagrass.

This ratio results in a problem when small samples are used. This is because the value of the carbonate separated is more likely to have associated errors – predominantly the retainment of some of the organic matter. As the carbonate value is so low, it is difficult to separate it further. Hence the calculation of $CaCO_3$ g/kg of seagrass produces large numbers. An exception to this was the calculation of $CaCO_3$ g/kg of seagrass for the loose sediment. Here it was necessary to use the sum of the biomass used in each quadrat.

$CaCO_3$ g/m^2 is used when analysing the effect of seagrass biomass on the carbonate abundance and when comparing the results with other studies. $CaCO_3$ g/kg of seagrass measurements were used for all other analyses as they allow evaluation of the carbonate independent of seagrass biomass.

2.4.2 Calcareous epiphyte productivity

The productivity rates from standing stock values, is achieved by multiplying the standing stock value by the number of crops per year, i.e. crop turnover. Crop turnover is estimated from leaf productivity and the lifespan of the blades. It was not within the scope of this project to estimate seagrass productivity. Hence values from previous studies were adopted (Table 1.2). This method of calcareous epiphyte productivity results in broader estimations than from other studies that determine calcareous epiphyte productivity by examining smaller areas or even individual blades (e.g. Nelsen & Ginsburg 1986).

2.4.3 Biomass (standing stock)

The term biomass is used to refer to the standing stock of the seagrass. (Standing stock is used only when referring to the epiphyte abundance). Two measurements of biomass were available i) total biomass ($\sum$bio) which was the dry weight of all biomass within each quadrat, multiplied by 4 (see 2.4.1), and ii) seagrass biomass which is $\sum$seagrass biomass in g/m^2 - $CaCO_3$ g/m^2. It is important to note that the values for seagrass biomass do not exclude the biomass from non-calcareous epiphytes. When comparing the biomass of genera and species it is assumed that 1 cm^2 of one species is equivalent to 1cm^2 of another species. The surface area of each plant represents the amount of potential surface for epiphytes to encrust and can be determined using measurements of blade/stem length and width. Surface area of typical *Amphibolis* and *Posidonia* plants was calculated by obtaining measurements of length and width of blades and stems.

2.4.4 Data analysis

Factors affecting biomass and carbonate quantity were analysed using Analysis of Variance (ANOVA) with SPSS 10.0 software and JMP 3.0.2. Variance heterogeneity was checked using Levene's test and normal distribution was tested using the Kolmogrov-Smirnov test, where the number of samples was greater than 20, otherwise the Shapiro-Wilk test was used. Data was transformed where necessary – the appropriate transformation estimated using Taylors power law and the ladder of powers. Most often log10 transformation was found to be appropriate. The probability of level of $\alpha = 0.05$ was assumed, unless transformed data failed Levene's test for variance homogeneity in which case a more conservative alpha value was adopted (i.e. $\alpha = 0.01$) (Underwood 1981). *Post hoc* comparison of means determining where significant differences lie was carried out using Tukeys-HSD test. Non-parametric Kruskall-Wallace analysis of variance was used where gross violations of normal distribution and failure of homogeneity occurred (Underwood 1981, Zar 1996). Significant differences were identified using the *post hoc* Tukey style, Nemenyi comparison of means. Seagrass species distribution was analysed by cluster analysis (JMP 3.0.2) and multi dimensional scaling (MDS) using the Bray-Curtis association measure for the similarity matrix (Pcord 4). Student t-test was used to test differences in carbonate abundances between genera. All averages given are means and standard errors are provided where possible.

2.5 FAUNAL ASSEMBLAGES

The methods described relate to Chapter 7.

The faunal assemblage data comprises the:

- identification of the calcareous epiphyte phyla/species at each site;
- quantification of the relative abundance of the calcareous epiphyte phyla/species; and
- distribution of calcareous epiphyte phyla/species on the seagrass shoots.

The most efficient method to estimate abundances of phyla and species was to collect and rank the relative abundances, i.e. obtain ordinal data. The ranks were calibrated using diagrams with known percentage coverage/composition. The ranks/classes used are shown in Table 2.6.

The following method was designed to address the described aims:

i. randomly select three quadrat samples for each site;
ii. select 10 mature *Posidonia* blades and/or 3 *Amphibolis* plants from each quadrat sample. Mature *Posidonia* blades were identified by blade length and the state of the tip;
iii. separate three clusters from the *Amphibolis* plant – the apex cluster, one near the middle of the plant and the lowest cluster. Further separate off the outer two blades of each cluster;
iv. soak the selected blades in de-ionised water for up to 15 minutes. This reconstitutes the blades to their (approximately) original size;
v. measure blade length and width and note the state of the blade (damaged, whole, brown, algal covered). Surface area was used rather than biomass for practical reasons and because previous studies have shown that biomass and leaf surface area are highly correlated (Jernakoff & Nielsen 1998);
vi. estimate the % coverage of calcareous epiphytes for each quarter of the blade, to assess the ontogeny differences;
vii. estimate the relative abundances of the different calcareous epiphyte taxa (coralline algae, bryozoans, spirorbids, serpulids, foraminifers, ostracods, bivalves and other);

Table 2.6. Ranks used to estimate epiphyte abundance.

Class	0	1	2	3	4	5	6	7
% Estimate	Absent	Present/ rare	1-5	6-10	11-25	26-50	51-75	76-100

Table 2.7. Morphological identification parameters for coralline algae.

Type	Descriptive	Genera and species types
1	Encrusting, nodular or blanket	*Hydrolithon* sp., *Pneophyllum,* sp., *Synarthrophyton* sp.
2	Encrusting, sheet	*Hydrolithon* sp., *Pneophyllum,* sp.,
3	Erect, thinly branching, filamentous	Jania sp.?
4	Erect, multiple branching, narrowly segmented	*Corallina* sp., *Arthocardia* sp., *Jania* sp., *Haliptilon* sp.
5	Erect, simple branch, broadly segmented	*Metagoniolithon radiatum*

Table 2.8. Classification of epiphytic bryozoans (adapted from Bone and James, 1993)

		Epiphytic example
Erect	Fenestrate	*Iodictyum* sp.
	Foliose	*Lanceopora smeatoni*
	Flat robust branching	*Adeonellopsis sulcata*
	Delicate branching	*Cellaria* sp.
Erect flexible	Articulated branching	*Crisia acropora*
	Articulated zooidal	*Emma rotunda*, Claviprella aurita
Encrusting	Robust sheet	*Petralia* sp.
	Delicate sheet	*Thairopora* sp a., *Celleporaria delta*
	Delicate branching	*Heterooecium* sp., *Aetea* sp.

Table 2.9. Classification table for epiphytic serpulids and spirobids based on morphological structure of the calcareous tubes.

5 ✓

Assigned no.	Descriptive	Identification
spirobids		
1	Dextral coil, rough surface, 1 indistinct longitudinal ridge, moderately involute	unknown
2	Dextral coil, 3 distinct longitudinal ridges, involute	*Janua* (*Dexiospira*) *lamellosa*?
3	Sinistral coil, smooth but with one obtuse longitudinal ridge, evolute	*Metalaeospira tenuis* ?
4	Dextral coil, 3 distinct longitudinal ridges, transverse furrows	*Janua* (*D.*) *fenestrata*
6	Sinistral coil, indistinct transverse growth striae, evolute, <3mm width	unknown
7	Dextral coil, multiple distinct transverse ridges, moderately involute	unknown
8	Sinistral coil, smooth, porcelain appearance, evolute	*Metalaeospira tenuis*
9	Sinistral coil, rough surface, 1 indistinct longitudinal ridge, Indistinct transverse growth striae, moderately involute	unknown
10	Sinistral coil, smooth, porcelain appearance, coils on top of each other	unknown
11	Sinistral, 1 distinct longitudinal coil, involute, outer whorls grossly larger then inner whorls	*Janua* (*D.*) *formosa*
serpulids		
1	Two distinct longitudinal ridges with violet colouring	*Pomaoceros taeniatus*
2	Indistinct transverse growth striae, no colouring	*Galeolaria* sp.

Table 2.10. Example of method to determine average % abundance of specific epiphyte taxa/species on whole *Posidonia* blade.

Estimate	Absent	Present/ rare	1-5	6-10	11-25	26-50	51-75	76-100	TOTAL
Class	0	1	2	3	4	5	6	7	
M_i	0	0.1	2.5	7.5	17.5	37.5	62.5	87.5	**215.4**
f_i	2	2	2	1	2	3	4	19	**30**
$M_i * f_i$	0	0.2	5	8	36	114	252	1672	**2087.2**
								Av. %	**69.57**

viii. identify the different species of each phyla, note the position on the blade (1st quarter, 2nd quarter etc.), their relative abundance to each other, the approximate number and whether the mode of encrustation (directly to blade, encrusting another epiphyte, loosely attached or not observed to be attached);

ix. repeat v-viii for each blade.

2.5.1 Species identification

2.5.1.1 Coralline algae

A morphological identification was adopted for both geniculate and non-geniculate coralline algae due to the difficulty of identifying, in particular, non-geniculate (encrusting) coralline algae to species level without cross-sections through the conceptacles (Table 2.7). Identification was aided by Womersley (1996).

2.5.1.2 Bryozoans

Bryozoan species identification was predominantly carried out by Rolf Schmidt, Geology and Geophysics Department, University of Adelaide (pers. comm. 2001) and with the aid of Bock (1982) and other literature. Bryozoans were also classified according to their growth form, using an adapted version of the morphotype classification by Bone & James (1993) (Table 2.8).

2.5.1.3 Foraminifers

Foraminifer species identification was undertaken by Qianyu Li, Geology and Geophysics Department, University of Adelaide (pers. comm. 2001) and with the aid of Yassini (1995) and other literature. In addition, foraminifers were also identified according to their attachment process; i) clinging, ii) adhesive, or iii) encrusting (Poag 1982).

2.5.1.4 Serpulids and spirorbids

Species identification of serpulids and spirorbids is not possible without examination of soft body parts, hence classification was carried out using the morphology of the calcareous tubes (Table 2.9). Some species were possible to identify using Knight-Jones & Knight-Jones (1973) and Hutchings (1982).

2.5.1.5 Ostracods

Ostracod identification was undertaken by Miles Davies, Geology and Geophysics Department, University of Adelaide (pers. comm. 2001) and with the aid of Yassini (1995) and other literature.

2.5.1.6 Bivalves

Only those bivalves which appeared to have some adaptation or ability to attach themselves to the seagrass were included in the study. Gastropods, although abundant within the seagrass environment, are permanently mobile.

2.5.2 Data analysis

The method to derive qualitative estimates of the relative abundances from ranked data is adapted from Saito & Atobe (1970 cited in English *et al.* 1997). The formula is:

$$A = \frac{\Sigma(M_i \times f_i)}{\Sigma f} \qquad \text{Eq.3}$$

where M_i = mid point value of each class

f_i = frequency of each class (number of blades with same class)

An example of this method, using data from this study is outlined in Table 2.10. A limitation of this procedure is that due to the mid point values, the average % that can be recorded is 88%.

2.5.3 Carbonate abundance of each species

Estimations of the amount of carbonate derived from each species within each taxa can be calculated using the abundance ratio of each species, the standing stock values of calcareous epiphyte abundance from each site on each seagrass species present.

$$\frac{\%sp_i}{100}C \qquad \text{Eq. 4}$$

Where $\%sp_i$ is the percentage of species 'i' present (on a seagrass species 'a' sample taken from a specific site 'b') and C is the carbonate abundance (g/kg of seagrass) on the same seagrass species at the same site. These calculations assume that the density (or specific gravity) of each calcareous epiphyte is the same. Carbonate mineralogy clearly shows this premise is incorrect.

CHAPTER 3

SEAGRASS BIOMASS AND DISTRIBUTION, SOUTH AUSTRALIA

3.1 INTRODUCTION

The dependence of calcareous epiphytes on their hosts requires the identification of the mechanisms that control the distribution and productivity of the host seagrass. This chapter addresses the geographical species distribution and parameters effecting seagrass biomass in South Australia (Fig. 3.1). The methods used are outlined in Chapter 2.

3.2 SEAGRASS SPECIES AND DISTRIBUTION

Six seagrass species from three genera were sampled:

- *Posidonia sinuosa* Cambridge & Kuo 1979;
- *P. angustifolia* Cambridge & Kuo 1979;
- *P. australis* J.D. Hooker 1858;
- *Amphibolis antarctica* (Labillardiere) Sonder & Ascherson ex Ascherson 1867;
- *A. griffithii* (J. Black) den Hartog 1970;
- *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog 1970.

Two additional genera (*Zostera* sp. and *Halophila* sp.) were found but, as with *Heterozostera tasmanica,* were considered insignificant in abundance compared to the other 5 species and were grouped as 'other' species. Table 3.1 gives the taxonomic descriptions used to identify the species. A glossary for seagrass terms is given on CD.data.

The distribution of seagrass species was examined to determine whether resulting patterns correlate with distribution patterns of calcareous epiphyte abundance and species. The distribution pattern of epiphytes is examined in later chapters. Figure 3.2 shows the distribution of the five predominant seagrass species found during this study. Analysis of the distribution of these species was carried out using cluster analysis and MDS (Fig. 3.2) which showed that:

- *Posidonia* and *Amphibolis* were found across the study region;
- *P. angustifolia* was more common in Gulf St. Vincent and towards the eastern side of the study area and it occurred largely in monotypic beds;
- *P. australis* reached its eastern-most extent on the southern edge of Yorke Peninsula (Port Moorowie; Fig. 2.1) and occurred predominantly in monotypic beds, although occasionally occurring with *P. sinuosa, A. antarctica* and 'other' species;

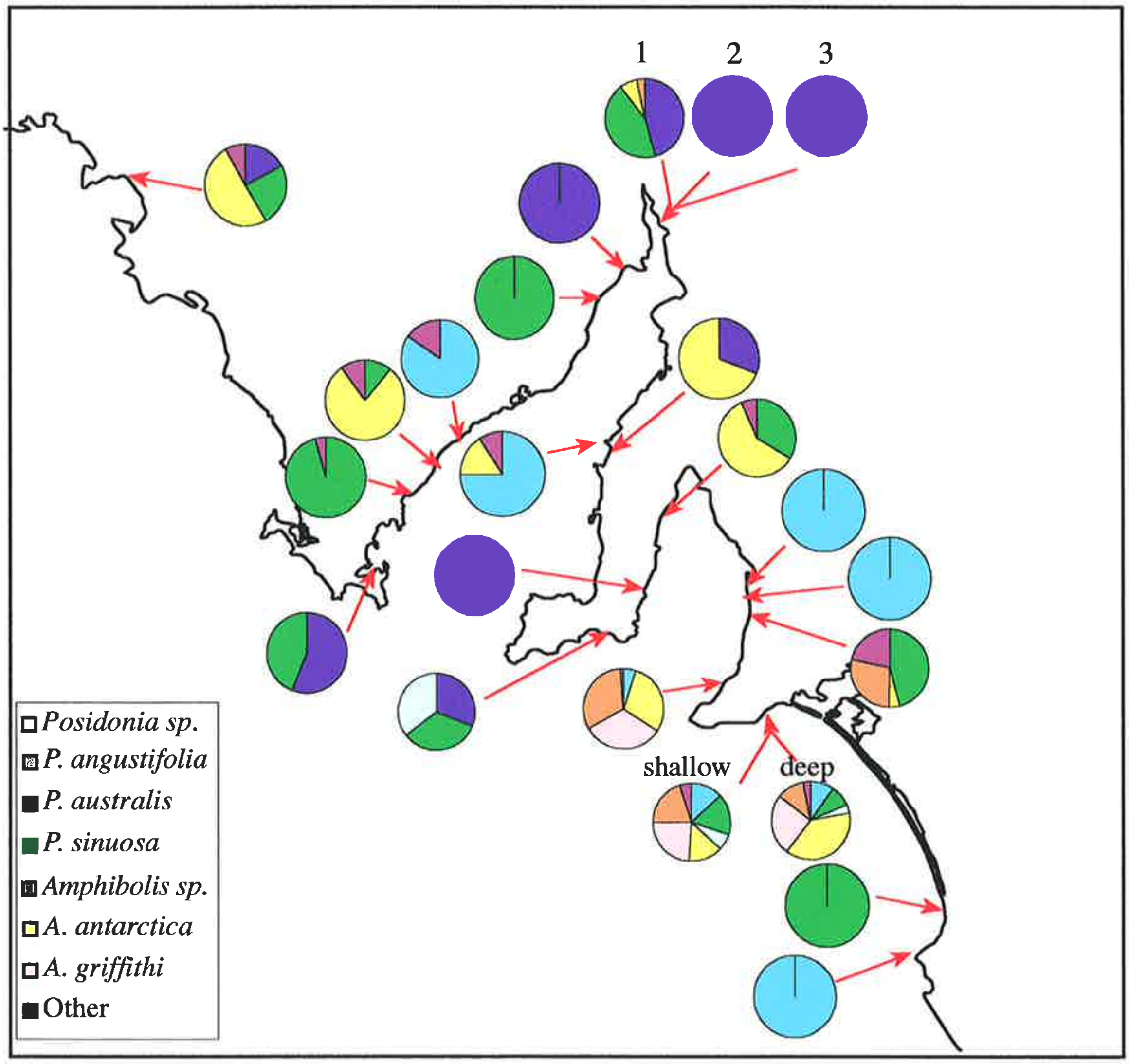


Fig. 3.1. Seagrass distribution map. Piecharts indicate species type and relative biomass.

Table 3.1. Ecological and morphological characteristics of seagrasses used in their identification (from Jernakoff et al., 1996,Womersley 1984)

Genus	species	habitat	temp.	depth	salinity	leaf longevity (days)	leaf length (cm)	leaf width (mm)	no. of leaves	description
Cymodoceaceae									creeping, monopodially or sympodially branched rhizomes. Leaves: distichous, with distinct blade and sheathing base; leaf sheath ligulate auriculate;leaf blade flat and linear or terete and subulate	
Halodule	*uninervis*	bays with sand and mud	tropical/ ristricted temperate	littoral, sublittoral to 30m	euryhaline to hyperhaline		6-15	0.5-3.5	2	leaf blade shed before the persistent sheath; blade narrow; blade veins 3, longitudinal, a midrib and 2 submarginal veins.Pioneer species and rapid coloniser
Thalassodentron	*pachyrhizm*	marine exposed rock & sand covered rock substratum	temperate	sublittoral to 30m	stenohaline	240	7-40	6-12	4	*Thalassondendron:* leaf blades with denticulate margins; apex rounded & coarsely denticulate. Stems unbranched or little branched, arising regularly at every fourth internode. Roots unbranched. *pachyrhizum:* leaf sheath compressed (3-4cm long), midrib prominant, 7-9 inconspicuous parallel veins either side of midrib connected by cross veinings.
Amphiboils	*antarctica*	near coastal & marine embayments	temperate	sublittoral to 23m	36-62.4	28-40	18-30	3.5-10	8-10	*Amphbolis:* leaf blades entire;apex bidentate. stems much-branched, arising at irregular intervals of 4-8 nodes. roots branched, arising at each node. *antarcitca:* leaf blades flat, usually twisted about 180° in the upper half; apex truncate or lunate with 2 acute marginal teeth. sheath margins overlapping lower half only
Amphibolis	*griffithii*	near coastal & marine embayments	temperate	sublittoral to 40m	stenohaline		3-10	3-7	3-5	leaf blade flat, not twisted, or only by 45-90° near the apex. apex notched with obtuse teeth. sheath margins completely overlapping.
Hydrocharitaceae									leaves: basal or arising along the stem.	
Halophila	*decipiens*									*Halophila:* leaves- in pairs,

paddleweed										petiolate, distinct blade, linear to ovate, with a midvein an an intramarginal vein connected by parallel crossveinsplant monoecious; leaf marins always finely serrulate; glabrous or hariy to a variable extent
Halophila	*ovalis*	marine and estuarine	above 10°C		euryhaline		15-25	0.4-1		Plants dioecious, leaf marings entire; blade always glabrous; leaf blade oblong to obovate, mostly rounded at base
Halophila	australis									Plants dioecious, leaf margins entire; blade always glabrous; leaf blade more or less ellipitc, narrowed towards the base
Potamogetonaceae										perennial herbs, rooted to substrate. Leaves; basal or cauline, commonly sheathing at the base, mostly ligulate. monopodial or sympodial rhizomes rooting at the nodes. roots unbranced. leaaves with sheathing base, eligulate.
Ruppia	*megacarpa*						20-200cm	0.4-1.0		Ruppia: roots 1-2 per node, unbranced, root hairs abundant. stems very short or absent, up to 2.5m long and flexuous. leaves alternate (except 2 immediatley below inflorescence which are sub-opposite), shealth open, edges overlapping, eligulate, auriculate, blade narrow-linear to filiform, more or less concavo-conves in x-section. megacarpa - leaf apex bidentate or truncate; robust perennia; erect stems conspicous; turions absent
Ruppia	*tuberosa*							0.1-0.5 mm		leaf apex rounded to acute; annual or delicate perennial; erect stems very short or absent; turions frequently presant. only tell by fruit
Ruppia	*polycarpa*	brackish, coastal lakes			<66‰			0.5 mm		leaf apex rounded to acute; annual or delicate perennial; erect stems very short or absent; turions frequently present
Posidoniaceae										
Posidonia	*angustifolia*	open nearshore waters	temperate	sublittoral 2-35m	stenohaline		20-75	4-6	2-3	leaf sheaths pale-yellow, becoming shaggy and fibrous disintegrating into a mass of pale hair like fibres. leaf blade epidermal cells in surface view with straight margin. epidermal cells in

										surface view elongate
Posidonia	*australis*	marine, sheltered and near coast	temperate	0-14m	35-55‰	67-75 (WA) 91-125 (NSW)	20-45	10-15	2-3	leaf blade flat, or somewhat concavo-convex, with upper and lower faces parallel. epidermal cells in surface view isodiametric. leaf sheaths pale-yellow, becoming shaggy and fibrous disintegrating into a mass of pale hair like fibres. leaf blade epidermal cells in surface view with straight margin
Posidonia	*ostenfeldii*							2-5		leaf blade thick & tough, biconvex to round in x-section. 5-9 longitudnial vascular bundles. not terete in any part
Posidonia	*aff. ostenfeldi*							1-1.5		leaf blade thick & tough, biconvex to round in x-section. leaf blade terete, round in x-section when fresh. becomes flattened then tapering higher up, terminating in a spathulate apex
Posidonia	*sinuosa*	marine, sheltered, near coastal, less sed. depo.	temperate	1-35m	stenohaline	84-168	30-70	7-9	1-2	leaf sheaths brown to red/brown, remaining entire and not disintegrating into hairy fibures, strawlike in texture when dry. leaf blade epidermal cells in surface view with sinuose margins
Zosteraceae										
Zostera										internode in transverse section showing 4-12 cortical vascular bundles; erect shoots apparenty vegetative,in older plants some times developing inflorescences.
Zostera	*mucronata*	extremely shlelterd shallow bays, sand and mud	temperate	upper middle intertidal	hypersaline in summer		2-22	0.75 - 1.75	2-5	leaf apex more or less tridentate, with central vein ending in a distinct mucro: roots two only at each node
Zostera	*muelleri*	marine protected bays sand and mud	temperate	intertidal	euryhaline		5-30	0.75 -2	2-5	Leaf apex truncate, or roundedand notched with central vein without a mucro; roots 2 to several at each node. leaf apex rounded and usually more or less deeply notched, frequently with some fine

										denticulations; leaf blade with 3 longitudinal veins, the two lateral ones submarginal.
Zostera	*capricorni*	marine, sand and mud	warm temperate	low water to about 6m	polyhaline		7-50	2-5	2-5	Leaf apex truncate, or roundedand notched with central vein without a mucro; roots 2 to several at each node. Leaf apex truncate; leaf blade with 4-5 longitudinal veins, the lateral ones on either side of the central vein well-spaced from the marginal veins.
Heterozostera	*tasmanica*									internode in tranvserse section showing only 2 vascular bundles in cortex, erect shoots always developing inflorescences

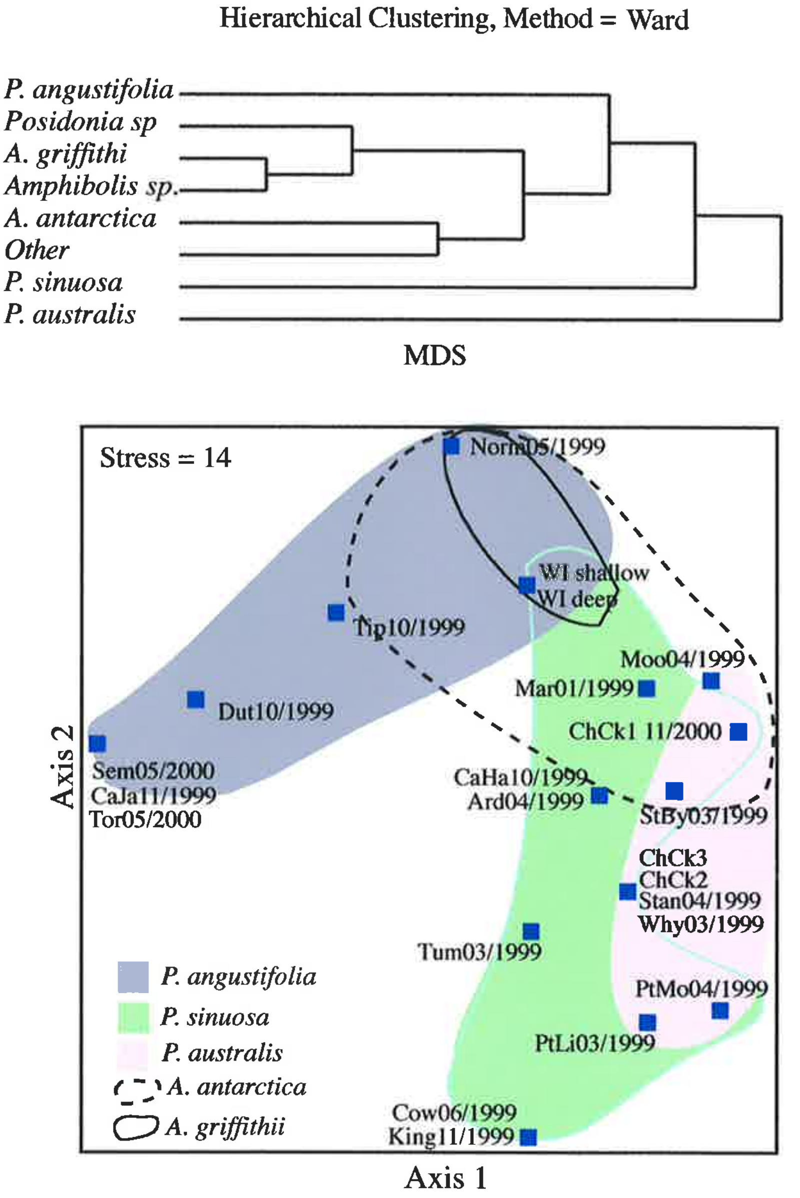


Fig. 3.2. Dendogram of cluster analysis and corresponding multi-dimensional scaling plot showing groupings of seagrass distribution relationships

A. antarctica occurred along the entire coastline but was always found with *P. australis* or *P. sinuosa*. It was also occasionally found with *A. griffithii* and 'other' species.

- *A. griffithii* was only found at the eastern edge of the study area and always with *A. antarctica* and *P. angustifolia*.

3.3 BIOMASS

The abundance of the above seafloor seagrass biomass was assumed to reflect the amount of surface area available for epiphyte recruitment. Identifying controlling parameters effecting distribution of the biomass of seagrass may enable the predictability and extrapolation of data for calcareous epiphyte abundance. The correlation between seagrass biomass and calcareous epiphyte abundance is examined in Chapter 4.

The averaged dry weight site value (West Island sites were aggregated as one site) was 401.3 g/m^2 (± 17.7 standard error) total dry biomass ($\sum$biomass), or 322.5 g/m^2 (± 12.48) seagrass biomass. The maximum quadrat biomass obtained was 1338.4 g/m^2 $\sum$bio or 883.9 g/m^2 seagrass biomass. Seagrass biomass and total dry biomass lay predominantly (>70% of samples) between 50-500 g/m^2. Averaged site values ranged from 57.7 g/m^2 $\sum$biomass (42.9 g/m^2 seagrass biomass) at Semaphore (Fig 2.1) to 781.5 g/m^2 $\sum$biomass (557.5 g/m^2 seagrass biomass) at Streaky Bay (Fig. 2.1, Table 3.2).

3.3.1 Parameters controlling biomass distribution

4.1 3.3.1.1 Geographic position (Fig. 2.1)

Geographical distribution of biomass within the scale of this project shows no relationship either with latitude or longitude (Fig. 3.1, 3.3). Relationships with latitude were determined using sites within the Spencer Gulf. Total dry biomass at Port Lincoln, on the west coast of the Spencer Gulf, was 354.3 g/m^2 $\sum$biomass [310.3 seagrass biomass]; at Dutton Bay it was 99.9 g/m^2 $\sum$biomass [85.4 seagrass biomass]; it then generally increased northwards to the head of the Gulf at Chinaman Creek where it ranged from 227.4 – 455.3 g/m^2 $\sum$biomass [203.9-442.9 seagrass biomass]. Biomass values on the east coast of the Spencer Gulf show an apparently random change in biomass (Fig. 3.3). Results indicate there was no clear reduction or increase in biomass with changes in latitude and no correlation between the two sides of the gulf.

Sites located at similar latitudes across South Australia were used to examine changes in biomass with longitude (Fig. 3.3). The first geographical transect used sites at Port Lincoln,

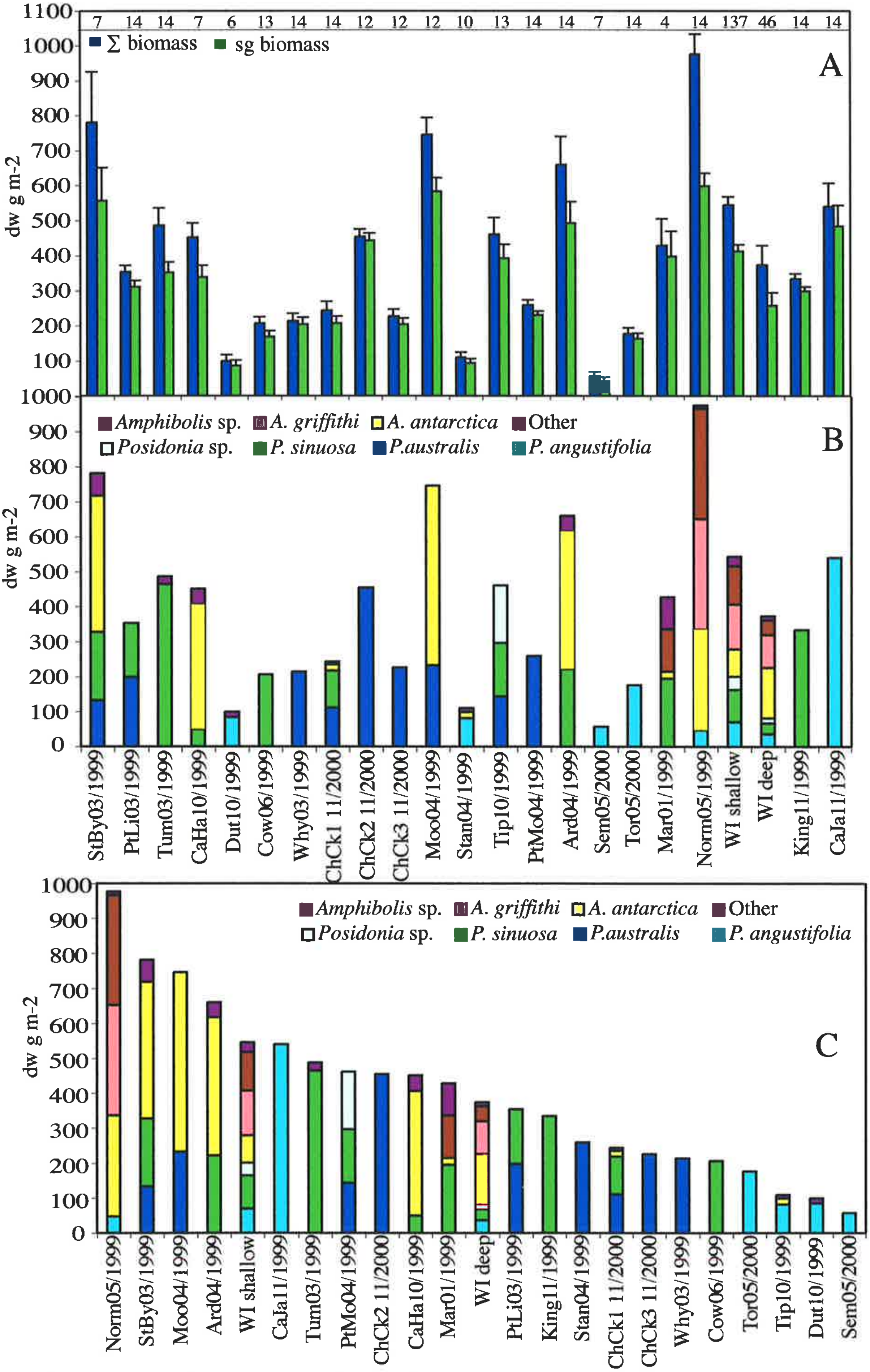


Fig. 3.3 . A.Total and seagrass biomass from all sites arranged from west to east. Numbers at top refer to the number of quadrats sampled at each site. B. Species contribution to biomass ordered from west to East. C. As for B, but arranged in numerical order. Mean ±SE

Stansbury and Semaphore which show a steady decline in biomass from west to east (354.3 g/m^2 Σbiomass [310.3 seagrass biomass] to 57.7 g/m^2 Σbiomass [42.9 seagrass biomass]). However, if Torrens site (Tor05/2000) is exchanged for the Semaphore site (Semaphore is located at a similar longitude and latitude as the Torrens site) (Semo5/2000) then the declining pattern no longer occurs and the minimum biomass is in the central part of the transect (Fig. 3.3). A second transect, using sites from Dutton Bay, Tiparra Reef and Moonta Bay, shows a peak in biomass in the centre of the transect. These results suggest that, at this scale, there is no regional correlation with longitude.

3.3.1.2 Depth

Kruskall-Wallis analysis of variance indicated a significant variation of biomass with depth, both with different genera and mixed genera ($P \leq 0.001$ *Posidonia* sp., $P \leq 0.05$ *Amphibolis* sp., $P \leq 0.001$ mixed genera) (Fig. 3.4). The significant variation is in the form of a negative correlation ($r^2 = 0.74 - 0.86$). Overall biomass decreases from 504 ± 34.5 g/m^2 at 2-4 m mwd to 155.7 ± 89.7 g/m^2 at >10 m (Fig. 3.4). The limited number of samples available from depths greater than 10 m mwd decreases the power of this analysis. It is also noted that biomass is greater at 2-4 m mwd depth than at 0-2 m mwd (Fig. 3.5).

3.3.1.3 Genera and species

The site average results include 8 different seagrass species types. ANOVA was used to determine if species diversity had an effect on the biomass. The test was run on the number of seagrass species present at a site against the average biomass at that site. The results showed no apparent correlation between seagrass diversity and biomass.

Different genera and species have high variance in biomass. For example, the average biomass of *A. antarctica* at Normanville was 852.8 g/m^2 Σbiomass [528.1 seagrass biomass] and at Tiparra Reef was only 19.4 g/m^2 Σbiomass [16.3 seagrass biomass] (Table 3.2). At Normanville biomass values of *A. antarctica* varied between 506.6 g/m^2 Σbiomass [324.5 seagrass biomass] and 1045.5 g/m^2 [736.9 seagrass biomass] (Table 3.2). Comparison of biomass values from each quadrat for *Posidonia* and *Amphibolis* showed that average biomass was higher for *Amphibolis* sp. (558.3 ± 4 g/m^2 Σ biomass [404.7 seagrass biomass] $n = 60$) than for *Posidonia* sp. (292 ± 11.8 g/m^2 Σ biomass [252.3 seagrass biomass] $n = 202$). On occasion, both genera occurred in one quadrat. Hence, the biomass values are not independent and it was not possible to determine significant differences using ANOVA. Instead each quadrat was classified for the dominant species and ANOVA was run on these.

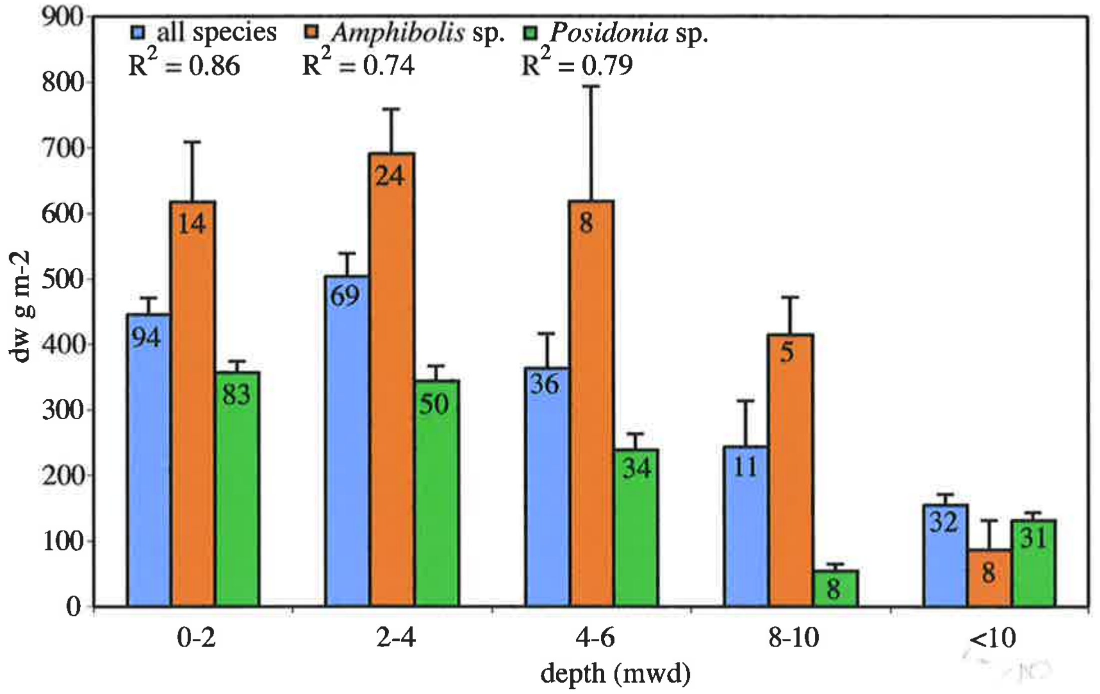


Fig. 3.4 Graphical distribution of seagrass biomass values with depth. Values grouped at 2mwd intervals, combined species and by genera. Number at top of column refers to number of samples collected. Mean ±SE

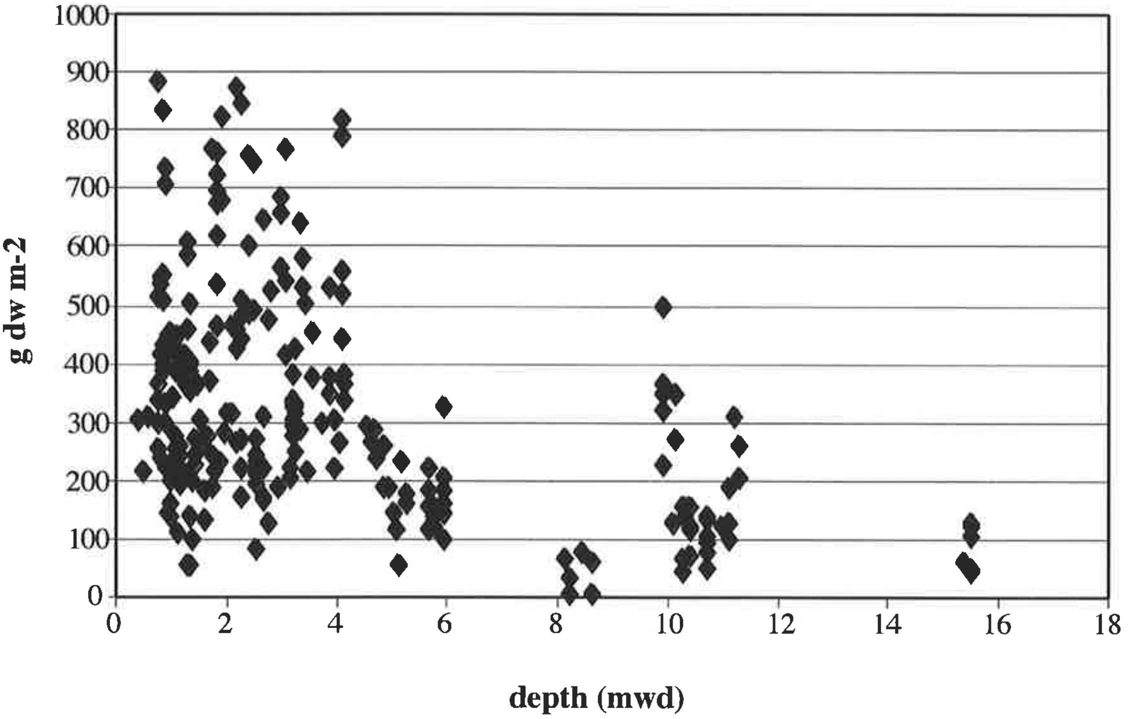


Fig. 3.5. Graphical distribution of seagrass biomass values with depth.. Values grouped by 2mwd intervals, combined species and by genera. Scatter plot of indivdual quadrat data

Table 3.2. Summary of total and seagrass biomass averages (g dw/m^2) from all sites. ∑bio = total biomass sg bio = seagrass biomass

Site	Total		*A. antarctica*		*A. griffithi*		*Amphibolis* sp.		*P. angustifolia*		*P. australis*		*P. sinuosa*		*Posidonia* sp.		Other	
	∑ bio	sg bio	∑bio	sg bio	∑bio	sg bio	∑bio	sg bio	∑bio	sg bio	∑bio	sg bio	∑bio	sg bio	∑bio	sg bio	∑bio	sg bio
Ardrossan	660.3	492.7	572.9	447.8									321.7	287.0			62.5	0.1
Cape Hardy	451.6	338.5	379.0	313.5									52.6	49.6			48.0	2.8
Cape Jaffa	540.5	484.1							518.8	462.6								
Chinaman Ck 1	244.2	206.9	38.6	33.2			18.0	14.8			244.0	212.9	233.3	194.3				
Chinaman Ck 2	455.3	442.9									455.3	442.9						
Chinaman Ck 3	227.4	203.9									227.4	203.9						
Cowlers Landing	206.6	168.9											206.6	168.9				
Dutton Bay	99.9	85.4							97.0	85.4							17.4	
Kingston	334.0	298.3											334.0	298.3				
Marino Rocks	428.8	397.8	39.3	36.7			242.5	228.0					394.3	377.5			184.7	164.3
Moonta Bay	746.0	583.1	724.1	563.6							329.0	265.9						
Normanville	976.0	599.0	852.8	528.1	932.7	571.9	928.0	551.6	140.2	126.3							29.4	25.2
Port Lincoln	354.3	310.3									365.4	325.5	287.3	219.1				
Port Moorowie	461.3	392.0									421.8	385.6	454.4	387.2	485.1	403.3		
Semaphore	57.7	42.9							66.0	49.2								
Stansbury	259.8	230.6									259.8	230.6						
Streaky Bay	781.5	557.5	697.7	576.7							237.9	210.3	349.0	294.1			113.1	
Tippara Reef	110.0	93.3	19.4	16.3					91.2	81.0							11.3	3.8
Torrens outlet	177.1	162.9							177.1	162.9								
Tumby Bay	487.1	352.5											457.1	328.4			21.8	
Whyalla	214.1	203.8									214.1	203.8						
West Island -6m	544.7	413.4	205.0	150.0	338.7	240.2	286.0	176.1	184.8	160.1			246.9	232.9	95.6	78.8	72.5	29.4
West Island-10m	374.5	257.5	578.8	377.0	376.4	281.4	168.8	111.5	147.5	138.5			126.5	114.5	57.1	53.6	48.7	9.2
AVERAGE	401.3	322.5	445.5	349.8	932.7	571.9	680.8	426.0	229.7	205.6	297.6	272.2	335.9	273.3	485.1	403.3		

Amphibolis-dominant quadrats still showed significantly (P>0.001) higher biomass values (745.7 ± 45 g/m^2 Σ biomass [522.9 seagrass biomass]) than *Posidonia* sp. (329.6 ± 14 g/m^2 Σ biomass [280.90 seagrass biomass]).

The high biomass of *Amphibolis* plants (Fig. 1.4c, d) is due to higher density of shoots per square metre and not due to higher biomass of individual plants. Individual plant biomass was determined assuming that seagrass biomass is directly related to surface area. Only values from West Island were used because the biometry of plants from other sites may reflect the habitat conditions rather than characteristic values for the species (Table 3.4). Measurements were obtained over several seasons (02/99 to 09/99) at West Island which provides better measurements for a 'typical shoot' and the biomass of *A. griffithii* and *P. sinuosa* dominated quadrats were significantly different (*A. griffithii* 708 ± 33 g/m^2 Σbiomass [509 ± 25.7 seagrass biomass] and *P. sinuosa* 434.9 ± 27.2 g/m^2 Σbiomass [360.0 ± 22.2 seagrass biomass]; Chapter 5). The statistics of blade/stem lengths/widths from West Island are given in Table 3.3 and the mean, median, maximum and minimum values were used as typical values for blade clusters (*Amphibolis*) or whole plants (*Posidonia*) (Fig. 1.4a, b, c, d).

The surface area calculated for a typical blade cluster of 3-4 blades of *A. griffithii* shoots is 37.7 to 49 cm^2 (includes both sides of blades) with 6-8 blade clusters per plant = 150 to 392 cm^2, plus the typical stem surface area of 123 cm^2 gave a total surface of 273 to 515 cm^2. The surface area for a typical shoot of *P. sinuosa* with 3-4 blades is 599 to 1019.2 cm^2 .

These results indicate that the surface area of a typical *A. griffithii* shoot is significantly lower than a typical shoot of *P. sinuosa* at West Island. It was assumed that 1 cm^3 of one plant has the same weight as 1 cm^3 of another, so the biomass of a typical shoot of *P. sinuosa* is greater than the biomass of *A. griffithii*. The higher biomass of *A. griffithii* per unit area must be related to a higher number of shoots per unit area than for *P. sinuosa*.

Variation of biomass within species was determined for *Posidonia* (Fig. 3.7). It was possible to use the biomass values from each species from each quadrat as no two *Posidonia* species occurred in the same quadrat and hence each value is independent. ANOVA indicates that there was a significant difference in biomass between species (P>0.01). Tukey-HSD shows that the biomass of *P. angustifolia* (227.5 ± 29.8 g/m^2, n = 57) was significantly lower than *P. sinuosa* (319.4 ± 17.2 g/m^2, n = 78) and *P. australis* (297.6 ± 14.3 g/m^2, n = 75). Analysis of

Table 3.3 Seagrass dimensions (in cm) from different sites sampled. L – average length, W – average width, No. – number sampled. Numbers in brackets refer to standard deviation. West Island samples include measurements from different seasons.

Site	*A. antarctica* blade			*A. antarctica* stem			*A. griffithii* blade			*A. griffithii* stem		
	L	W	No.	L	w	No.	L	W	No.	L	W	No.
Ard04/1999	3.6(0.1)	0.5(0.1)	60	43.2(0)	0.1(0)	6						
CaHa10/1999	3.2(0.1)	0.5(0.1)	60	36.6(0)	0.1(0)	12						
ChCk11/2000-1	5.2(0.1)	0.6(0.1)	10	47	0.1	1						
ChCk11/2000-2												
ChCk11/2000-3												
Cow06/1999												
Dut10/1999												
King11/1999												
Mar01/1999	4(0.1)	0.5(0.1)	58	29.6(0)	0.1(0)	6	7.8(0.1)	0.6(0.1)	30	24.3(0)	0.1(0)	3
Moo04/1999	3.3(0.1)	0.6(0.1)	92	35.5(0)	0.1(0)	13						
Norm05/1999	2.5(0.1)	0.6(0.1)	58	39.2(0)	0.1(0)	7	6.6(0.1)	0.6(0.1)	78	29(0)	0.1(0)	8
PtLi03/1999												
PtMo04/1999												
Sem05/2000T1	4.9	0.6	1	34.4	0.1	1						
Stan04/1999												
StBy03/1999	4.3(0.1)	0.6(0.1)	40	41.8(0)	0.1(0)	4	9.5(0.1)	0.8(0.1)	18	31.5(0)	0.1(0)	4
Tip10/1999	3.4(0)	0.5(0)	4	38	0.1	1						
Tor05/2000												
Tum03/1999												
Why03/1999												
West Island	3.7(0.6)	0.7(0.6)	50	57.4(17.8)	0.1(0)	7	8(1.9)	0.7(1.9)	232	49(11.7)	0.1(0)	37

Site	*Het.tasmanica*			*P. angustifolia*			*P. australis*			*P. sinuosa*		
	L	W	No.	L	W	No.	L	W	No.	L	W	No.
Ard04/1999										32.5(0.1)	0.7(0.1)	20
CaHa10/1999				74.8(0.1)	0.8(0.1)	25						
ChCk11/2000-1							57.3(0.1)	1.1(0.1)	4	68.4(0.1)	0.7(0.1)	24
ChCk11/2000-2							54.2(0.1)	1(0.1)	30			
ChCk11/2000-3							90.5(0.1)	1.1(0.1)	30			
Cow06/1999										48(0.1)	0.6(0.1)	30
Dut10/1999				35.1(0.1)	0.5(0.1)	20						
King11/1999										60(0.1)	0.6(0.1)	30
Mar01/1999				60.8(0.1)	0.6(0.1)	20						
Moo04/1999							29.9(0.1)	1.2(0.1)	10	30.5(0.1)	0.7(0.1)	10
Norm05/1999				21.5(0.1)	0.6(0.1)	15				26.1(0.1)	0.5(0.1)	5
PtLi03/1999							27.5(0.1)	1.1(0.1)	19	43.7(0.1)	0.7(0.1)	10
PtMo04/1999							44.8(0.1)	1.5(0.1)	14	44.3(0.1)	0.7(0.1)	27
Sem05/2000T1										37.3(0)	0.6(0)	25
Stan04/1999							32(0.1)	1.2(0.1)	27			
StBy03/1999							29.8(0.1)	1.4(0.1)	15	37.6(0.1)	0.7(0.1)	15
Tip10/1999	29(0)	0(0)	1							47.1(0)	0.5(0)	28
Tor05/2000				40.6(0.1)	0.5(0.1)	30						
Tum03/1999										45.4(0.1)	0.8(0.1)	29
Why03/1999							25.8(0.2)	1.1(0.2)	30			
West Island	46(10.8)	0.1(10.8)	15	41.9(13.5)	0.6(13.5)	20				48.8(16.8)	0.6(16.8)	80

Table 3.4. Statistics of *A. griffithii* and *P. sinuosa* blades and stems from West Island

	A. griffithii blade		*A. griffithii* stem		P. sinuosa	
	Length (mm)	Width (mm)	Length (mm)	Width (mm)	Length (mm)	Width (mm)
Average (mean)	80	7	490	0.8	488	6
Average (median)	82	7	478	0.8	459	6
max	159	9	71	1	1014	8
min	29	2	154	0.6	162	1
Number samples	227	227	38	38	80	80

Table 3.5. Results of Kruskall-Wallis test for correlation between abiotic parameters and seagrass biomass. α0.05.
*** $p \leq 0.001$, ns = not significant

	Amphibolis sp.	*Posidonia* sp
Salinity ‰	ns	***
Air temperature (°C)	ns	***
Water temperature (°C)	ns	***
Sediment composition (%)	ns	ns
Nitrate (µg N/L)		***
Nitrite (µg N/L)		***
Ammonia (µg N/L)		***
FRP (µg P/L)		***

Table 3.7. Nutrient concentrations of water samples collected just above the seagrass canopy. West Island sites are average values from over *8 and **4 seasons, shallow and deep sites respectively. Sites ordered from West to east.

Site	Month	Nitrate (µg N/L)	Nitrite (µg N/L)	Ammonia (µg N/L)	FRP (µg P/L)
Port Lincoln	March 1999	43	<0.5	10	6
Semaphore	May 2000	222	5	396	129
Chinamans Creek	November 2000	13	1	33	9
West Island (shallow)	*	35.6	1.7	18.1	9.8
West Island (deep)	**	22.8	1		9.2
Cape Jaffa	November 1999	8	0.9	25	21

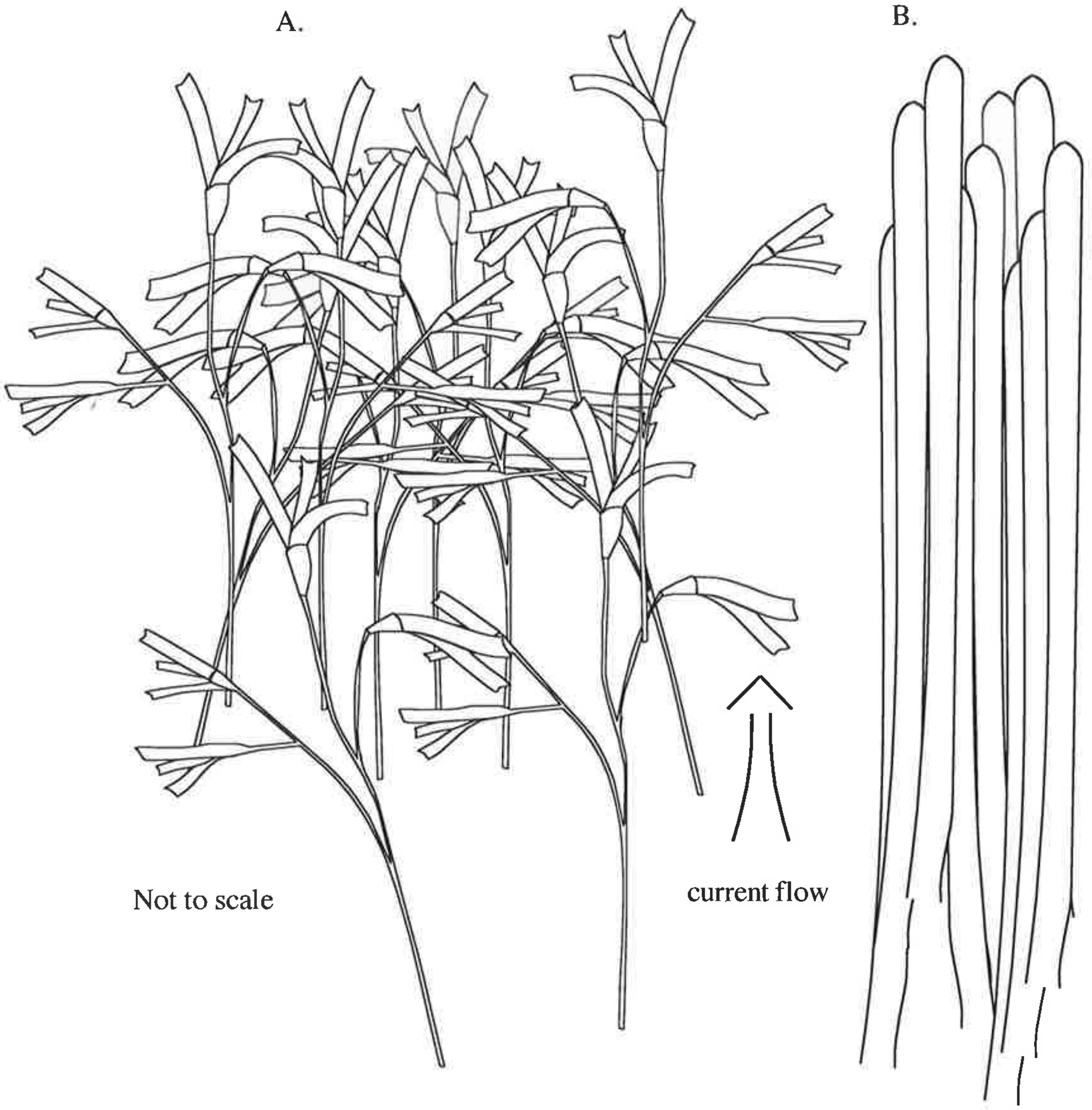


Fig. 3.6. Schematic plan view demonstrating susceptibility of *Posidonia* sp. (B) to self-shading, when plants are flattened in the current, in comparison to *Amphibolis* sp (A), due to morphological structure of the plants. The shaded plant indicates the bottom plant. Plan view.

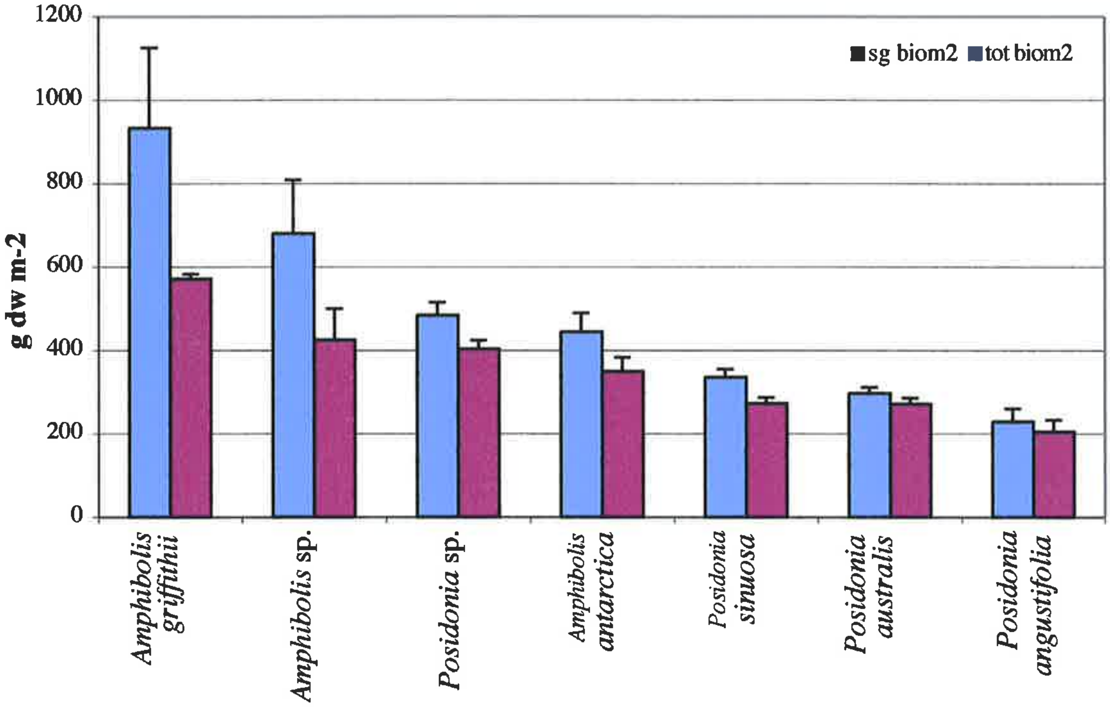


Fig 3.7 Average seagrass biomass for the different seagrass species sampled. Mean ±SE

the different biomass of *Amphibolis* species could not be carried out because of the limited number of samples of *A. griffithii* found from different sites.

3.3.1.4 Temperature and salinity

Samples were collected in water temperatures ranging from 14.1 – 27.9°C and salinity measurements of 32.2 – 43.7‰ (Fig. 3.8). However, regression analysis of biomass with temperature and salinity showed no relations with a change in temperature and salinity. Temperature and salinity values were ranked by 2°C and 1‰, respectively, to determine if any relationships existed whilst reducing the effect of outliers. Non-parametric Kruskall-Wallis tests were run for each genera and each parameter (Table 3.5). However, *Amphibolis* sp. showed no significant variation, but *Posidonia* sp. did show significant variation with changing temperature and salinity (Fig. 3.9) although no trends were apparent.

3.3.1.5 Grain size

Sediment composition ranged from 80% CaCO3 (Cowlers Landing) to 100% quartz (Table 3.6). Grain size varied from coarse sand (e.g. Whyalla) to silt (e.g. Tumby Bay; Table 3.6) but biomass or species type showed no correlation, both with ANOVA and regression analysis (see both CDs).

3.3.1.6 Nutrients

Nutrient analysis was carried out by the "Australian Centre for Tropical Freshwater Research", James Cook University. The lack of filtering on collection may have caused some alteration of the nutrient concentration, in particular the FRP (filterable reactive phosphate). However, comparison of filtered and unfiltered samples taken from West Island indicates that the alteration was minimal. Nutrient concentrations at Semaphore were particularly high in comparison to the other 6 sites (Table 3.7). This was potentially due to the proximity of anthropogenic input. The high nutrient concentration at Semaphore correlates with the lowest biomass at any site. Kruskall-Wallis test of nutrient concentrations on biomass, from the other sites, indicates that *Posidonia* biomass does show significant variation. It was not possible to examine the effects of nutrient concentrations on *Amphibolis* as the sites where *Amphibolis* occurred did not coincide with the sites where nutrient data was obtained. The nutrient concentrations obtained are shown in Table 3.7.

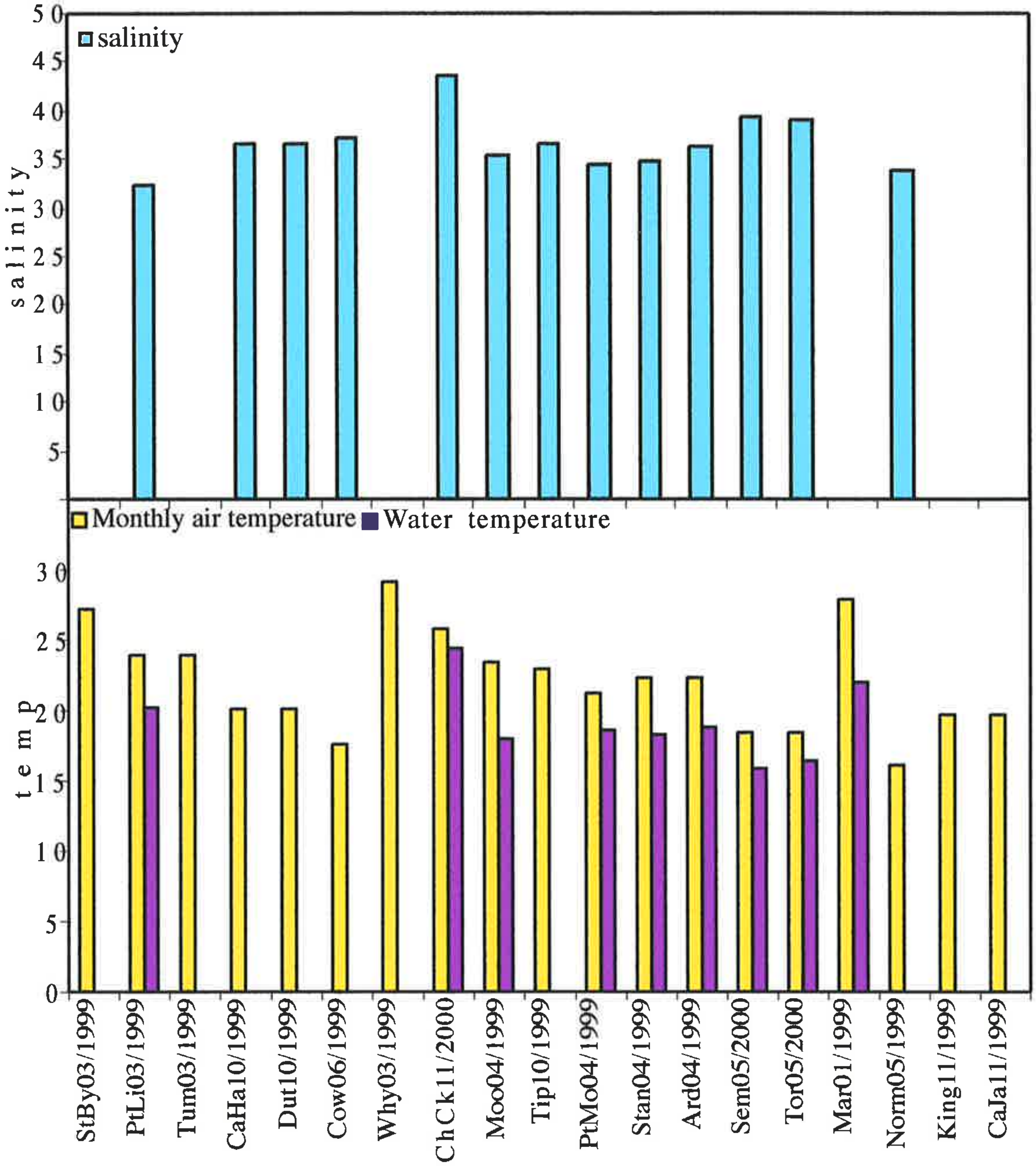


Fig. 3.8. Salinity and temperature values recorded from sample sites. Air temperatures are monthly averages obtained from Australian Bureau of Meteorology.

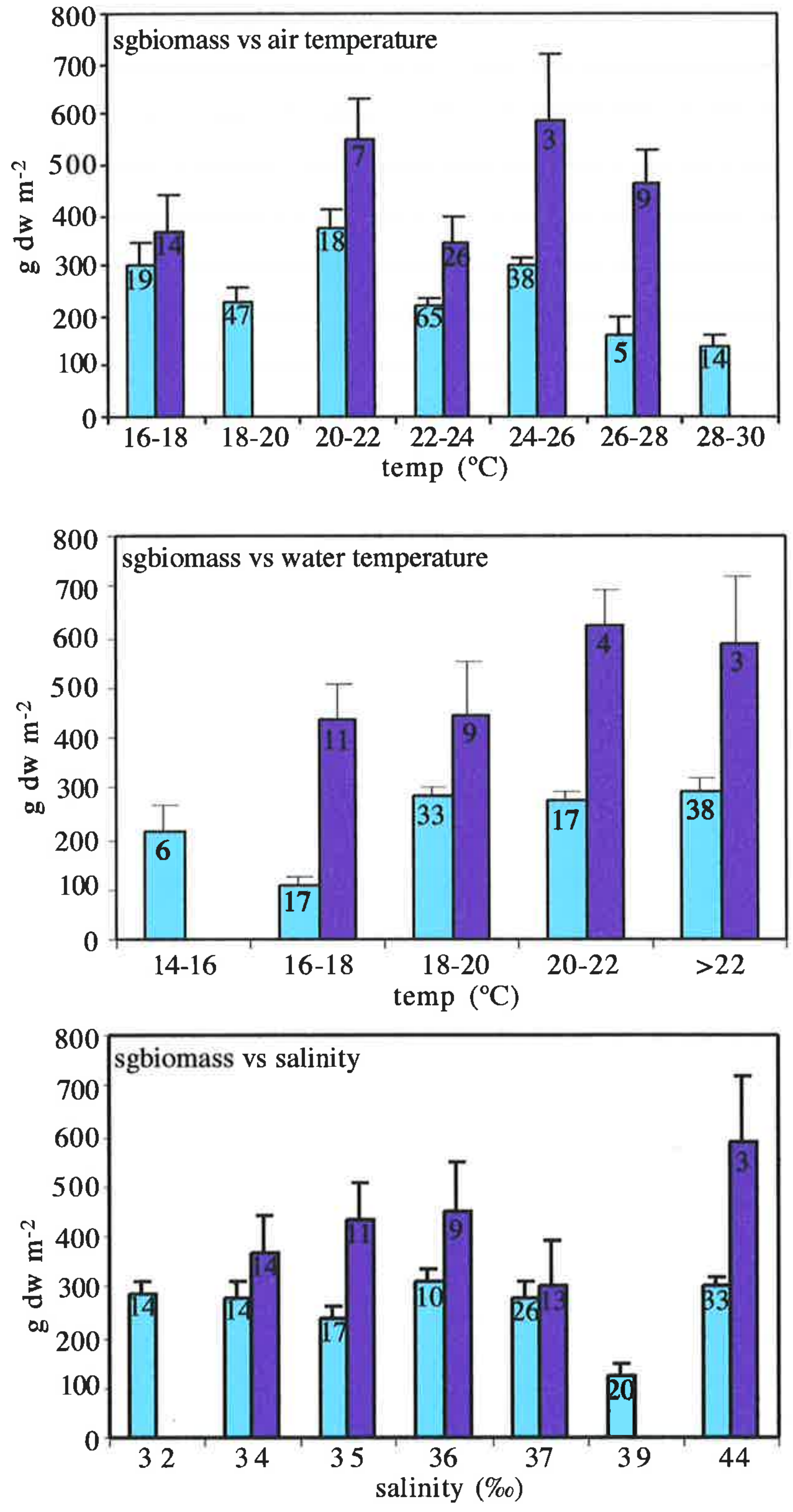


Fig. 3.9. Average seagrass biomass values of *Posidonia* sp. 🟦 and *Amphibolis* sp. 🟪 plotted against ranked temperature and salinity values. Number at top of column refers to number of samples collected. Mean ± s.e.

Table 3.6. Field site results. Grain size refers to the dominant size fraction of the sediment: fs = fine sand, f-ms = fine to medium sand, ms = medium sand, cs = coarse sand.

Location	Seagrass species collected	$CaCO_3$ % in sed	Grain size
Ardrossan jetty (Ard04/1999)	*A. antarctica,* *P. sinuosa*	2.1	fs
Cape Hardy (CaHa10/1999)	*A. antarctica,* *H. australis,* *P. sinuosa*	15.8	ms
Cape Jaffa jetty (CaJa11/1999)	*P. angustifolia*	-	ms
Chinaman Ckk 1 (ChCk 1 11/2000)	*A. antarctica,* *P. australis,* *P. sinuosa,*	37.0	silt
Chinaman Ck 2 (ChCk 2 11/2000)	*P. australis*	77.8	ms
Chinaman Ck 3 (ChCk 3 11/2000)	*P. australis*	46.7	ms
Cowlers Landing (Cow06/1999)	*P. sinuosa*	80.5	ms
Dutton Bay (Dut10/1999)	*P. angustifolia*	13.4	ms
Long Beach, Kingston (King11/1999)	*P. sinuosa*	44.8	silt
Marino Rocks (Mar01/1999)	*A. antarctica,* *P. sinuosa*	6.3	ms
Moonta Bay (Moo04/1999)	*A. antarctica* *P. angustifolia*	31.6	silt
Normanville jetty (Norm05/1999)	*A. antarctica,* *A. griffithi,* *P. angustifolia*	5.2	fs
Port Lincoln (PtLi03/1999)	*P. australis*	77.5	ms

Port Morrowie (PtMo04/1999)	*P. australis,* *P. sinuosa*	63.2	fs
Semaphore (Sem05/2000)	*P. angustifolia,* *Hal. australis.*	20.8	fs
Stansbury jetty (Stan04/1999)	*P. australis*	31.6	ms
Streaky Bay (StBy03/1999)	*A. antarctica,* *P. australis,* *P. sinuosa,* *Zostera sp.*	61.5	fs
Tiparra Reef (Tip10/1999)	*A. antarctica,* *H. tasmanica,* *P. angustifolia*	57.2	silt
Torrens outlet (Tor05/2000)	*P. angustifolia*	0.0	ms
Tumby Bay (Tum03/1999)	*P. sinuosa*	7.9	silt
West Island shallow (WI shallow)	*A. antarctica,* *A. griffithi,* *Het. tasmanica,* *P. angustifolia,* *P. sinuosa*	#	f-c
West Island deep (WI deep)	*Halophila* sp., *A. griffithi* *A. antarctica* *P. sinuosa* *P. angustifolia*	55.6	m-fs
False Bay, Whyalla (Why03/1999)	*P. australis*	76.4	m-cs

3.4 DISCUSSION

3.4.1 Seagrass biomass

Seagrass biomass values recorded from this study (Table 3.2) largely agree with the findings of the same species elsewhere (Table 1.4). *P. australis* biomass values from the coast of South Australia (203.8-442.9 g/m^2) are similar to those from New South Wales and Western Australia (140-453 g/m^2). *P. sinuosa* biomass range recorded during this study (49.6-387.2 g/m^2) was lower than that from Western Australia (140-660 g/m^2). The only known recorded biomass of *P. angustifolia* biomass from W.A. (254.6 g/m^2, Marbà & Walker 1999) is approximate to the average value found from this study (av. 205.6 g/m^2). *A. griffithii* biomass range, from this study (240.4 - 571.9 g/m^2), is also similar to those from W.A. (97-531.7 g/m^2). *A. antarctica* biomass values in South Australia (16.3 – 576.7 g/m^2) fall within the range of biomass values measured in Western Australia (71 – 2000 g/m^2). The approximate similarities of biomass between the findings of this study in South Australia and those from Western Australia and New South Wales indicate that correlations between biomass and calcareous epiphytes in South Australia may be extrapolated to other areas.

The small changes in depth encountered along each transect do not account for the high variance found at each site (Fig. 3.5). High variance at 50 – 100 m scale, was also recorded by Kendrick *et al.* (1998a, b), who attributed the variation to processes that vary across shoots and meadows, i.e. patchiness. Causes of patchiness include competition between species, lack of equal seagrass growth expansion, limited dispersal of seedlings, non-uniform availability of resources, grazing patchiness, unfavourable sediment conditions, blowouts and anthropogenic influences.

Chinaman Creek has the highest biomass of *P. australis* recorded in the literature (Table 3.2; West & Larkum 1979). These biomass recordings, plus another two at Chinaman Creek (227.4 g/m^2 $\sum$biomass [203.9 seagrass biomass] site 3; and 244 g/m^2 $\sum$biomass [212.9 seagrass biomass] site 1), indicate that patchiness occurs not only at the metre scale (i.e. along transect), but also at the 100s of metres scale. The data from this study indicates that the cause of the patchiness at this scale, as opposed to within transect patchiness as above, is caused by depth changes and hence light availability. The lower biomass values occurred at the deeper sites (site 1 – 5 m mwd & site 3 – 2.5 m mwd), and the higher values at the shallowest depths (site 2 – 1 m mwd). Patchiness at this scale has ramifications for the validity of the representativeness of the sampling method and should be taken into account when examining the controlling parameters of biomass and calcareous epiphyte abundance.

Seventy four percent of all seagrass biomass samples (Table 3.2) lie between 50 and 500 g/m^2, which suggests that conditions enabling higher biomass are relatively rare. Biomass is taken to indicate both the density (number of shoots per area) and the volume of plant material, i.e. high biomass may indicate high density and/or large plants, as well as large surface area for epiphyte recruitment. The high biomass of *P. australis* in the region of Chinaman Creek is probably a result of a relatively atypical environment. Chinaman Creek is situated at the head of a reverse estuary and the seagrass is subjected to high temperatures, high salinity and low current velocity, all of which appear to be favourable for the growth of *P. australis*. This situation provides two possible alternative consequences for epiphyte productivity. Firstly, the conditions that stimulate large seagrass biomass may be unfavourable for epiphytic growth, consequently reducing shading and further enhancing the seagrass productivity. Secondly, the high biomass provides a large surface area for recruitment of the epiphytes and consequently epiphyte abundance may be higher in this region compared to other sites. Chinaman Creek is an excellent natural laboratory to test some of the probable parameters controlling epiphyte growth (Chapter 4).

3.4.2 Geographical distribution of seagrass

The distribution of seagrass species for this project compares well with the findings of Shepherd & Roberston (1989) and Edyvane (1999b) although *P. coriacea*, *P. denhartogii*, *P. ostenfeldii,* and *P. kirmanii* were not sampled at any location. This was probably because these 4 species generally occur in isolated patches (Shepherd & Roberston 1989) and the sampling range did not extend to these sites. The regional distribution is probably a function of evolutionary dispersion patterns, as suggested by den Hartog (1989) although it has been implied that the eastward reducing influence of the Leeuwin Current across the southern margin has resulted in the reduced number of *Amphibolis* and *Posidonia* species towards the east because of their warm temperate affinities (Kirkman 1997). Locally the distribution is controlled by water depth, sediment composition, turbidity, nutrient availability and coastal topography (Shepherd & Roberston 1989). Temperature does not make a significant difference to the distribution of seagrass locally (Kirkman 1997). There was no correlation between biomass and changes in latitude or longitude, indicating that the variance in biomass is controlled by local parameters.

3.4.3 Biomass and taxon relationships

The results show that *Amphibolis*-dominated communities have higher biomass than *Posidonia* dominated communities (Fig. 3.3, 3.7). This has also been documented from Success Bank, Western Australia. where *A. griffithii* had a higher biomass than *P. coriacea* (Kendrick *et al.* 1998a, b). A general overview of biomass recordings from different sites also indicates that *Amphibolis* can have significantly higher biomass than *Posidonia*, although biomass may also be present at low biomass values (*Amphibolis* 71-2000 g/m^2, *Posidonia* 101-660 g/m^2). There are several reasons for this:

- the number of shoots per m^2 is higher for *Amphibolis;*
- the biomass of an individual shoot of *Amphibolis* is greater than for *Posidonia;* or
- a combination of these.

The weight or biomass of individual shoots was not measured, but an indication of the biomass of individual shoots was obtained using the measured surface area and the assumption that the weight of 1 cm^3 of one species was the same as for any other. If the assumption holds, then this study showed that *P. sinuosa* would equivalently have a higher biomass per shoot. Consequently, the higher biomass found of *Amphibolis*-dominated quadrats, must be attributed to a higher number of shoots per area. Results of other studies do not agree with this as they generally indicate that *Posidonia* has a higher shoot spatial density than *Amphibolis* (*Posidonia* 11-2060 shoots/m^2; *Amphibolis* 2-1250 shoots/m^2). Genetic physio/physical characteristics suggest that *Amphibolis* shoots would be expected to have greater spatial packaging than *Posidonia,* because of the relatively narrow rhizome/stem thickness of *Amphibolis* (2-3 mm *Amphibolis*; 4-15 mm *Posidonia*; Womersley 1984). Rhizome thickness has an allometric relationship with distance between shoots (Duarte 1991), i.e. the thicker the rhizome the further apart the shoots. Hence, *Posidonia* would be expected to have lower shoot densities than *Amphibolis*. Also, the data from previous studies of *Amphibolis* shoot density are relatively limited and may represent local conditions.

The implications of these findings suggest that calcareous epiphyte recruitment might be expected to be greater per unit area in *Amphibolis*-dominated quadrats although the amount of epiphytes per individual shoot might be greater on *Posidonia*. The finding that biomass is significantly different between *Posidonia* species also suggests that calcareous epiphyte abundance may be greater on *P. sinuosa* and *P. australis* than *P. angustifolia*.

3.4.4 Environmental controls

When examining the data for the controlling parameters of biomass, it should be remembered that the data comes from a number of separate sites and hence apparent generalised controlling parameters shown below may not be satisfactory for each individual site. Time and financial restraints did not allow detailed analysis from each site.

The results indicate a correlation of biomass with water depth. The biomass levels peaked at a depth of 2-4 m and then steadily declined with increasing water depth. Declining biomass of seagrass with decreasing light is a well-established fact (Burkholder & Doheny 1968, Backman & Barilotti 1976, Bulthuis & Woelkerling 1981, Dennison & Alberte 1986, Gordon, *et al.* 1990, Hillman & McComb, 1990; Masini et al 1990; Dennison *et al.* 1993; Fitzpatrick & Kirkman 1995, Walker *et al.* 1999, Abal 1996, Abal & Dennison 1996, Cambridge & Hocking 1997). Decrease in biomass can be attributed to the attenuation of incident light (photosynthetically active radiation) with increasing water depth. Samples below 15 m mwd were not sampled, but it is speculated that biomass would continue to decrease at the same rate until the minimum light levels are reached. This depth depends on species type and local conditions, such as turbidity (Dennison *et al.* 1993). In general, seagrass does not penetrate below 30 m mwd, although exceptions are known, e.g. *Halophila decepiens* has been recorded at 70 m mwd in tropical water. To determine whether some species are more sensitive to low light levels Dennison *et al.* (1993) devised experiments to calculate the minimum light requirements. The study showed that *A. antarctica, P. angustifolia* and *P. sinuosa* all had the same minimum light requirements - 24.7% of the incident light measured just below the water surface. These three species co-occur at approximately the same depth (e.g. Shepherd & Robertson 1989). This study showed that biomass of *Amphibolis* decreased more rapidly with depth than *Posidonia,* suggesting that *Amphibolis* is more sensitive to light than *Posidonia.* Experiments by Dennison *et al.* (1993) indicate otherwise, suggesting that the findings from this study may be a function of limited *Amphibolis* sampling at depth. The peak at 2-4 m mwd, rather than shallower, is attributed to the possibility of photosynthetic inhibition and desiccation in shallower water (Seddon 2000).

This study showed that temperature, salinity and nutrient availability affect biomass. The resolution used was coarse (2°C temperature, 1‰ salinity) but allowed examination for patterns, whilst excluding outliers. Other studies examine the affects of these parameters on the productivity of seagrass and have shown that photosynthesis and respiration is affected by temperature (e.g. Bulthuis 1987, Hillman *et al.* 1989, Masini *et al.* 1990, Walker 1991, Walker & Cambridge 1995, Masini & Manning 1997), nutrient concentration (e.g. Short 1987, Hillman *et al.* 1989, Cambridge & Hocking 1997, Moore *et al.* 1996, Udy & Dennison 1997, 1999a, b, Alcoverro *et al.* 2000) and salinity (e.g. Walker 1985, Hillman *et al.* 1989, Walker & McComb 1990). Optimum temperatures for photosynthesis by *P. sinuosa* have been measured at 13-23°C in comparison to 23°C or above for *P. australis, A. griffithii* and *A. antarctica* (Masini & Manning 1997). The temperature range for this study was between 14.1°C – 27.9°C, hence did not fall outside of the known optimum range for all species. Walker (1985) measured biomass changes of *A. antarctica* over a salinity range of 35-64‰ and showed that peak biomass occurred at 42.5‰ salinity. The range of salinity values during this study was only 32.2-39.4‰ and was therefore comparatively limited.

3.5 CONCLUSION

Greater than 74% of the quadrats obtained had seagrass biomass values between 50-500 g/m^{-2}. The limited numbers of sites which have higher values indicate that the more favourable conditions for plant growth are relatively atypical, i.e. low velocity and relatively high salinity, as found at Chinaman Creek. The distribution of the 8 seagrass species found agrees well with the biodiversity study by Shepherd & Roberston (1989) and Edyvane (1999) and is attributed to evolutionary dispersion, regional temperature changes due to the presence of the Leeuwin Current and more local conditions of salinity, current velocity, sediment type, temperature and nutrient concentrations. The significantly higher biomass of communities dominated by *Amphibolis* sp., compared with those dominated by *Posidonia* sp., is attributed to higher shoot density of Amphibolis per unit area. *Posidonia* sp. has a greater surface area for a typical shoot at West Island and hence it is assumed that the biomass of a single shoot of *Posidonia* is also greater than an individual shoot of *Amphibolis*. Seagrass biomass has a peak value at 2-4 m depth attributed to the level at which photosynthetic inhibition and desiccation are reduced. Below 4 m mwd seagrass biomass decreases and this is probably in response to light attenuation. Variance at each depth level is high, indicating that there are other controlling factors for seagrass biomass. It was not possible from this study to ascertain what these parameters are, although other studies indicate salinity, nutrients and temperature are important.

CHAPTER 4
QUANTIFICATION AND CONTROLLING PARAMETERS OF EPIPHYTE CALCIUM CARBONATE

4.1 INTRODUCTION

This chapter analyses the standing stock of calcareous epiphytes associated with dominant seagrass species in South Australia. Standing stock values were used to evaluate controlling parameters because they are more accurate than productivity values that have additional assumptions within the calculations (Chapter 7). Different environmental settings were examined in order to assess the most important physical/chemical parameters controlling carbonate productivity.

4.2 RESULTS

The data was obtained from the same samples as those used for the seagrass biomass and distribution aspects of this study. In total, 425 quadrat (50 x 50 cm) samples were collected from 20 sites (Fig. 3.1), with 182 of these from West Island (these were treated separately to prevent sampling bias). Only one transect was sampled when samples obtained appeared to be representative of the general surroundings. Consequently, of the 20 locations sampled, 15 locations were sampled with two transects and five with only one transect. Values of carbonate abundance are standing stock $CaCO_3$ g/m^2 and $CaCO_3$ g/kg.

4.2.1 Geographical distribution

No two sites produced the same abundance of epiphytes on the same seagrass species and the variance between sites is significant. Quadrat values of calcareous epiphyte quantities ranged from 3.06 to 655.6 g/m^2 (av. 78.7, SD = standard deviation 105.1 g/m^2) or 11.21 to 767.32 g/kg of seagrass (av. 164, SD 107.8 g/kg of seagrass). Average site values range from 10.3 g/m^2 (SD 4.6) at Whyalla, to 364.6 g/m^2 (SD 138.9) at Normanville and 27.8 g/kg (SD 13.6) at Chinaman Creek to 373.5 g/kg of seagrass (SD 88.2) at Normanville (Tab. 4.1, Fig. 2.1).

The sites of maximum and minimum carbonate production are of particular interest as they can be used as upper and lower limits. Normanville is the most favourable site for both seagrass and epiphyte growth, having the maximum seagrass biomass of 976.0 g/m^2 $\sum$biomass, 600 g/m^2 (seagrass biomass) and calcareous epiphyte abundance (364.6 g/m^2, 373.5 g/kg of seagrass). Semaphore, on the other hand, although favourable for epiphyte growth, was not for seagrass growth. It had the lowest seagrass biomass (57.7 g/m^2 $\sum$biomass, 42.9 g/m^2 of seagrass), but one of the highest productions of epiphytes per plant

Table 4.1 Examination of site variance indicating the relative significance of patchiness epiphyte and seagrass biomass. Patchiness is considered high when ratio of abundance (abund) to the standard deviation (s.d.) is less than 1:2.2, is moderate when ratio is between 1:2.5 and 1:3.5 and is low where >1:3.5. sg = seagrass.

	Sgbiomass g/m^2				CaCO$_3$ g/m^2				CaCO$_3$ g/kg sg			
	Abund	s.d.	Ratio	Seagrass patchiness	Abund	s.d.	Ratio	Apparent Seagrass patchiness	Abund	s.d.	Ratio	Apparent Epiphyte patchiness
Streaky Bay	499.9	280.6	1.8	high	223.9	142.9	1.6	high	263.0	62.4	4.2	low
Port Lincoln	310.3	68.0	4.6	low	43.9	16.8	2.6	mod	127.9	55.5	2.3	mod
Tumby Bay	352.5	107.7	3.3	mod	134.6	99.8	1.3	high	254.0	104.2	2.4	mod
Cape Hardy	338.5	86.5	3.9	low	113.1	26.0	4.4	low	252.0	28.2	8.9	low
Dutton Bay	85.4	38.9	2.2	mod/high	14.5	8.1	1.8	high	156.2	87.6	1.8	high
Cowlers Landing	168.9	59.2	2.9	mod	37.3	11.9	3.1	mod	187.0	45.7	4.1	low
Whyalla	203.8	68.7	3.0	mod	10.3	4.6	2.2	mod/high	47.4	13.5	3.5	low
Chinaman Creek (1)	206.9	73.0	2.8	mod	37.3	20.2	1.8	high	146.8	40.2	3.7	low
Chinaman Creek (2)	442.9	67.3	6.6	low	12.4	5.6	2.2	mod/high	27.8	13.6	2.0	high
Chinaman Creek (3)	203.9	61.5	3.3	mod	23.6	8.4	2.8	mod	104.2	17.0	6.1	low
Moonta Bay	583.1	134.0	2.8	mod	162.9	51.6	3.2	mod	217.3	49.8	4.4	low
Tiparra Reef	93.0	41.0	2.3	mod	16.7	7.9	2.1	high	150.5	35.2	4.3	low
Port Moorowie	392.0	143.3	2.7	mod	69.3	34.4	2.0	high	149.3	39.9	3.7	low
Stansbury	230.6	43.7	5.3	low	29.2	12.4	2.4	mod	109.7	29.9	3.7	low
Ardrossan	492.7	228.8	2.2	mod/high	167.5	88.1	1.9	high	256.3	74.2	3.5	low
Semaphore	40.5	30.9	1.3	high	14.8	8.6	1.7	high	324.7	220.4	1.5	high
Torrens outlet	162.9	59.2	2.8	mod	14.1	4.6	3.1	mod	81.5	14.8	5.5	low
Marino Rocks	397.8	144.2	2.8	high	31.1	18.6	1.7	high	74.4	31.9	2.3	mod
Normanville	594.7	133.5	4.5	low	364.6	138.9	2.6	mod	373.5	88.1	4.2	low
WI shallow	413.4	206.8	2.0	high	131.4	97.3	1.3	high	229.4	111.3	2.1	high
WI deep	257.5	250.9	1.0	high	117.0	137.6	0.9	high	303.1	180.1	1.7	high
Kingston	298.3	47.8	6.2	low	35.7	18.0	2.0	high	105.3	43.9	2.4	mod
Cape Jaffa	484.1	221.3	2.2	mod/high	56.3	36.4	1.5	high	108.0	39.1	2.8	mod

(324.7 g/kg of seagrass, 14.8 g/m^2). The three sites at Chinaman Creek show the extent to which the variability of calcium carbonate can occur within a relatively isolated region (27.8 to 146.8 g/kg of seagrass). Chinaman Creek site 2 was of particular interest because it showed the highest biomass for *P. australis* (443 g/m^2 of seagrass; Fig 4.1) but the lowest abundance of epiphytes per plant (27.8 g of $CaCO_3$/kg of seagrass). Potential explanations for the apparent data anomalies for these sites are tested and discussed below.

There is no apparent relationship between carbonate quantities and latitude or longitude at the scale of this study (Figs 2.1, 4.2, 4.3). Sites within Spencer Gulf, the same as those used for seagrass biomass, were used to determine the influence of latitude and longitude at a smaller scale. The distribution within the Gulf indicated a decrease in carbonate/kg of seagrass moving north on the west coast to a minimum at the head of the Gulf (Chinaman Creek). On the east coast epiphyte abundance peaked half way down the coast and then decreases southwards. Latitudinal variation shows no correlation. Sub-dividing the $CaCO_3$/m^2 values at each site into their seagrass species components indicated that latitude and longitude are not correlated with the abundance at the species level either, at this scale.

4.2.2 Biomass

Regression analysis shows that calcareous epiphyte abundance per unit area is closely associated with the abundance of seagrass substrate (equiv. biomass) available within that area (biomass; Fig. 4.4). Seagrass biomass is used because it is independent of calcareous epiphytes, as opposed to total biomass, which includes all epiphytes present.

Data was grouped within 100 g biomass bins (categories) to minimise the effects of outliers and to highlight any patterns (Fig. 4.5). The bin size was selected to ensure that the frequency of the samples within each group was greater than 5. The binned calcareous epiphyte abundance vs seagrass biomass yields an exponential curve with a correlation of $R^2 = 0.8$ (Fig. 4.5). A scatter plot of all individual quadrat data (excluding West Island data) produces an exponential relationship with a correlation of $R^2 = 0.4$ (Fig. 4.4) The relationship between the two variables can be described by the following equation:

$$Y = aX^b \qquad \text{Eq. 4.1}$$

where Y = biomass, X = $CaCO_3$ g/m^2 and a and b are constants.

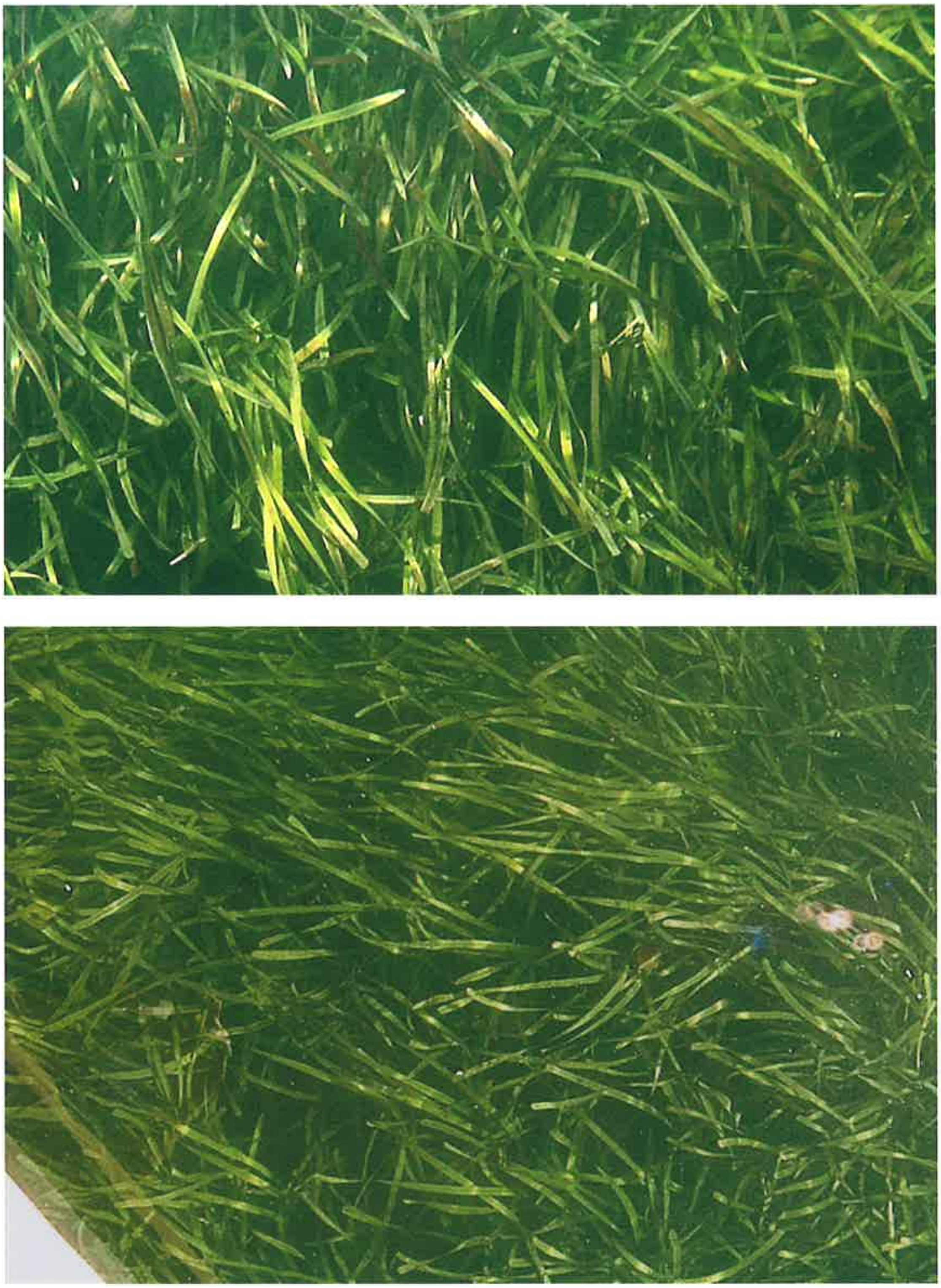


Fig. 4.1. *Posidonia australis* meadows at Chinaman Creek, showing the density of the Seagrass at this site. The *P. australis* at Chinaman Creek is relatively unencrusted by calcareous epiphytes compared to the other South Australian sites, (e.g. Figs 1.2, 1.4). The field of view in the upper photo is approximately 50 cm and is just under 1 m in the lower photo.

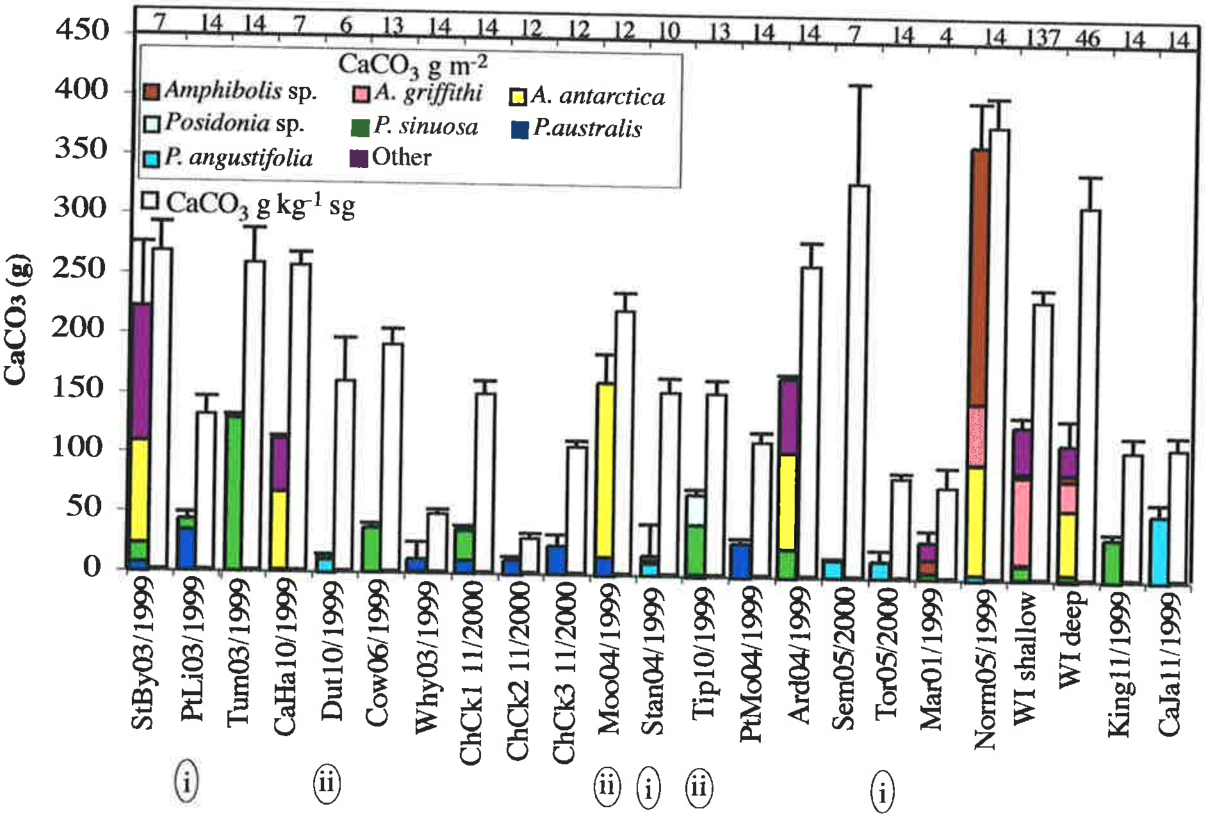


Figure 4.2. Average epiphyte abundance from all sites sampled, arranged from west to east. Values are in $CaCO_3$ g m^{-2} & g kg^{-1} sg. Numbers at top refer to the number of quadrats sampled at each site. i & ii = longitude transects. Mean ±SE

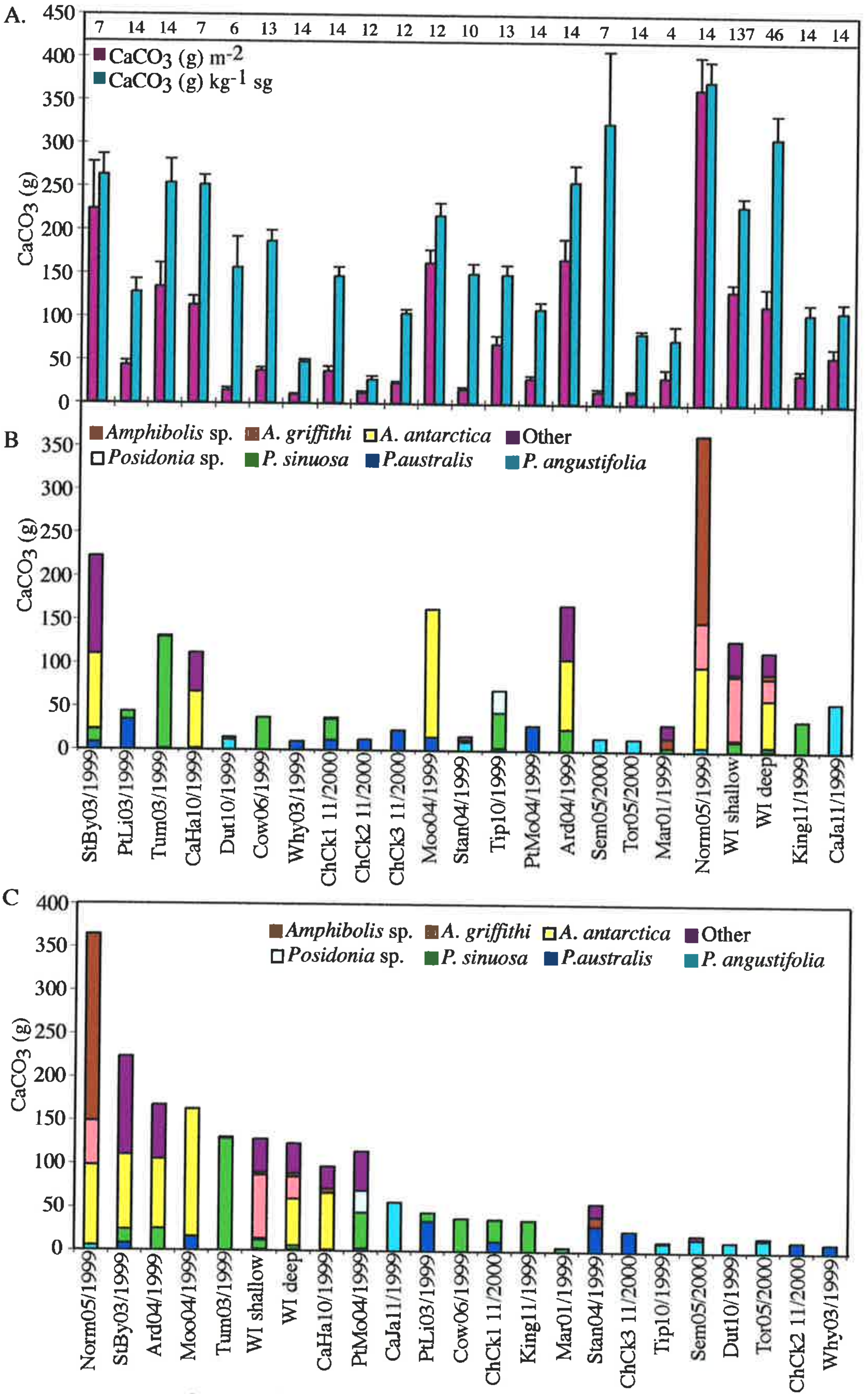


Fig 4.3. A. $CaCO_3$ m^{-2} and kg^{-1} sg from all sites arranged from west to east. Numbers at top refer to the number of quadrats sampled at each site. B. Seagrass species break down of $CaCO_3$ m^{-2} ordered from west to East. C. As for B, but arranged numerically. Mean ±SE

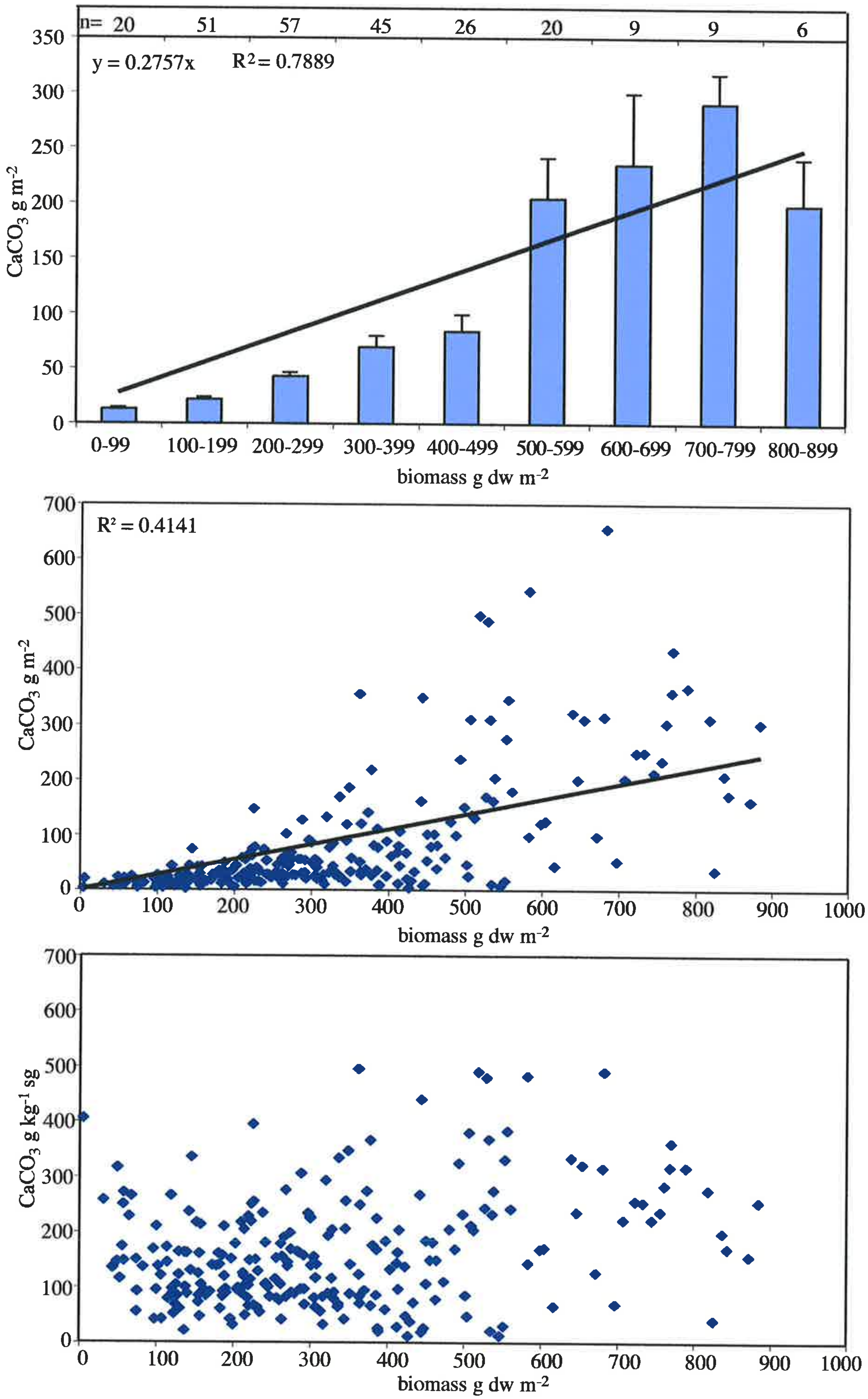
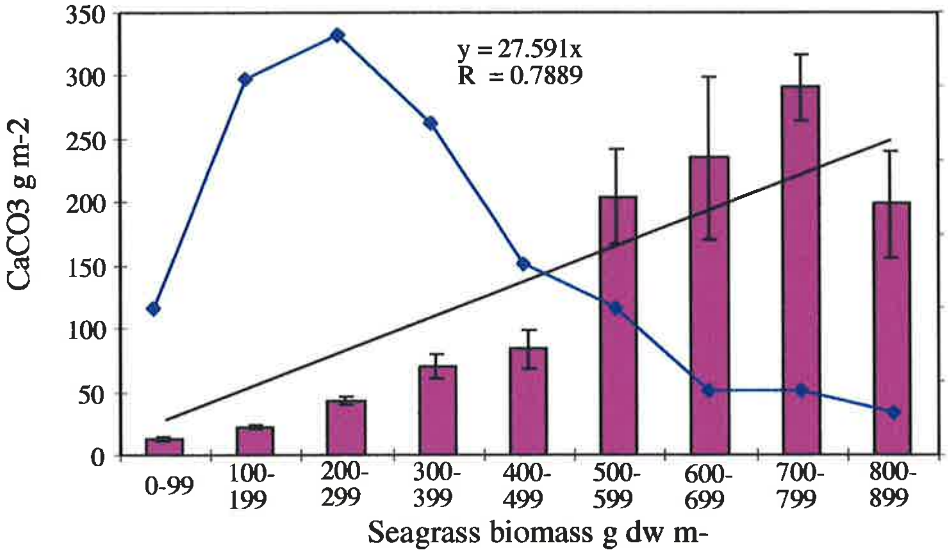
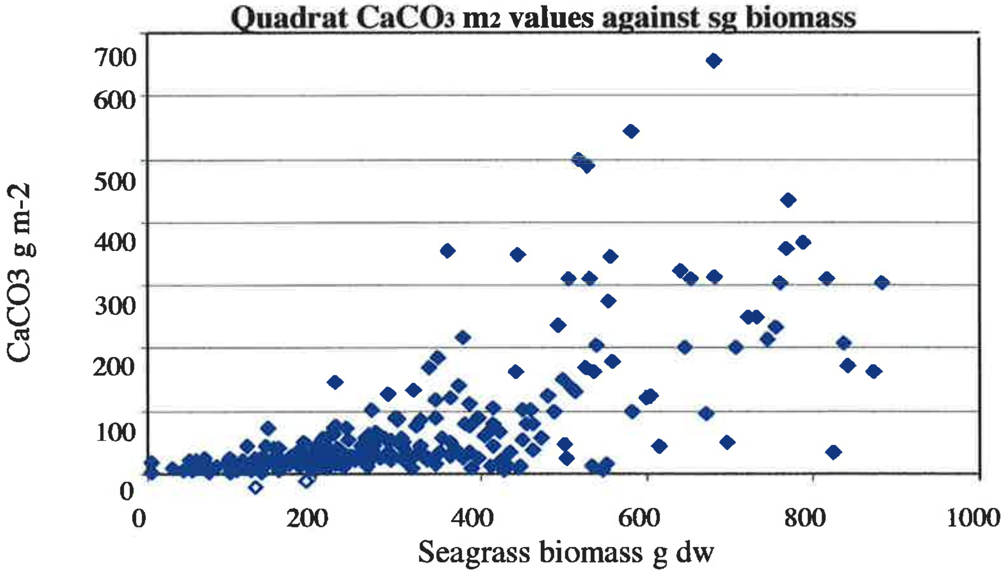


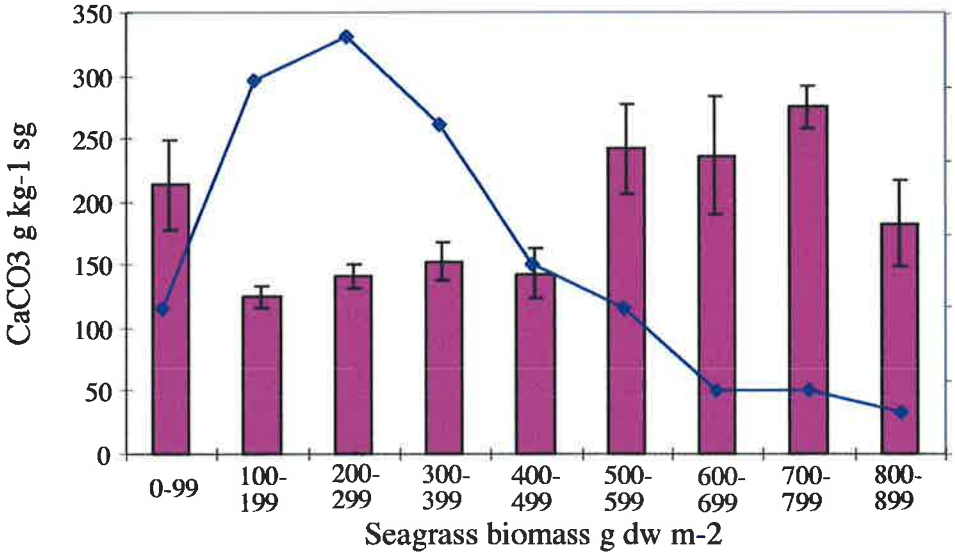
Figure 4.4. Graphical demonstration of relationship between epiphyte $CaCO_3$ and seagrass biomass. A. Epiphyte $CaCO_3$ g m^{-2} ranked by 100g seagrass biomass bins B.Quadrat values of $CaCO_3$ g m^{-2} C. quadrat values of $CaCO_3$ g kg^{-1} sg. Mean ±SE, n = number samples.



CaCO3 g m-2 grouped by 100g seagrass biomass bins



Quadrat CaCO3 m2 values against sg biomass



CaCO3 g kg-1 sg grouped by 100g seagrass biomass bins

Fig. 4.5. Data grouped into 100 g biomass "bins". This minimises the effects of outliers and also highlights any patterns.

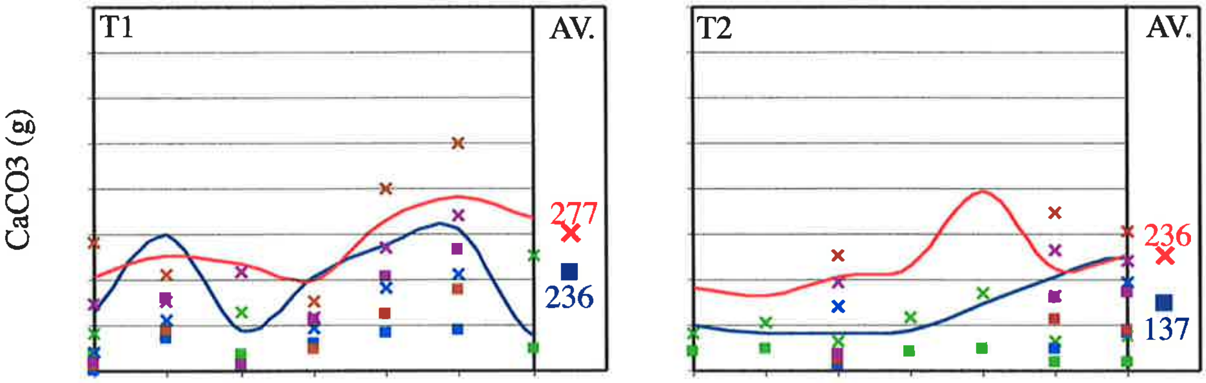
This equation describes an allometric relationship, i.e. there is a constant ratio between the two parameters. A logarithmic plot of the two variables (Y & X) produces a straight line (Fig. 4.2) where the strength of the relationship is characterised by the coefficient of determination (r^2) = 0.48, the log-transformed intercept (a) = -1.19 ± 0.19 SE = standard error and the log-transformed slope (b) = 1.16 ± 0.08 SE.

The correlation of biomass with calcareous epiphyte abundance per unit area is observed with overall mixed seagrass species data, and at genera/species and components (e.g. stems, leaves, etc.) level (Fig. 4.6). Regression analysis of *Posidonia* sp. data shows a similar trend to the combined data se, but a poor correlation ($R^2 = 0.3$). The correlation also varies depending on the seagrass species. *P. angustifolia* had the greatest correlation ($R^2 = 0.6$), followed by *P. sinuosa* ($R^2 = 0.35$), *P. australis* does not show a clear correlation. *Amphibolis* sp. shows a low correlation ($R^2 = 0.4$).

4.2.3 Site variance and patchiness

Variance of carbonate production along transects was high at some locations, e.g. Semaphore and Tumby Bay (Table 4.2). The relationship between calcareous epiphyte abundance m^2/kg of seagrass (Section 2.4.1.2) and seagrass biomass made it possible to estimate whether variance was a result either of patchiness of calcareous epiphytes or of the seagrass. Values measured by $CaCO_3$ g/m^2 were closely related to the abundance of seagrass present and hence it was assumed that high variation along transects was related to changes in seagrass biomass (patchiness). Values measured by $CaCO_3$ g/kg of seagrass are independent of changing seagrass biomass and hence reflect patchiness in calcareous epiphytes (Table 4.2). Standard deviation values were used as in indication of the variability. Ratio was used because it evaluates the variance at each site independent of the actual abundance of carbonate. A high ratio, (>1:3.5) indicates low variance, a moderate ratio (1:2.5 – 1:3.5) indicates moderate variance and a low ratio (<1:2.2) indicates high variance. NB The categories are subjective and are only meant to give an indication of the relative variation. The effectiveness of this method was tested by comparing the seagrass biomass variability (Table 4.3). The seagrass biomass and $CaCO_3$ g/m^2 data used to determine the amount of seagrass patchiness showed very similar results, hence supporting the ability to use a similar technique to indicate calcareous epiphyte patchiness.

Ardrossan
04/1999 1 mwd



Cape Hardy
10/1999 10 mwd

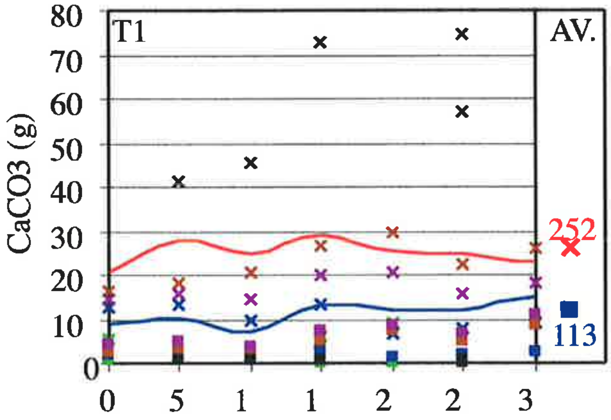
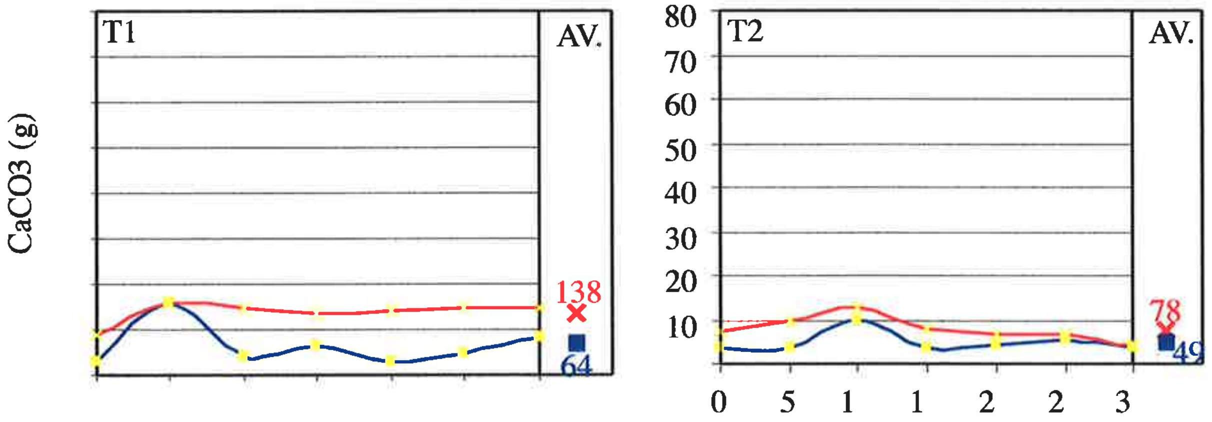
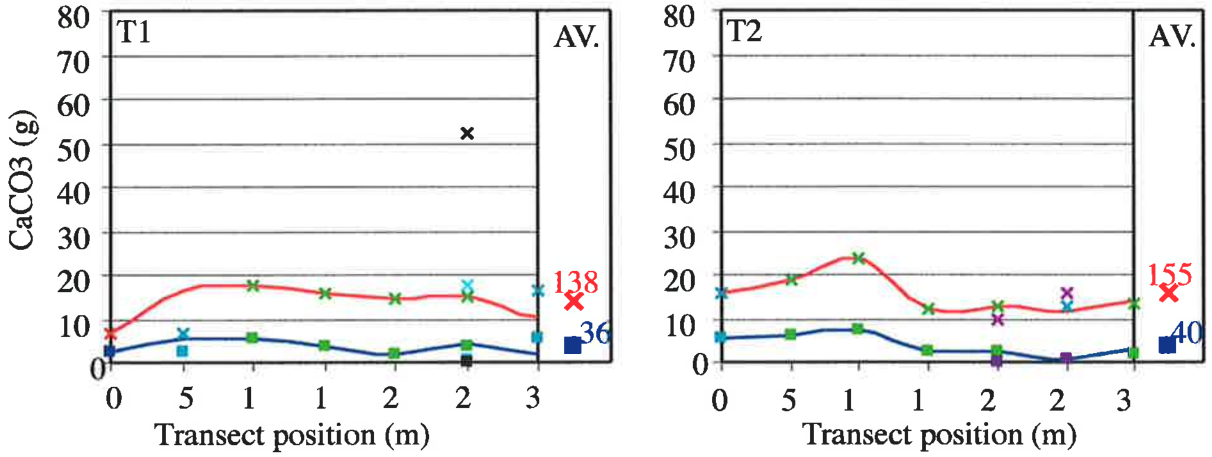


Fig. 4.6. Weight of calcareous epiphytic material from seagrass collected at 1 m intervals along transects at various sites. Legend is given below the last plots on the 6th page.

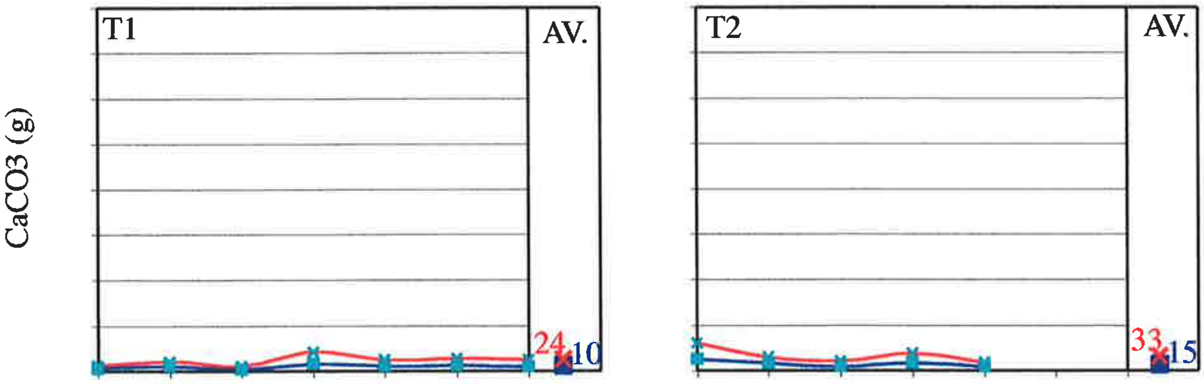
Cape Jaffa
11/1999 2 mwd



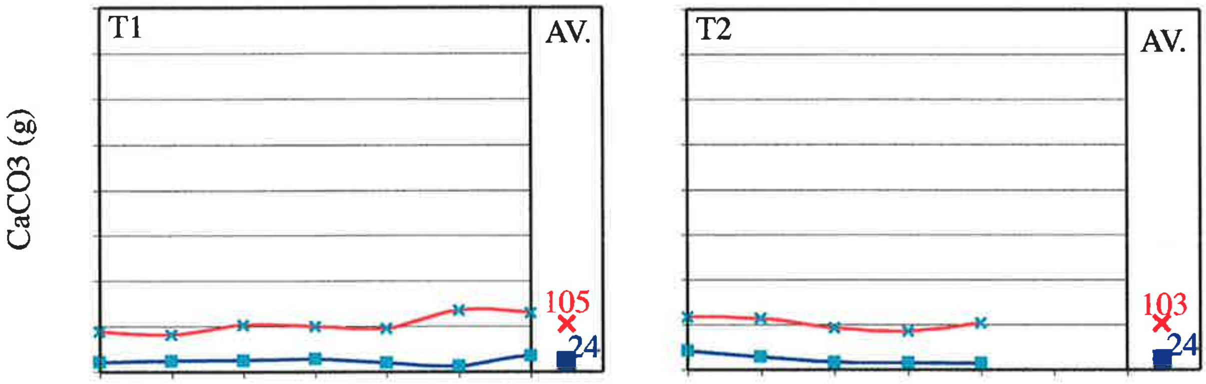
Chinaman Creek (1)
11/2000 5 mwd



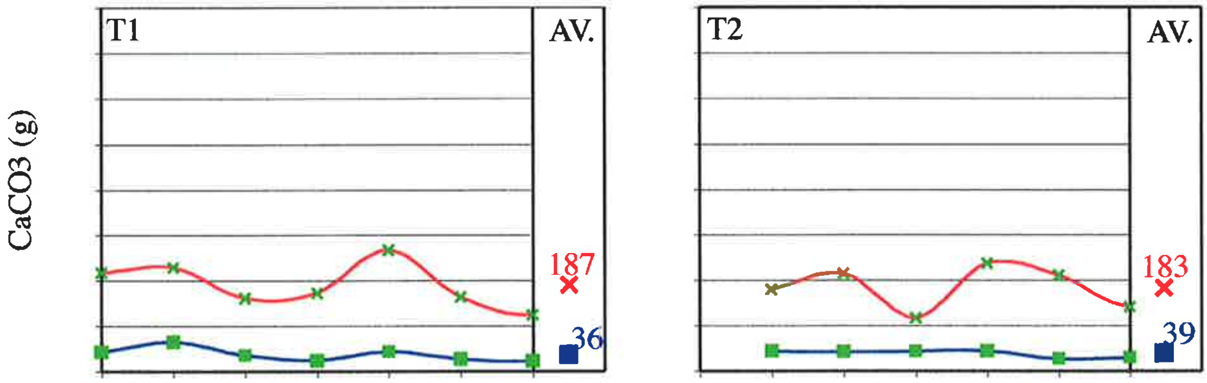
Chinaman Creek (2)
11/2000 1 mwd



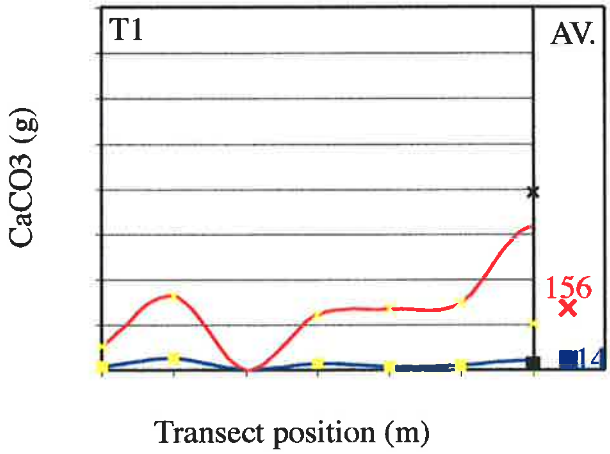
Chinaman Creek (3)
11/2000 2.5 mwd

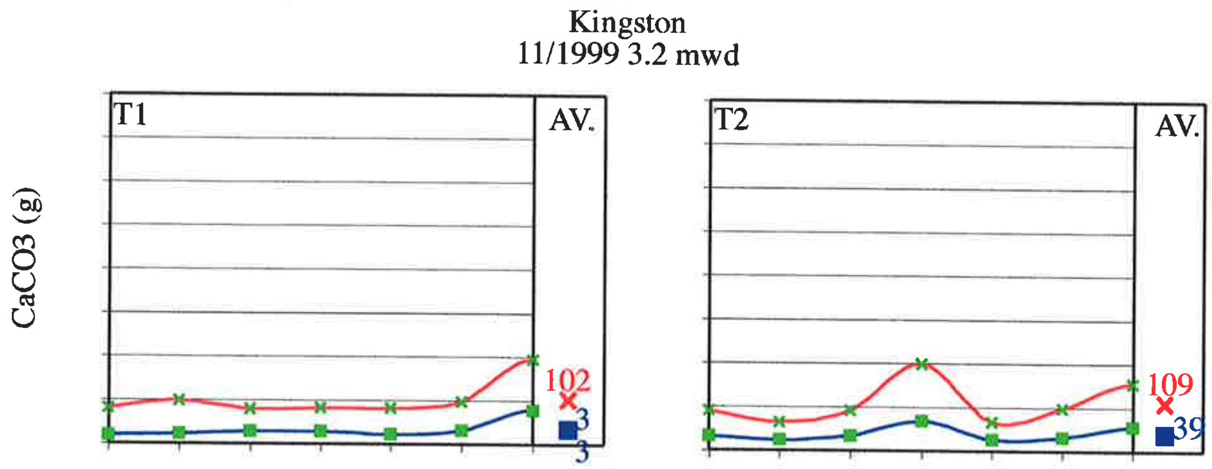


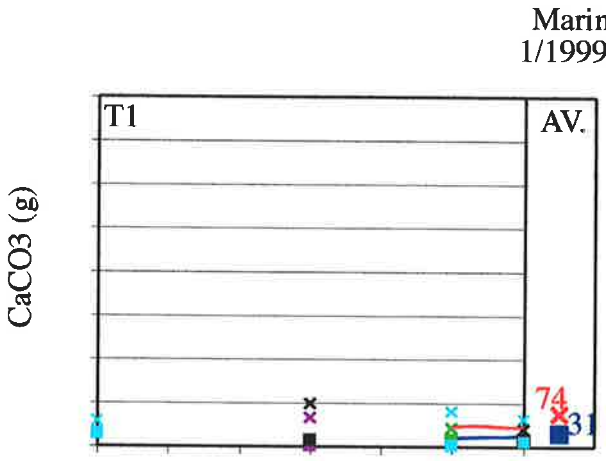
Cowlers Landing
06/1999 5.8 mwd

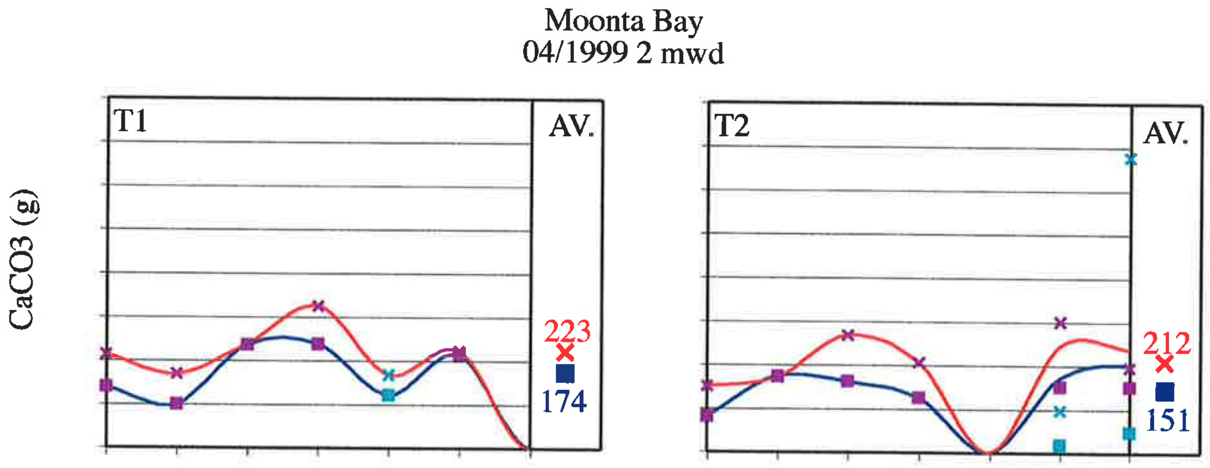


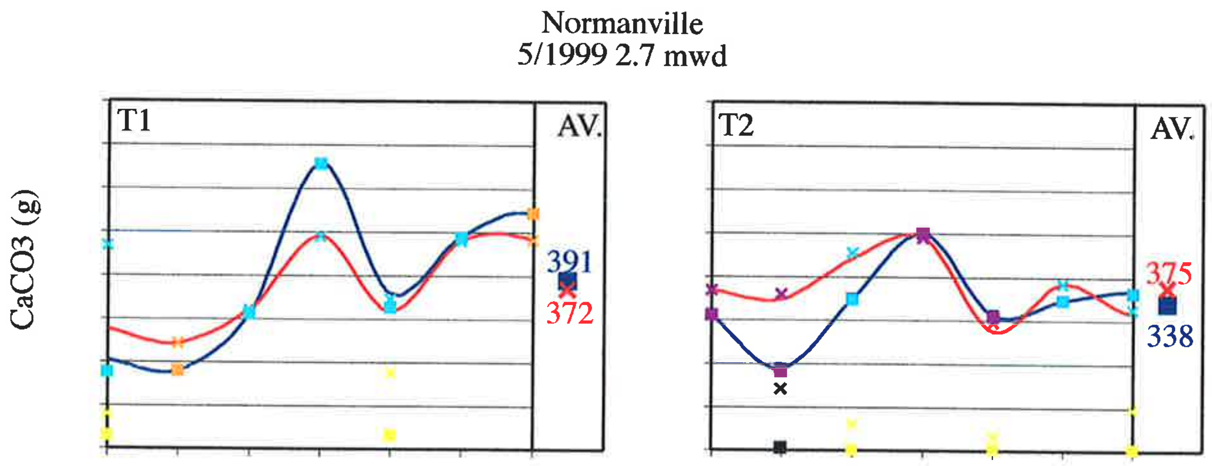
Dutton Bay
10/1999 15.5 mwd



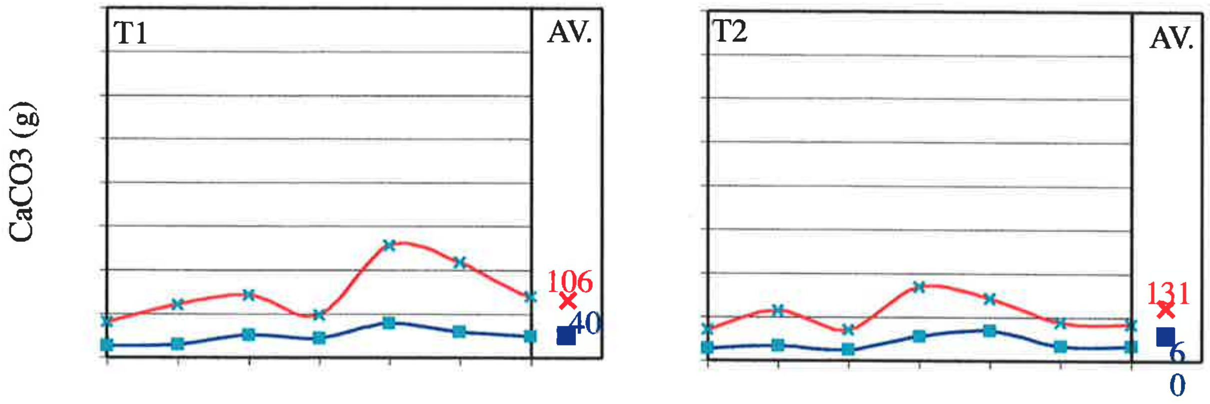

Kingston
11/1999 3.2 mwd
CaCO3 (g)
T1
AV.
102
3
3
T2
AV.
109
39


Marino Rocks
1/1999 3.1 mwd
CaCO3 (g)
T1
AV.
74
31

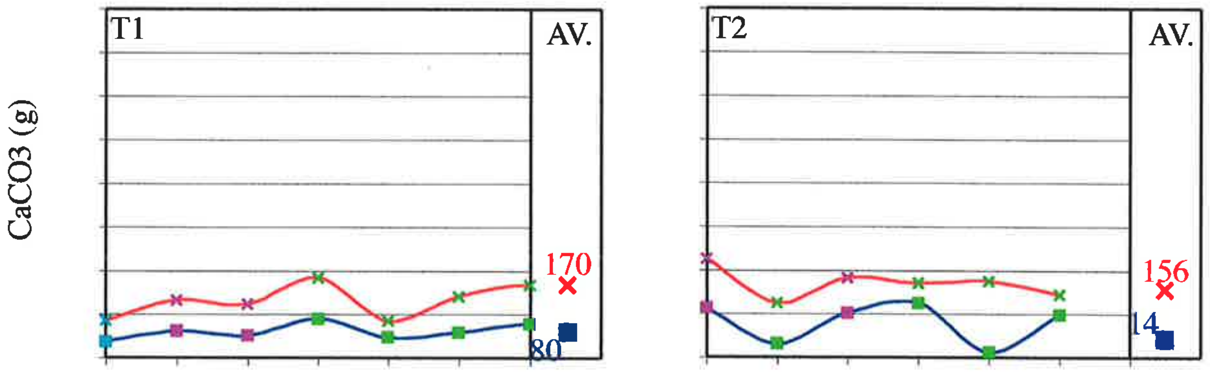

Moonta Bay
04/1999 2 mwd
CaCO3 (g)
T1
AV.
223
174
T2
AV.
212
151


Normanville
5/1999 2.7 mwd
CaCO3 (g)
T1
AV.
391
372
T2
AV.
375
338
Transect position (m)
Transect position (m)

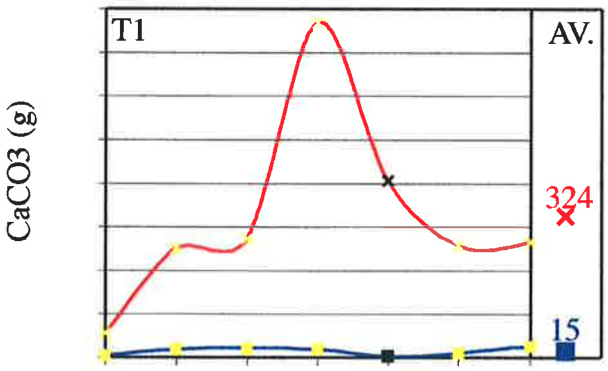
Port Lincoln
3/1999 1 mwd



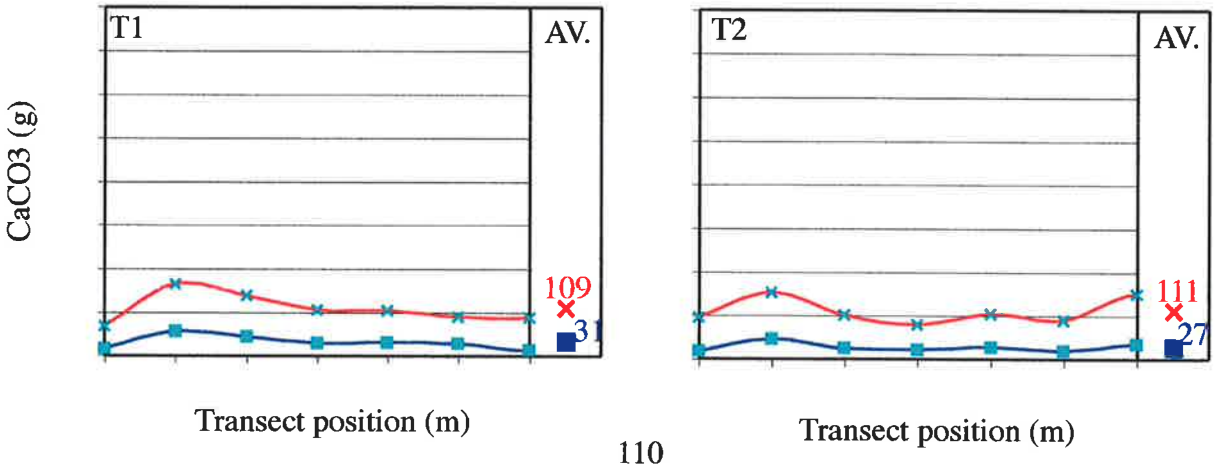
Port Morrowie
04/1999 2.3 mwd



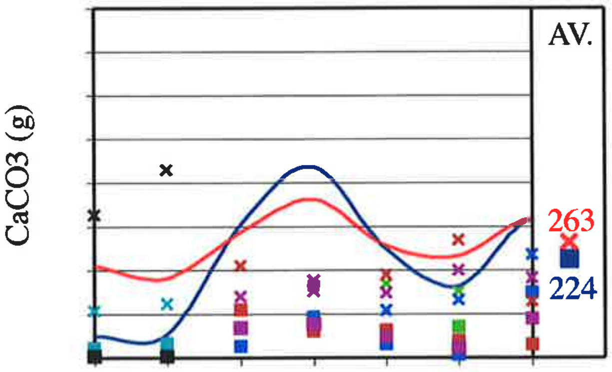
Semaphore
05/2000 9.2 mwd



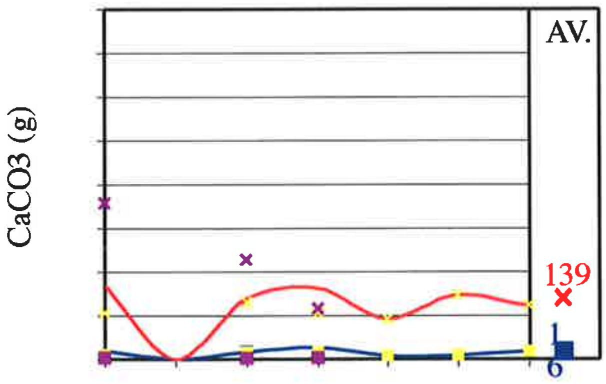
Stansbury
04/1999 2.6 mwd



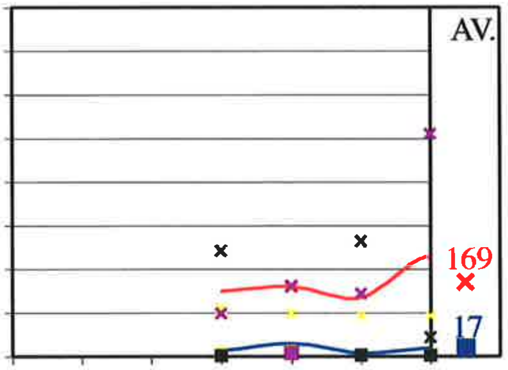
Streaky Bay T1



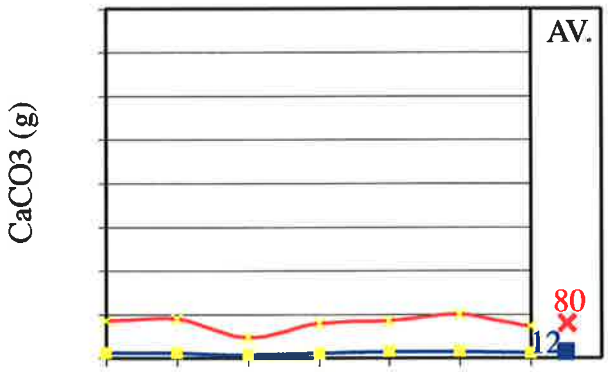
Tiparra Reef T1



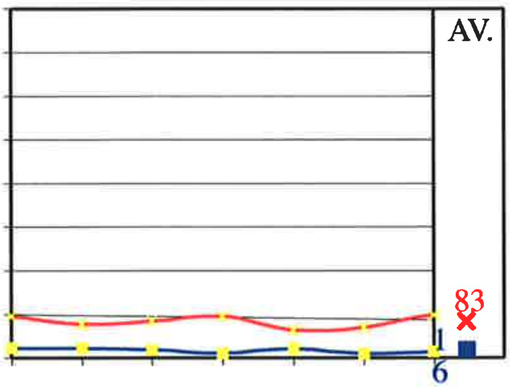
Tiparra Reef T2



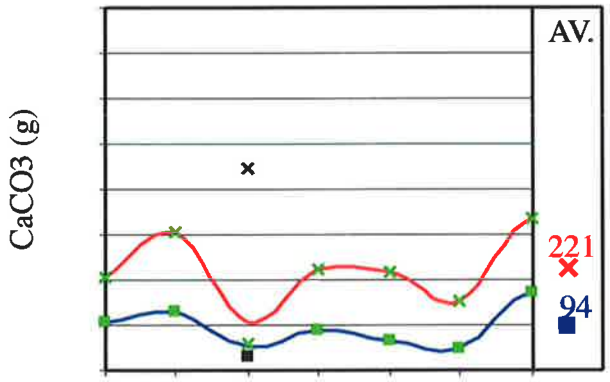
Torrens T1



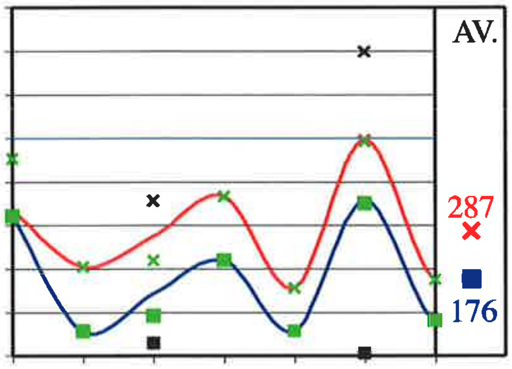
Torrens T2

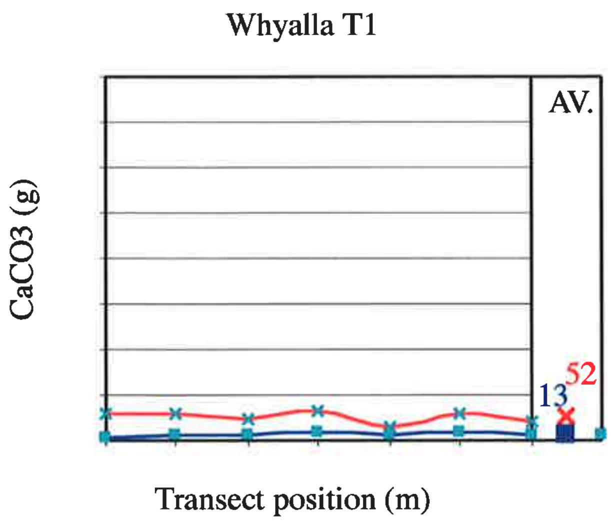


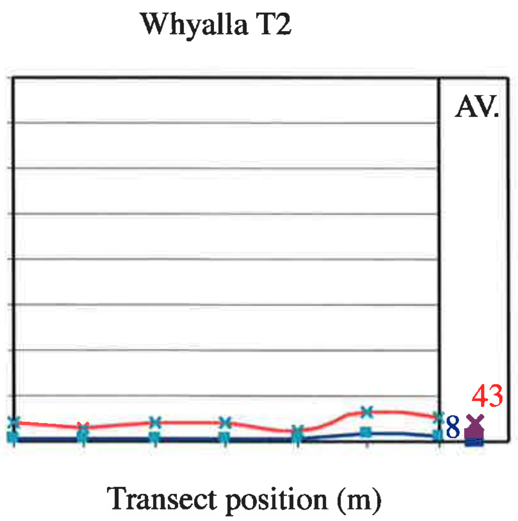
Tumby Bay T1



Tumby Bay T2







Key for Figure 4.6 (6 parts)

✖ Average $CaCO_3$ g m^{-2}

🟦 ✕ Amphibolis sp.

Amphibolis antarctica

🟦 ✕ blades

🟫 ✕ stem

🟪 ✕ whole plant

Amphibolis griffithi

blades

stem

🟧 ✕ whole plant

⬛ Average $CaCO_3$ g kg^{-1} sg

🟩 ✕ Posidonia sinuosa

🟦 ✕ Posidonia australis

🟨 ✕

🟪 ✕ Posidonia sp.

⬛ ✕ Other

Posidonia angustifolia

Table 4.2. Average standing stock values of carbonate derived from epiphytes at each of the 21 sites sampled in South Australia. Overall average values of the site and carbonate derived from the individual seagrass species are shown. sg = seagrass, n refers to the number of samples used to obtain average, number in brackets indicates SE.

	Total carbonate			*A. antarctica*			*A. griffithi*			*P. angustifolia*			*P. australis*			*P. sinuosa*		
	g/m^2	g/kg sg	n	g/m^2	g/kg sg	n	g/m^2	g/kg sg	n	g/m^2	g/kg sg	n	g/m^2	g/kg sg	n	g/m^2	g/kg sg	n
Ardrossan	167.5	256.3	14	125.1	216.2	9										34.6	113.7	10
	(23.6)	(19.8)		(29.6)	(23.9)											(4.3)	(18.5)	
Cape Hardy	113.1	252	7	65.5	169.3	7										3.1	67.9	3
	(9.8)	(10.7)		(9.9)	(9.4)											(1.5)	(10.8)	
Cape Jaffa	56.3	108	14							56.3	108	14						
	(9.7)	(10.4)								(9.7)	(10.4)							
Chinaman Creek (1)	37.3	146.8	14	5.4	126.8	2							31.2	124.5	5	39	159	9
	(5.4)	(10.8)		(3.3)	(31.8)								(10.3)	(17.4)		(6.8)	(12.2)	
Chinaman Creek (2)	12.4	27.8	12										12.4	27.8	12			
	(1.6)	(3.9)											(1.6)	(3.9)				
Chinaman Creek (3)	23.6	104.2	12										23.6	104.2	12			
	(2.4)	(4.9)											(2.4)	(4.9)				
Cowleds	37.7	187	13													37.7	187	13
	(3.3)	(12.7)														(3.3)	(12.7)	
Dutton	14.5	156.2	6							11.6	120.4	6						
	(3.3)	(35.8)								(3.1)	(16.2)							
Kingston	35.7	105.3	14													35.7	105.3	14
	(4.8)	(11.7)														(4.8)	(11.7)	
Marino	31.1	74.4	4	2.6	65.8	1										16.9	42.8	1
	(9.3)	(16)																
Moonta	162.9	217.3	12	160.5	223.1	11							63	314	3			
	(14.9)	(14.4)		(15.5)	(16.7)								(30.4)	(182.3)				
Normanville	364.6	373.5	14	324.7	378.1	4	360.4	362.1	2	13.9	88.3	5						
	(37.1)	(23.6)		(65.1)	(40.6)		(181.6)	(120)		(6.9)	(24.2)							
Port Lincoln	43.9	127.9	14										39.9	109.8	12	68.3	236.5	2
	(4.5)	(14.8)											(4)	(9.5)		(9.6)	(18.7)	

Table cont.	Total carbonate			*A. antarctica*			*A. griffithi*			*P. angustifolia*			*P. australis*			*P. sinuosa*		
	g/m²	g/kg sg	n	g/m²	g/kg sg	n	g/m²	g/kg sg	n	g/m²	g/kg sg	n	g/m²	g/kg sg	n	g/m²	g/kg sg	n
Port Moorowie	69.3	149.3	13										36.1	85.7	1	67.2	149.1	8
	(9.5)	(11.1)														(13.2)	(11.4)	
Semaphore	14.8	324.7	7							16.7	311.1	6						
	(3.2)	83.3)								(3.1)	(97.3)							
Stansbury	29.2	109.7	14										29.2	109.7	14			
	(3.3)	(8)											(3.3)	(8)				
Streaky Bay	223.9	263	7	121	182	5							27.6	114.7	2	54.9	160.1	2
	(54)	(23.6)		(23.6)	(16.6)								(5.9)	(8.1)		(15.1)	(8.9)	
Tiparra	16.7	150.5	10	3.1	184.3	6				10.1	109.9	10						
	(2.5)	(11.1)		(0.8)	(39)					(1.5)	(5.8)							
Torrens	14.1	81.5	14							14.1	81.5	14						
	(1.2)	(4)								(1.2)	(4)							
Tumby	134.6	254	14													128.7	255.1	14
	(26.7)	(27.8)														(27.1)	(32.3)	
Whyalla	10.3	47.4	14										10.3	47.4	14			
	(1.2)	(3.6)											(1.2)	(3.6)				
Total (excluding WI)	78.9	163.5	243	117.5	209.6	45	360.4	362.1	2	24.1	123.3	55	25.3	93.1	75	56.6	161.6	76
	(6.7)	(6.9)		(15.6)	(12.7)		(181.6)	(120)		(3.6)	(13.9)		(2.2)	(9.3)		(6.7)	(9.7)	
West Island (shallow)	131.4	229.4	137	54.9	330.4	4	98.6	315.8	102	24.8	124.2	5				14.1	55.3	108
	(8.5)	(9.5)		(29.4)	(68)		(7.9)	(12.6)		(7.8)	(26.2)					(1.1)	(4.4)	
West Island (deep)	117.0	303.1	45	201.8	368.9	12	95.1	356.8	12	9.0	69.2	7				13.7	129.3	14
	(20.5)	(26.8)		(40.5)	(56.9)		(19.6	(52.6)		(1.6)	(14.1)					(3.6)	(111.2)	
West Island	127.8	247.6	182	165.1	359.3	16	98.2	320.1	114	15.6	92.1	12				14.0	63.8	122
	(8.1)	(10)		(34.9)	(45)		(7.4)	(12.6)		(3.9)	(15.3)					(1.1)	(5.6)	

The results showed that variance in calcareous epiphyte abundance was generally higher (low ratio) g/m^2 than g/kg of seagrass (Table 4.2). This implies that epiphyte abundance per shoot was more constant than it was per area, in turn indicating that patchiness of seagrass has a stronger influence than patchiness of epiphytes. The high variance of $CaCO_3$ g/m^2 and low variance of $CaCO_3$ g/kg of seagrass at Ardrossan and Streaky Bay show that epiphyte abundance is relatively constant on each plant, although the actual abundance of substrate available varies strongly. At other sites, e.g. Cape Hardy, Cowlers Landing and Moonta Bay, there is little patchiness in either seagrass or calcareous epiphyte distribution. Moderate or high patchiness in calcareous epiphytes generally coincided with high seagrass patchiness. West Island data shows high patchiness in both seagrass and epiphytes, but, as this mean covers a range of seasons and years, this may vary within individual seasons.

4.2.4 Seagrass species

Student t-test shows that there was a significant difference between carbonate associated with *Amphibolis* and that associated with *Posidonia* ($P \leq 0.001$). *Amphibolis* had a significantly greater abundance of calcareous epiphytes compared to *Posidonia* (238.5 g/kg of seagrass *vs.* 127.2 g/kg of seagrass respectively) (Table 4.2). *P. sinuosa* had significantly higher quantities of carbonate compared to *P. angustifolia* and *P. australis*. *A. antarctica* and *A. griffithii* show no significant difference. The higher values of carbonate associated with higher biomass values, as described previously, also coincides with an increase in carbonate from *Amphibolis* sp. compared to from *Posidonia* sp., i.e. lower biomass, lower carbonate for *Posidonia* sp. and higher biomass, higher carbonate for *Amphibolis* sp.

4.2.5 Other parameters

There was variation in carbonate abundance with depth (Fig. 4.7). Water depth values were grouped into 2 m mwd intervals to determine clear patterns without the affect of anomalous data points. It was necessary to use $CaCO_3$ g/kg of seagrass values for each genus to determine the effects of depth. The maximum values occur at 8-10 m mwd for epiphytes associated with *Posidonia* and at 4-6 m mwd for calcareous epiphytes associated with *Amphibolis*.

Water temperature and salinity measurements are reported in Chapter 3. Non-parametric analysis of variance using the Kruskal-Wallis test indicates that epiphytic carbonate associated with *Posidonia* is more sensitive to changes in water temperature and salinity than those associated with *Amphibolis* sp (Table 3.5). No clear distribution pattern was shown for

Table 4.3. Mean, maximum and minimum epiphytic $CaCO_3$ standing stock values obtained from the 5 main seagrass species. These values do not include data from West Island.

	Amphibolis		*A. antarctica*		*A. griffithii*		*Posidonia*		*P. angustifolia*		*P. sinuosa*		*P. australis*	
	m^{-2}	kg^{-1}	m^{-2}	kg^{-1}	m^{-2}	kg^{-1}	m^{-2}	kg^{-1}	m^{-2}	kg^{-1}	m^{-2}	kg^{-1}	m^{-2}	kg^{-1}
Mean	151.1	238.5	95.64	191.3	360.8	362.1	37.39	127.2	24.1	123.3	62.6	193.6	25.3	93.1
Max	655.6	510.4	498.1	510.4	542.5	482.1	350.7	767.3	161.5	767.3	350.	493.3	121.	676.3
Min	1.29	56.9	1.29	52.5	197.2	242.1	3.1	11.2	1.8	32.1	11.9	42.8	3.1	11.2

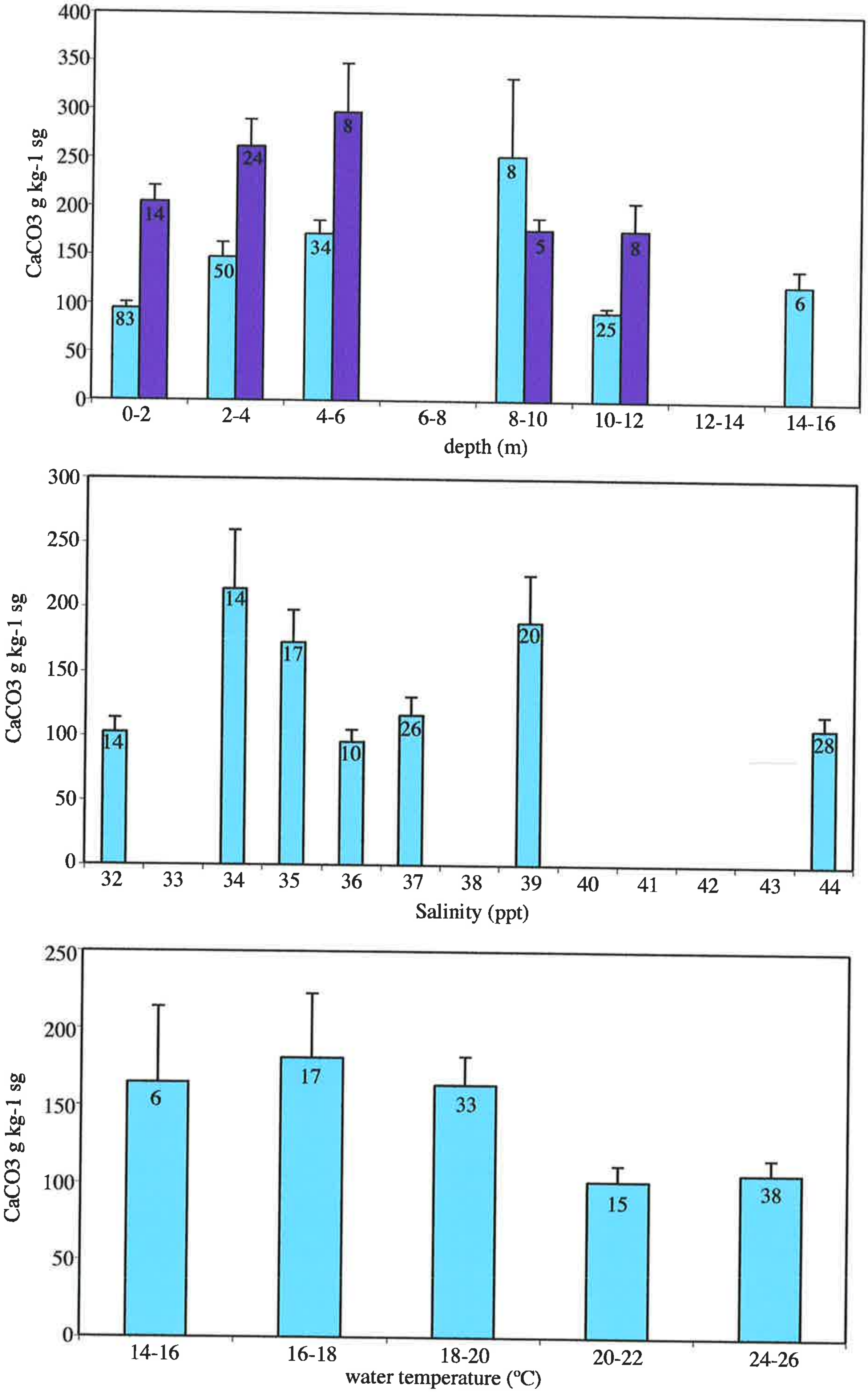


Figure 4.7. Average epiphyte standing stock $CaCO_3$ g kg^{-1} sg values of *Posidonia* sp. ▨ and *Amphibolis* sp. ■ plotted against ranked a) depth b) salinity c) water temperature. Number at top of column refers to number of samples collected. Mean ± s.e.

salinity even though significant variation was found (Fig. 4.7). The maximum variation of temperature occurs at 16-18°C, followed by a decrease in abundance with water temperature over 20°C (Fig. 4.3).

There was not enough nutrient data for *Amphibolis* to carry out analysis. *Posidonia* sp. only showed significant variation when the anomalously high values from Semaphore were included (see Section 3.3).

4.3 DISCUSSION

The epiphytic quantities obtained are of standing stock values only (Table 4.2), with productivity values discussed in Chapter 7. Comparison with standing stock data from other studies shows a wider range in values for the minimum-maximum abundances for individual seagrass species data, but average values lie within the range of the previous studies. The range of epiphytic $CaCO_3$ abundances obtained from this study for *A. antarctica* was 1.29 – 498.1 g/m^2, averaging 95.6 g/m^2, which compares with the findings of Sim (1991) of 42.1-178.8 g/m^2 in summer, and 74.4-168.9 g/m^2 in winter. The range of epiphytic $CaCO_3$ abundances for *A. griffithii* was 197.2 –542.5 g/m^2, averaging 360.8 g/m^2, compared to a value of 157.8 g/m^2 (Lavery *et al.* 1998) and 415.0 g/m^2 (Lord Associates 1998a, b). The only standing stock abundances known for Australian *Posidonia* are for *P. coriacea* and range from 14.1 to 77.9 g/m^2 (Lavery *et al.* 1998 and Lord Associates 1998a, b, respectively), which compares to 3.1-350.7 g/m^2, average 37.4 g/m^2 for this study from *P. angustifolia, P. sinuosa* and *P. australis*. The range of values shown for this study are individual quadrat data, hence are more susceptible to local variations and reflect the maximum variability. The high range of values may also be attributed to sampling over several years and all seasons, or just a larger sample size than previous studies. Chapter 5 addresses the subject of seasonal affects on epiphyte productivity. Calcareous epiphyte standing stock values from the tropical seagrass *Thalassia* sp. tend to lie between the average values of *Posidonia* and *Amphibolis*, e.g. 0.2-182.9 g/m^2 (Frankovich & Zieman 1994), 1.19-140.95 g/m^2 (Nelsen & Ginsburg 1986) and 7.2 – 48 g/m^2 (Land 1970).

4.3.1 Biomass correlation

The results indicate that there is a strong positive relationship between the abundance of epiphytic $CaCO_3$ g/m^2 and biomass of seagrass. Sim (1991) determined that there was no correlation between epiphyte abundance and the density (i.e. number of shoots per unit area), of *A. antarctica* stems and blades. He, however, partially attributed the variations between sites as largely corresponding to the different sizes of the plants – i.e. the biomass. There are no other reported studies that have examined the relationship between epiphyte abundance and seagrass biomass. The relationship found during this study can be described as being allometric, i.e. there is a constant ratio between the two variables. This relationship described by equation 4.1 allows the predictability, within the calculated errors, of epiphyte abundance from any known biomass and the predictability of any seagrass biomass from known epiphyte abundance. The ability to predict the abundance of epiphytes from seagrass biomass means that extrapolation of carbonate abundance data to larger areas, e.g. 9,612 km^2 of seagrass in South Australia, is feasible (see Chapter 7). Predicting the amount of seagrass biomass from epiphyte abundance has ramifications for interpreting paleoenvironments from the rock record, i.e. it is now possible to estimate the seagrass biomass present at the time of deposition from the abundance of recognisable epiphytes found in sediment Other variables, such as sediment loss through transportation, breakdown, dissolution etc., need to be considered These are discussed in detail in Chapter 7.

The relationship between $CaCO_3$ g/m^2 and biomass is almost certainly a function of the surface area that biomass provides, i.e. high biomass equals a large surface area. This indicates that the surface area available for recruitment largely restricts the abundance of epiphytes per unit area. The fact that the relationship is not linear indicates that some other process is involved. The exponential curve is probably a function of the proximity of epiphytes to their conspecific adults, i.e. more surface area equals more calcareous epiphytes, more adult epiphytes equals greater numbers of adults reproducing, and an increase in spores and larvae (hereon in referred to as propogules) available for recruitment, which in turn results in higher abundance of epiphyte recruitment (limited by the surface area). An increase in biomass may also reduce the amount of light available for algal epiphytes below the canopy. These algal epiphytes can also be used as additional substrate for epiphytes to settle. In addition to the proximity of the conspecific adults, it has been speculated that as seagrass biomass increases, so current velocity decreases and the ability and success rate of epiphyte settlement and establishment increases (Eckman 1983). Alternatively, a decrease in current velocity is suggested to increase the surface boundary layer (Vogel 1981 and Koehl 1984 cited in Sim 1991) in increasing the barrier for the exchange of nutrients and waste products which may be limiting to algal calcification (Sim 1991). If the latter process is occurring then according to the findings of this study it is insignificant.

The exponential growth of calcareous epiphyte abundance with biomass may have an influence on limitation of biomass abundance due to the shading effect of epiphytes. In Chapter 3, it was found that the majority of biomass values were found between 50-500 g/m^2

and it was suggested that where biomass values were higher, the environments were 'atypical'. Could these 'atypical' environments be unfavourable or even inhibit epiphyte growth, rather than being favourable for seagrass growth as suggested in Chapter 3? If the conditions were unfavourable for epiphyte growth then it would be expected that epiphyte abundance per shoot would actually decrease at a certain limit of biomass. The $CaCO_3$ g/kg of seagrass data from this study does appear to show a decrease in epiphyte abundance per shoot above a seagrass biomass of 700 g/m^2 (Fig. 4.4). The $CaCO_3$ g/m^2 data also indicates a downturn in the abundance of epiphytes above 800 g/m^2 (Fig. 4.5). The quadrats that contained the high biomass occurred at a number of sites (Ardrossan, Cape Jaffa, Moonta Bay, Normanville and Streaky Bay) and also had quadrats with lower biomass values and high epiphyte abundance. This indicates that the environments are not 'atypical' and therefore are not the cause for the apparent decreasing epiphyte abundance. The number of quadrats with high biomass was also low, thereby biasing the data. In general, evidence does not indicate that the exponential abundance of calcareous epiphytes inhibits the seagrass biomass, but it is clear that biomass (analogous to surface area) strongly influences the abundance of calcareous epiphytes in an area.

Surface area is not the only constraining parameter on epiphyte abundance as shown by i) the lower correlation of the ungrouped data ($r^2 = 0.5$) as opposed to the grouped data ($r^2 = 0.9$) and ii) the lack of correlation with biomass when epiphyte abundance is measured in kilograms of seagrass, i.e. the amount of calcareous epiphytes on each plant is controlled by other factors. These other potential factors are investigated and discussed in the following sections.

4.3.2 Intra-site variance

The results indicate that variance of carbonate quantities along transects, at different sites (Fig. 4.1), is related predominantly to patchiness of seagrass. Causes of seagrass patchiness have been discussed in Chapter 3. The overall lower variance of calcareous epiphyte abundance per kilogram of seagrass indicates that the availability of calcareous epiphyte propogules is relatively homogenous at each site. This is not contradictory to the finding that calcareous epiphyte availability exponentially increases with increasing seagrass biomass because this homogenous availability is at site level only. For example, it could be predicted that two sites of differing biomass would each have a homogenous abundance of calcareous epiphyte propogules available, and only the site with the higher biomass would have a higher abundance of calcareous epiphyte propogules.

Not all sites showed equal distribution of epiphytes per kilogram of seagrass, e.g. Dutton, Semaphore and West Island (deep site). Where patchiness of calcareous epiphytes was high, patchiness of seagrass was also high. It is consequently suggested that this patchiness may be caused by a competition for space. Along an individual transect, a quadrat with a relatively low biomass would be expected to have a relatively high abundance of calcareous epiphytes on each blade, and vice versa. The epiphyte abundance/m^2 in these circumstances would be relatively consistent. This did not occur at all sites although it was clearly the case at Semaphore where the $CaCO_3$ g/m^2 was constant, $CaCO_3$ g/kg of seagrass was highly variable and the pattern along the transect mirrors the seagrass biomass. Where this pattern did not occur, patchiness in epiphytes is attributed to a number of possibilities;

- proximity to the conspecific adult (Keough 1983);
- competition with algal epiphytes;
- structure of host plant;
- epiphyte species type; or
- recruitment mechanism (active/passive).

It is apparent that the host type will also have an affect on the distribution of epiphyte abundance. The effects of different seagrass genera and species are discussed below.

4.3.3 Seagrass genera/species correlation

This study indicates that the abundance of calcareous epiphytes, independent of seagrass biomass, was significantly greater on *Amphibolis* sp, than on *Posidonia* sp. Studies of calcareous epiphytes from Success Bank, Western Australia, also show similarly higher abundance of epiphytes on *A. griffithii* (157.8 - 415.0 g/m^2) than *P. coriacea* (14.1 g/m^2 - 77.9 g/m^2) - Lavery *et al.* (1998) and Lord Associates (1998a, b). It has also been stated that *Amphibolis* sp. has the largest biomass of epiphytic (calcareous and non-calcareous) organisms of any species of seagrass (Borowitzka & Lethbridge 1989).

The current study also showed a close correlation between sites of low carbonate quantities/high dominance of *Posidonia* sp. and between sites with high carbonate quantities/high dominance of *Amphibolis* sp. (Fig. 4.6). This agrees with the findings in Chapter 3 that *Amphibolis*-dominated quadrats tend to have higher biomass values than *Posidonia*-dominated quadrats. The high value of epiphyte carbonate associated with *Amphibolis* sp. has also been noted by Jernakoff & Nielsen (1998).

The significantly greater abundance of epiphytes on *Amphibolis* is attributed to the longevity of *Amphibolis* sp. stems. *Amphibolis* stems are biennial (Walker 1985, Coupland 1997), whereas *Amphibolis* blades and *Posidonia* blades have life-spans of only 60-100 and 65-130 days, respectively. Hence, calcareous epiphytes have a longer time to accumulate on stems. Analysis of epiphytes on stems of *Amphibolis,* rather than on the blades, was examined from the West Island sites and is described in Chapter 5. Settlement plate studies have shown that longer immersion times result in higher species abundance and higher species diversity (Turner & Todd 1993).

Species of *Posidonia* also showed significantly different abundances of calcareous epiphytes associated with them. The higher abundance of epiphytes on *P. sinuosa* may be attributed either to the habitat in which *P. sinuosa* occurs, or that this species occurs more frequently than *P. angustifolia* or *P. australis*. The more frequent occurrence may bias the data. On the other hand, the conditions that are favourable for *P. sinuosa* are probably also favourable for calcareous epiphytes. The literature does not offer clear reasons as to why *P. sinuosa* is the most widely distributed species, although the strong rooting system may be a contributing factor (Womersley 1984).

The difference in abundance of epiphytes associated with *Posidonia* and *Amphibolis,* as well as between species, is likely to be a contributing factor to the cause of epiphyte patchiness as described above. The ramifications of these findings are similar to those for the relationship between carbonate abundance and biomass. These findings i) enable more accurate extrapolation of the calcareous epiphyte abundance data to regional areas, and ii) allow palaeo-environmental interpretation of, not only the biomass present at the time of deposition, but also the genera type.

4.3.4 Depth correlation

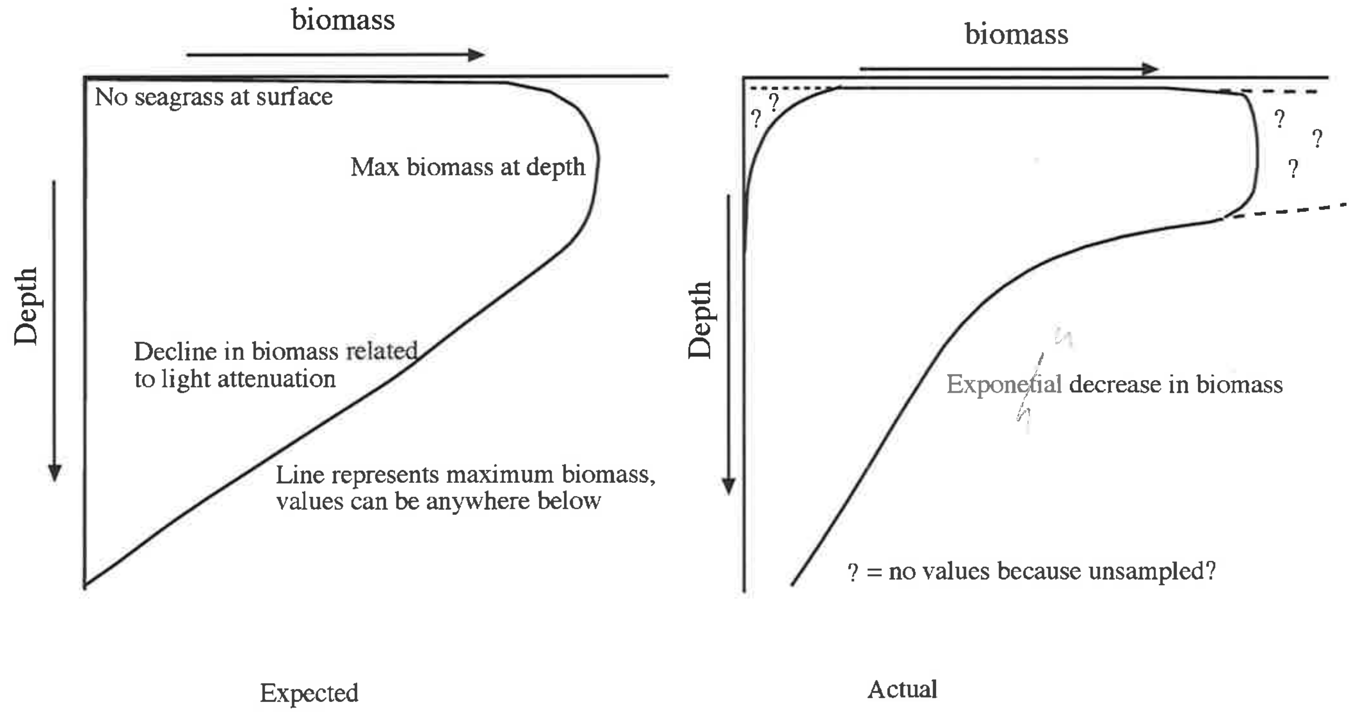
Epiphytic carbonate production appears to be affected by increasing depth independently of biomass (Fig. 4.8). The $CaCO_3$ g/kg of seagrass indicates that there is an increase in carbonate production to a maximum depth of 10 m, after which carbonate quantities reduce (Fig. 4.7). Depth is intrinsically linked with reducing light penetration and current velocity, the former generally accepted as the main controlling parameter for photosynthetic productivity (Wetzel & Penhale 1983, Dennison & Alberte 1986, Fairhead 2001). The only photosynthetic calcareous epiphytes are coralline algae, which are known to tolerate low light levels (Johansen 1981, Leukart 1994). It seems unlikely therefore, that light is the direct controlling factor for calcareous epiphyte abundance with depth. Other algal epiphytes are not tolerant of low light and hence an increase in depth would reduce the abundance of non-calcareous algal epiphytes, making more space available for calcareous epiphytes. Reduction in carbonate below 10m mwd may reflect the critical depth at which the epiphytic coralline algae species begin to be affected by light reduction, although this is probably not the case as coralline algae are often found at depths of up to 40 m (N. James pers. comm. 2002). Alternatively or additionally, non-photosynthetic calcareous epiphytes may be limited by the reduction or change in the species of their photosynthetic dependent food source, i.e. phytoplankton. This seems unlikely as the depths involved during this study are unlikely to produce such stratification in phytoplankton, although the possibility should not be ruled out. Correlated with increasing depth is a reduction in current speed that may be detrimental to filter-feeding calcareous epiphytes because of reduced flow across the surface of the organisms resulting in decreased particulate matter available for feeding (Peterson *et al.* 1984), although there is an alternative theory that speculates that reduced velocities may concentrate particulate matter in the region of seagrass beds, hence increasing the availability to filter-feeders (Eckman *et al.* 1984 cited in Sim 1991). There is evidence to indicate that the hydrodynamic conditions alter the abundance of certain epiphytic species over certain depths, e.g. Blanc-Vernet (1984) and Ribes *et al.* (2000) showed that benthic foraminifers increased in diversity and quantity over depths of 5-13 m. This was attributed to calmer deep water enabling more foraminifers to stay attached to the blades, rather than the consequences of deeper light penetration or change in particulate matter available as food. Even though the data from this study shows the variation with depth as described, the low correlation ($R^2 = 0.16$) suggests that, without more detailed measurements, the true nature of the relationship between calcareous epiphyte abundance and depth, and the causes of the variation, can not be clarified. It is therefore suggested that the data from this project only be used as a rough guide to predict the change in $CaCO_3$ g/kg of seagrass with depth.

Calcareous epiphytes appear to be more affected by depth when associated with *Posidonia* sp. than when associated with *Amphibolis* sp. This is most likely to do with the long lifespan and hence accumulation time for epiphytes on *Amphibolis* stems compared to *Posidonia* blades. This relationship indicates that, with time, calcareous epiphytes out-compete non-calcareous epiphytes. Such competition has been noted by Borowitzka *et al.* (1990) who surmised that the distribution of species on *A. griffithii* was partially driven by the competitive abilities of non-calcareous algal epiphytes (see Section 3.3.2).

4.3.5 Other parameters

The lack of any significant effects of temperature and salinity on epiphytes associated with *Amphibolis* sp. may be attributed to one of three things;

- numbers of samples studied;



Expected

Actual

Fig. 4.8. Diagrammatic profiles of expected and actual seagrass biomass changes with water depth

- limited range in temperatures; and
- longevity of *Amphibolis* sp. covering any variability.

The temperature effect on calcareous epiphytes associated with *Posidonia* sp. is more likely to reveal any effects because of the larger sample size. The results indicated that temperatures above 20°C reduce calcareous epiphyte abundance. Intuitively, increasing temperatures would increase the productivity of epiphytes due to increased metabolism and that 20°C is too low to be inhibitive. Ichiki *et al.* (2000), however, reported that the sporelings of the coralline algae *Lithophyllum essoense* Foslie had an optimum growth temperature of 15°C, indicating that optimum and inhibiting temperatures may be low. There are few studies that establish the optimum temperatures for growth and reproduction of temperate calcareous epiphytes. Hence, the findings of apparently low inhibiting temperatures cannot be excluded.

The reason why there was no apparent significant effect caused by nutrient changes of calcareous epiphytes on either *Amphibolis* sp. or *Posidonia* sp. when the anomalously high values from Semaphore are excluded, is not clear. It could be that too many other variables influence their abundance and hence the multiple site sampling covers up nutrient control effects, or that the nutrient variability (excluding those from Semaphore) was not sufficient to cause any change. The correlation between extremely high nutrient levels, low seagrass biomass and high $CaCO_3$ g/kg of seagrass at Semaphore could be interpreted as an indication that either the high nutrients levels prohibit seagrass growth, or that low nutrients inhibit calcareous epiphyte productivity.

4.3.6 Geographical distribution

Some sites produce epiphyte abundances apparently anomalous to the other sites. The low biomass and high epiphyte abundance per kilogram of seagrass at Semaphore is attributed to the high nutrient levels that were found at this site. The source of the nutrients is likely to be anthropogenic, given its proximity to the Adelaide metropolitan coastline. The northward current direction and the relatively normal values of seagrass biomass, epiphyte abundance and nutrient levels at the Torrens site indicate that the source of the nutrients is located somewhere between Torrens and Semaphore. Both sites were 2 km offshore, so it is unlikely that the source is direct runoff from the metropolitan area as any affected waters would be dispersed at this distance offshore. The Port Adelaide sludge outfall was situated 1.5 km offshore and 2 km south of Semaphore and seems the most likely source for the nutrients. However, this outfall was deactivated in 1992. It is likely that, during the time in which the outfall was operational, organic material was deposited and built up in the sediment. The resulting break down of the organic matter would be released back into the water column over time, and it is deduced that this is the source of nutrients measured at Semaphore. The long-lasting effect of nutrient input was also noted during a study by Delgado *et al.* (1999) who found that, even after 4 years closure of a fish farm and the return to normal water conditions, there was still a decline in seagrass biomass. It was concluded from this that the continuing decline was due to a build up of excess organic matter in the sediment originating from the fish farm (Delgado *et al.* 1999).

The variation in biomass and calcareous epiphyte abundance at the three Chinaman Creek sites has been attributed to patchiness caused by changes in depth and current regime. Site 2 occurred at the shallowest site, which appears to be favourable for seagrass growth, but not for epiphyte growth, i.e. the highest biomass, but lowest epiphyte abundance of the 3 sites. The parameters favourable for *Posidonia australis* growth at Chinaman Creek are attributed to shallow, low turbidity waters with low current velocity and possibly high salinity. High salinity is the most likely contributing factor to the low epiphyte abundance, although low velocity may also reduce the abundance of filter feeders.

Normanville is considered to be a 'pristine' (or 'ideal') site for calcareous epiphyte and seagrass biomass, having the maximum seagrass biomass and calcareous epiphyte abundance. However, the conditions that make this so, are unclear. Normanville is situated 60 km south of Marino, and is relatively sheltered and oceanic conditions are 'normal' for the lower Fleurieu Peninsula region. Normanville has a population of 3800 and no industrial outfalls, and although there may be some anthropogenic influence, it does not appear to be limiting. Nutrient data was not available from the site, but despite three small rivers in the vicinity (Yankalilla River, Bungala River and Carrickalinga Creek) the coastal environment here is relatively pristine.

The lack of any regional geographical correlation with the quantities of calcareous epiphytes indicates that the parameters that are controlled by latitude and longitude at this scale, have no significant effect on epiphyte quantities. This is explained by local parameters that override regional variations at this scale and the general restriction of seagrass to more sheltered environments. The apparent decrease northwards on the west coast and the southward decrease on the east coast of the Spencer Gulf could be interpreted as a function of the cyclic clockwise current circulation within the Spencer Gulf (an inverse estuary). However, the different regimes, seagrass species and the effect of depth at the different sites render this correlation inconclusive.

4.4 CONCLUSIONS

Standing stock values of epiphytic carbonate have average values of 79 g/m^2 or 162 g/kg of seagrass. The fact that each of the 21 sites had different abundances of calcareous epiphytes, indicates that estimations of regional abundance may be difficult without a more detailed understanding of the controlling factors. The predominant control on the abundance of epiphytes was seagrass biomass, i.e. the more seagrass, the more surface area for recruitment, the greater the abundance of calcareous epiphytes. It is possible to predict the abundance of calcareous epiphytes because of the allometric relationship between biomass and $CaCO_3$ g/m^2. The exponential increase in epiphyte abundance is attributed to the proximity to the conspecific adults, reduced current velocity allowing higher settlement success rates and light availability below the canopy reducing competition for space with non-calcareous epiphytes. Variance at sites is attributed largely to patchiness in seagrass biomass, but calcareous epiphyte patchiness can be extensive at some locations. Greater abundance of calcareous epiphytes was associated more with *Amphibolis* than with *Posidonia* due to the accumulation of calcareous epiphytes over time on the relatively long-lived *Amphibolis* stems. Epiphytic carbonate significantly changes with depth, apparently increasing with depth to 10m mwd and then decreasing with further depth. Increasing $CaCO_3$ g/kg of seagrass to 10 m mwd is probably a function of reduced competition from algal non-calcareous epiphytes, but beyond 10m mwd light for coralline algae, and food source for other epiphytes, becomes limited. There is no apparent correlation between salinity or nutrient concentration, at levels normal for the local environment, with calcareous epiphyte abundance, but temperature data indicates the optimal temperature is 16-18°C. The elevated nutrient levels at Semaphore appear result from the sediment that was previously sourced from the Port Adelaide sludge outfall and has resulted in low seagrass biomass, but high epiphyte abundance. No clear regional trends were found.

WEST ISLAND

CHAPTER 5

SEASONALITY EFFECTS ON CALCAREOUS EPIPHYTE ABUNDANCE: WEST ISLAND - A CASE STUDY

5.1 INTRODUCTION

Previous chapters analysed epiphyte carbonate standing stock at two spatial scales – metres and kilometres. The dominant factors putatively controlling the quantities of epiphytes at these scales were also described and discussed. This chapter uses information collected from West Island as a case study to extend knowledge gained from the larger-scale investigations and to add temporal and seasonal variations to the equation. This enables better estimations of the productivity and furthers the knowledge on the controlling parameters affecting calcareous epiphyte colonisation and growth.

Seasonal variation is a common phenomenon, especially amongst primary producers. Seasonal variation is also expected, as some calcareous epiphytes are primary producers whereas others are intrinsically linked to primary producers (the seagrass). Seasonal variation, independent of seagrass seasonal variation, is also described.

5.2 METHODS

5.2.1 West Island

West Island was selected for a detailed study of seagrass calcareous epiphytes because of:

- the presence of dense seagrass beds;
- accessibility;
- previous marine scientific knowledge; and
- relatively pristine conditions.

West Island is situated south-west of Encounter Bay, South Australia (35°36’25”S latitude, 138°35’27”E longitude (Fig. 5.1) and approximately 800 m offshore. It is subjected, predominantly, to Southern Ocean and to Gulf St. Vincent waters bodies (Fig. 2.1). The rocks of West Island belong to the Encounter Bay granitoid suite which was intruded into Cambrian sediments during the Delamerian Orogeny in the Cambrian/Ordovician (Drexel *et al.* 1993). It is composed entirely of granite, with large K-feldspar phenocrysts (<7 cm) and numerous xenoliths (5-50 cm). The granite is

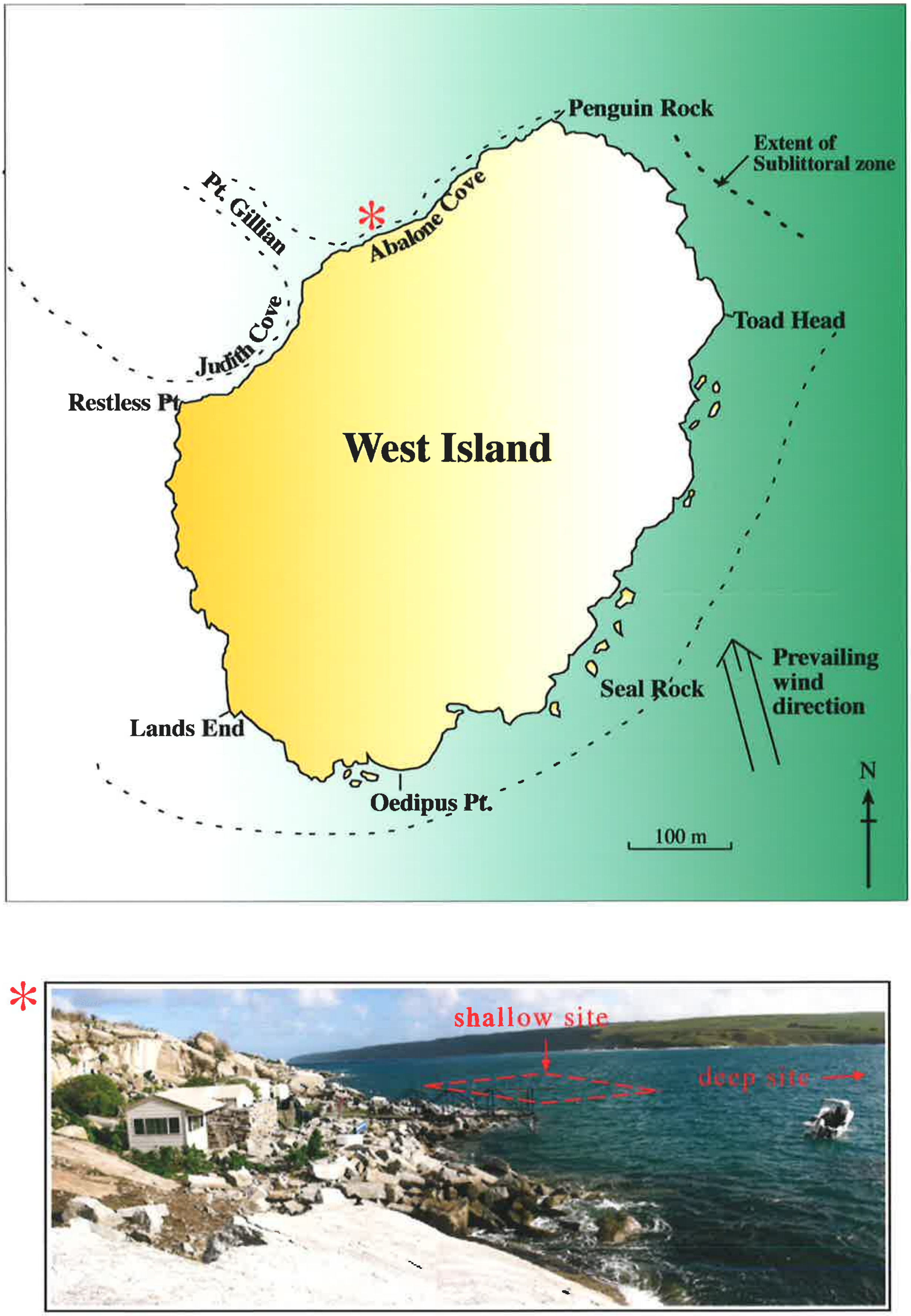


Fig. 5.1. West Island field site(see Fig. 2.1 for location.. A. Schematic map of West Island B. Photograph of West Island marine laboratory in abalone cove and study sites. Photograph taken from * in a south-westerly direction.

resilient to erosion and forms the rocky sublittoral zone that extends 2-10 m offshore to a depth of 3 m. The granite was mined from 1913 to 1939 and was used in the building of South Australia's Parliament House (Robinson *et al.* 1996). The quarry site, located on the northwest side of the island, is now occupied by the research station (Fig. 5.1). The only evidence of quarrying in the offshore environment is a number of fresh granite blocks in Abalone Cove.

The only marine disturbance since quarrying ceased has been from boat moorings and from scientific studies. The moorings have removed seagrass within a 5 m radius of the mooring block. Scientific studies have had minimal impact on the natural ecosystem.

West Island was designated a Conservation Park in 1972, with an aquatic reserve extending 100 m offshore (Robinson *et al.* 1996). The reserve was initially used to study abalone (Shepherd 1973), but is now utilised for a wide range of studies, including: productivity and significance of the macro-algal communities (e.g. Shepherd 1970, Shepherd & Thomas 1982, Cheshire *et al.* 1996, Fairhead 2001, Copertino 2002); Fairy Penguin (*Eudyptula minor*) breeding patterns (N. Gilbert pers. comm. 1999); and territory identification of Leafy Seadragons (Connolly *et al.* 2002).

Terrestrial sources of 'new' nutrients are limited to three rivers. The River Murray reaches the sea 24 km east of West Island. The flow is minimal and drifts south-east away from West Island. The only other possible sources of 'new' nutrients to the Island are the Inman and Hindmarsh Rivers and no quantitative data is available.

5.2.2 Sample sites and sample collection

Sites were selected at two depths: 4-6 m mwd in Abalone Cove, approximately 10 m offshore (herein referred to as the 'shallow' site; (Fig. 5.1) and 11 m mwd, approximately 500 m offshore located between the mainland and the island (herein referred to as the 'deep' site).

Samples were collected using the transect method (Fig. 2.2) approximately every 3 months (weather permitting). Samples from a total of 182 quadrats were collected; 137 from the shallow site, 45 from the deep site (Table 5.1). Shallow site samples were collected over a 2.5 year period and the deep site samples were collected over a 1 year period. The Australian calendar seasons are as follows: summer – December to

Table 5.1. Summary of the number of samples obtained from West Island, South Australia.

	Total samples	Shallow	Deep
Total *Amphibolis* sp.	143	113	30
A. griffithii whole plants	116	104	12
A. griffithii stem/blade	83	75	8
A. antarctica whole plants	18	5	14
A. antarctica stem/blade	14	4	10
Total *Posidonia* sp.	138	114	24
P. sinuosa	117	105	12
P. angustifolia	12	5	7

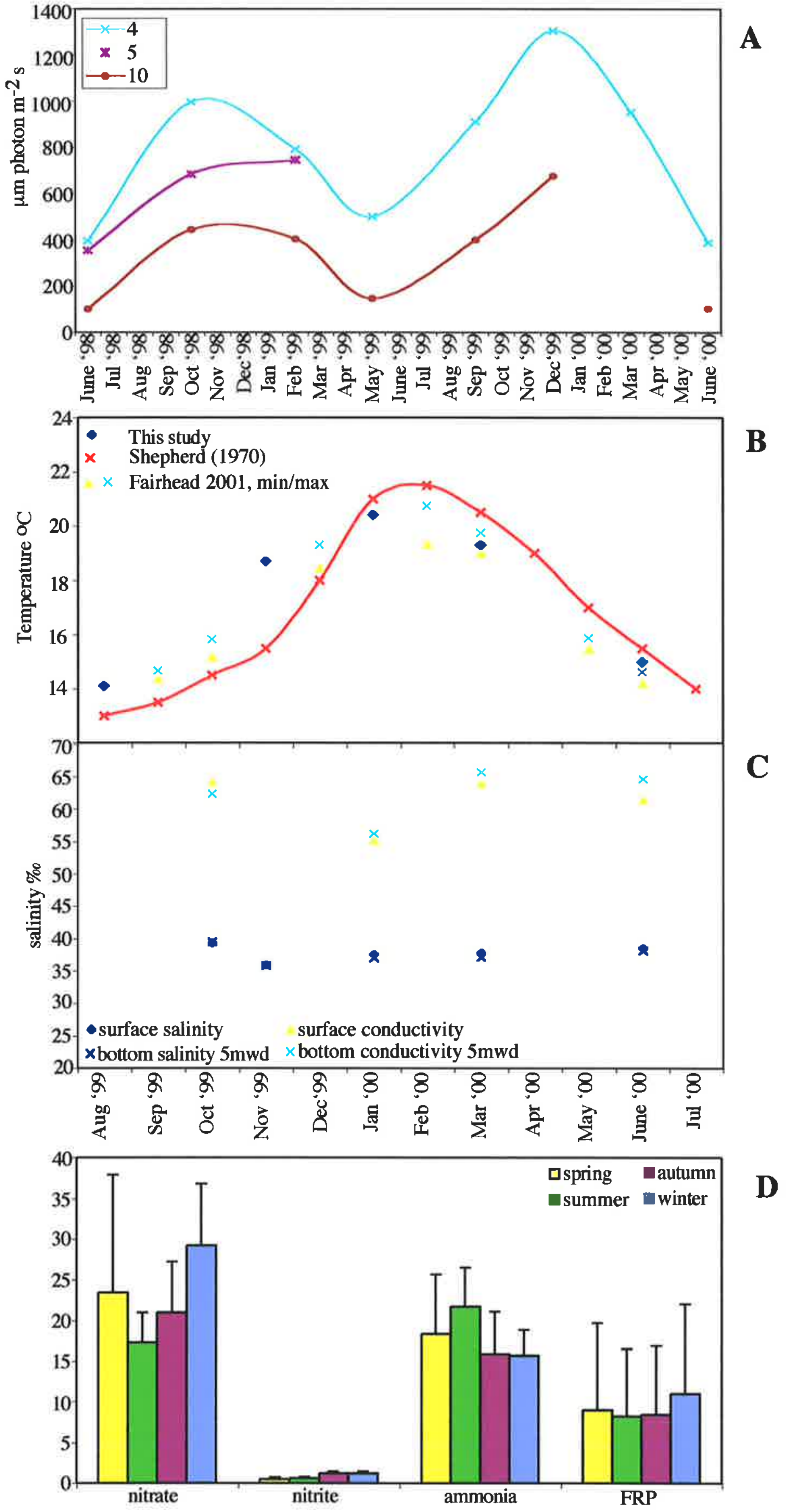


Fig. 5.2. West Island abiotic variables. **A**. Light intensity variation with depth and season (PAM light sensor corrected to logger LICOR-absolute maximum values) (data kindly donated by Fairhead 2000; Copertino, 2002) **B**. Sea surface temperature, measurements from 3 sources. **C**. Surface and bottom salinity and conductivity measurements from this study only. **D**. Seasonal average nutrient values. FRP= Filterable reactive phosphate. Mean ± s.e.

February, autumn – March to May, winter – June to August, spring – September to November. Transects were orientated NW-SE (140°) at both sites. The transect locations were repositioned 10 m further south each season, for one year and then returned close to the original site for the 2nd year of sampling to reduce the chances of re-sampling quadrat sites. The shallow sites were located by identifying underwater landmarks. The 10 m mwd was located using a combination of landmark bearings and GPS (Magellan 300).

5.2.3 Environmental parameters

5.2.3.1 Light

Light measurements (photon flux density; μmol photons/m^2/s) were obtained from studies at West Island by Fairhead (2001) and Copertino (2002). Light intensity was measured using a LICOR light sensor and a diving-PAM light sensor. The LICOR light sensor was kept at a constant depth of 4 m for 24 hour periods. Values given are average maxima (Fig. 5.2A). Diving-PAM readings were taken from a variety of depths and the values are instantaneous, i.e. a moment in time. LICOR data was corrected using light meters fixed underwater. The PAM data was corrected to the logger LICOR data. It should be noted that the10 m mwd site was measured at a location adjacent to the Island and hence may differ slightly from the true values at the 'deep' site for this study.

5.2.3.2 Temperatures and salinity

Records of average mean maximum monthly air temperatures for the period of the study were obtained from the Bureau of Meteorology's station at Victor Harbor (CD). Surface water temperatures (Fig 5.2B) and salinity (Fig. 5.2C) were recorded using a calibrated TPS WP-84 from November 1999 to March 2001. Salinity was recorded at the surface and at the bottom.

5.3 RESULTS

There were 5 seagrass species sampled at West Island (Table 5.1). Their natural patchiness resulted in differing quantities of species being collected during each season of the study period. Fewer samples were obtained from the deeper sites due to the shorter collection period. *Amphibolis* sp. blades and stems were considered as separate entities where biomass samples were >10 g, due to their different morphological attributes and growth rates.

5.3.1 Environmental variables

5.3.1.1 Light

Average maximum photon flux density showed strong seasonal variation. Values at 4 m mwd ranged from 1305 μmol photons/m^2/s in December to 388 μmol photons/m^2/s in June (Fig. 5.2A). These values are higher than those found by Cheshire *et al.* (1996) of 600-700 μmol photons/m^2/s in January and 200 μmol photons/m^2/s in June, although these were measured at 4.5 m. Light reduced by half from 5 m to 10 m (590 →325 μmol photons/m^2/s) (Fig. 5.2A).

5.3.1.2 Temperature and salinity

Air temperatures (average mean maximum monthly) ranged from 15-25°C and showed strong seasonal variation. Temperature did not vary strongly between years, although temperatures in early 1999 were slightly cooler. Daily air temperatures during the sampling months were within the normal range. Surface water temperatures varied from 14.1°C (September) to 20.4°C (January). These temperatures are within the range found by Shepherd (1970), but are seasonally slightly offset (Fig. 5.2B). This offset may be attributed to the limited data points or may be a real phenomenon suggesting that water temperature has been warming and cooling slightly earlier in the year.

Only surface water temperatures were recorded. It was assumed that temperature variation would be limited due to the shallow depth and relatively high energy environment. Shepherd (1970) stated that thermoclines only developed during periods of calm, and even then a change was only noticeable at depths of 15-20 m. Cheshire *et al* (1996) recorded temporal pulses of warm water causing a temperature flux of 2°C during the summer. This was attributed to a warm water plume forming in the shallow waters of Encounter Bay and then flowing past West Island (Cheshire *et al.* 1996).

Salinity varied from 36-39.4 ‰ (av. 37.9 ‰) (Fig. 5.2C). There was no significant difference relative to depth and no clear seasonal variation. The salinity values were higher than expected and may be attributed to unavoidable problems with calibrating the TPS.

5.3.1.3 Nutrients

Average nutrient values recorded from West Island samples over 2 years show that nutrients were not significantly different at the two depths when the standard errors taken into account (Table 5.2D). The large standard error values observed in Table 5.2 show the high flux that occurs at West Island. Repeated measurements at any one time, or over the space of a few days at the same location and water depth, showed high variation (e.g. shallow site 22/2/99 to 1/3/99). This flux, over a period of days, may be related to storm or current activity. Variation within the same day may be caused by changes in photosynthetic activity of plants in close proximity or rapid input of guano from the bird life that inhabits the island (Paton & Paton 1977).

Nitrite and filterable reactive phosphate (FRP) values are relatively consistent throughout the year (Fig. 5.2D). The consistency of the phosphate levels agrees with the findings of Kirkwood (1967), who indicated that organic and inorganic phosphate remained constant around Kangaroo Island, a neighbouring island. Nitrate values were highest in winter, reduced in spring and summer and then increased in autumn again. Ammonia values peak during summer.

5.1.1.4 Sediment type

The sediment is a coarse/medium-grained, well-sorted, high sphericity immature sand. It has an equal composition of lithic and carbonate fragments. Lithic fragments, derived from the island granite, consist of quartz, feldspar and biotite. The carbonate fraction comprises fragments of bivalves, gastropods, bryozoans and echinoids. A considerable fraction is also composed of foraminifers and polychaete worm tubes. Both pristine (white in colour) and relict (stained red/brown) carbonate fragments are present, suggesting that reworking processes are important and that the deposition has occurred over a considerable length of time (James *et al.* 1992). This mixture of pristine and relict sediment is termed palimpsest. Areas of coarser sediment (>pebble size) occur in blowouts. There is also the occasional boulder amongst the seagrass beds. Presumably derived from previous marine experiments.

5.1.1.5 Wind, waves & currents

Mean monthly wind speeds (obtained from the Bureau of Meteorology) varied between 7-25 km/hr during the study period (CD). No clear seasonal trend was shown. Average

Table 5.2. Nutrient values from 5 (shallow site) and 10mwd (deep site) at West Island. Average from seasonal data collected over two years ± standard error (outliers removed)

Collection date	Season	Nitrate (NO_3) (μg N/L)	Nitrite (NO_2) (μg N/L)	Ammonia (NH_3) (μg N/L)	Filterable reactive phosphate (FRP μg P/L)
Shallow site	**Average**	**17.2 (± 13.5)**	**0.99 (± 0.6)**	**16.8 (± 14.4)**	**8.26 (± 3.0)**
22/2/1999	summer	6	0.8	9	8.1
22/2/1999	summer	16	0.5	9	7.5
25/2/1999	summer	8	0.7	14	8
25/2/1999	summer	10	0.1	40	7
1/3/1999	autumn	8	0.9	38	7
1/3/1999	autumn	6	1.7	33	7
27/5/1999	autumn	30	0.9	7	8.1
27/5/1999	autumn	41	1	7	7.9
2/6/1999	winter	56	0.7	10	10
2/6/1999	winter	36	1	9	8
6/6/1999	winter	11	0.9	6	19
6/6/1999	winter	13	6	17	10
10/9/1999	spring	5	<0.5	7	7.9
10/9/1999	spring	8	<0.5	6	6.1
30/11/1999	spring	12	1	50	19
11/12/1999	summer	10	1	9	5.9
11/12/1999	summer	23	<0.5	10	7.5
8/10/2000	spring	11	0.9	2	4
Deep site	**Average**	**32.7 (± 27.9)**	**1.1 (± 0.7)**	**19.9 (± 13.4)**	**10.5 (± 2.23)**
25/2/1999	summer	21	0.8	28	10
25/2/1999	summer	19	1.7	49	10
27/5/1999	autumn	32	16	9	8
27/5/1999	autumn	223	2	13	11
2/6/1999	winter	23	0.9	7	10
2/6/1999	winter	94	1	13	10
6/6/1999	winter	14	0.8	8	12
6/6/1999	winter	19	0.9	9	12
10/9/1999	spring	268	0.8	22	16
10/9/1999	spring	81	0.2	23	11
1/12/1999	summer	6	1	14	5.9
11/12/1999	summer	22	<0.5	12	11
11/12/1999	summer	49	<0.5	45	9.7
23/6/2000	winter	12	2	27	11

wind speeds were lower during 1999 (average 11 km/hr) compared to the year 2000 (average 19 km/hr), with the start of 2001 being similar to 2000. Wind direction is variable, depending on the season, but during the study period the dominant direction was southerly. Local winds produce a local swell, with a 5-6 second period in early summer (November and December) from the south to south-east (Shepherd 1970). Seagrass beds at the shallow site are subjected to reduced energy waves that have been refracted around the island. The unprotected deeper site is subjected to more normal wave energy from the south.

5.3.2 Seagrass

Both species of *Posidonia* and *Amphibolis* occur at the shallow and deep sites and grow in mixed and mono-specific patches (Fig. 5.3). *A. griffithii* and *P. sinuosa* are the dominant species at 5 m of the 5 seagrasses found at West Island. *Heterozostera tasmanica* is only present in 2-4 m mwd, proximal to West Island and in niches of unstable or disturbed sediment.

5.3.2.1 Seagrass biomass

Seagrass biomass ranges from 10.1 - 977.5 g/m^2 (Table 5.3). The average seagrass biomass was 408.2 g/m^2, although the majority (71%) of quadrats had biomass values of between 0 and 449 g/m^2 (Fig. 5.4). The biomass distribution was not controlled by species type, as there was an equal distribution of species through the biomass range (Fig. 5.4). Average biomass values of each of the dominant genera (Fig. 5.5), *A. griffithii* and *P. sinuosa,* showed no significant difference (217.8 g/m^2 and 244.5 g/m^2 respectively), however, where average biomass of quadrats dominated by certain genera are compared, significant biomass differences are found (745.7 ± 45 g/m^2 [522.9 seagrass biomass] *Amphibolis* vs 329.6 ± 14 g/m^2 [280.9 seagrass biomass] *Posidonia*).

5.3.2.2 Depth and seasonality

The data from the shallow site was restricted to the same collection period as the deep site, i.e. May 1999, September 1999, November 1999, March 2000 and June 2000, to determine if biomass quantities vary with depth. This data set was also analysed for depth/season interaction. Average seagrass biomass from the mixed species and the individual genera found at the two depths for the 5 collection times are shown in Table 5.3. Depth variations were examined at the genus taxonomic level rather than at the

Table 5.3. Average seagrass biomass (g/m^2) from 5 m mwd and 10 m mwd sites at West Island from February 1999 to March 2001. Mean ± SE. n = number of quadrats sampled. *Overall values from period of deep site collection.

Period	Overall		*Posidonia* sp.		*Amphibolis* sp.		*Amphibolis* sp. blades		*Amphibolis* sp. stem	
	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
*Overall	413.4 ± 17.8 (n=83)	257.5 ± 37.4 (n=44)	223.2 ± 17.8 (n= 66)	122.7 ± 20 (n=24)	250.4 ± 29.9 (n=70)	280.4 ± 53 (n=28)	173.3 ± 18.6 (n=78)	206.8 ± 32.5 (n=19)	102.8 ± 9.9 (n=78)	200.8 ± 30 (n=19)
Feb 1999	546.5 ± 49.6 (n=13)	-	333.7 ± 50.4 (n=9)	-	315.7 ± 51 (n=11)	-				
May 1999	440.2 ± 50.4 (n=18)	82.8 ± 17.8 (n=5)	144.4 ± 20.6 (n=13)	85.0 ± 14.4 (n=4)	302.0 ± 65.1 (n=18)	160.3 ± 135 (n=3)	174.6 ± 46.4 (n=18)		127.2 ± 23.1 (n=18)	
Sep 1999	348.3 ± 35.6 (n=25)	243.2 ± 50 (n=7)	207.6 ± 24 (n=20)	127.5 ± 20.2 (n=5)	158.5± 37.8 (n=23)	107.4 ± 72.6 (n=3)	137 ± 38 (n=17)	173.6 ± 13.2 (n=3)	67.4 ± 9.4 (n=17)	170.9 ± 34.4 (n=3)
Nov 1999	577.1 ± 66.1 (n=4)	399.3 ± 99 (n=6)	407.2 ± 57.2 (n=10)	227.4 ± 57.2 (n=10)	324.4 ± 78.6 (n=11)	348.8 ± 164 (n=4)	193.4 ± 43.2 (n=11)	247 ± 141.3 (n=2)	131.2 ± 38.2 (n=11)	239.9 ± 69.6 (n=2)
Mar 2000	525.8 ± 75.2 (n=13)	329.1 ± 90.3 (n=12)	232.7 ± 57.1 (n=10)	81.1 ± 18.2 (n=6)	423.8 ± 107 (n=9)	386.8 ± 111 (n=9)	394 ± 60.3 (n=6)	229.7 ± 55.9 (n=9)	207.3 ± 29.6 (n=6)	214.3 ± 48.2 (n=9)
June 2000	265.3 ± 21 (n=13)	174.1 ± 60.3 (n=14)	177 + 16.1 (n=13)	38.8 ± 7.3 (n=3)	113.1 ± 29.7 (n=9)	296.3 ± 85.2 (n=9)	101.2 ± 32.7 (n=5)	169.6 ± 62.2 (n=5)	58.5 ± 11.7 (n=5)	178.8 ± 57.7 (n=5)
Oct 2000	285.9 ± 24.8 (n=14)	-	190.1 ± 57.2 (n=13)	-	158.5 ± 37.8 (n=11)	-	89.7 ± 19.2 (n=5)		47 ± 7.1 (n=5)	
Jan 2001	389.1 ± 52 (n=14)	-	188 ± 36.5 (n=13)	-	257.4 ± 93.1 (n=9)		253.6 ± 62.3 (n=7)		129.5 ± 31.4 (n=7)	
Mar 2001	390.9 ± 29.3 (n=13)	-	278.2 ± 26.4 (n=13)	-	137.7 ± 51 (n=11)	-	91.9 ± 23.9 (n=9)		51.4 ± 12.4 (n=9)	

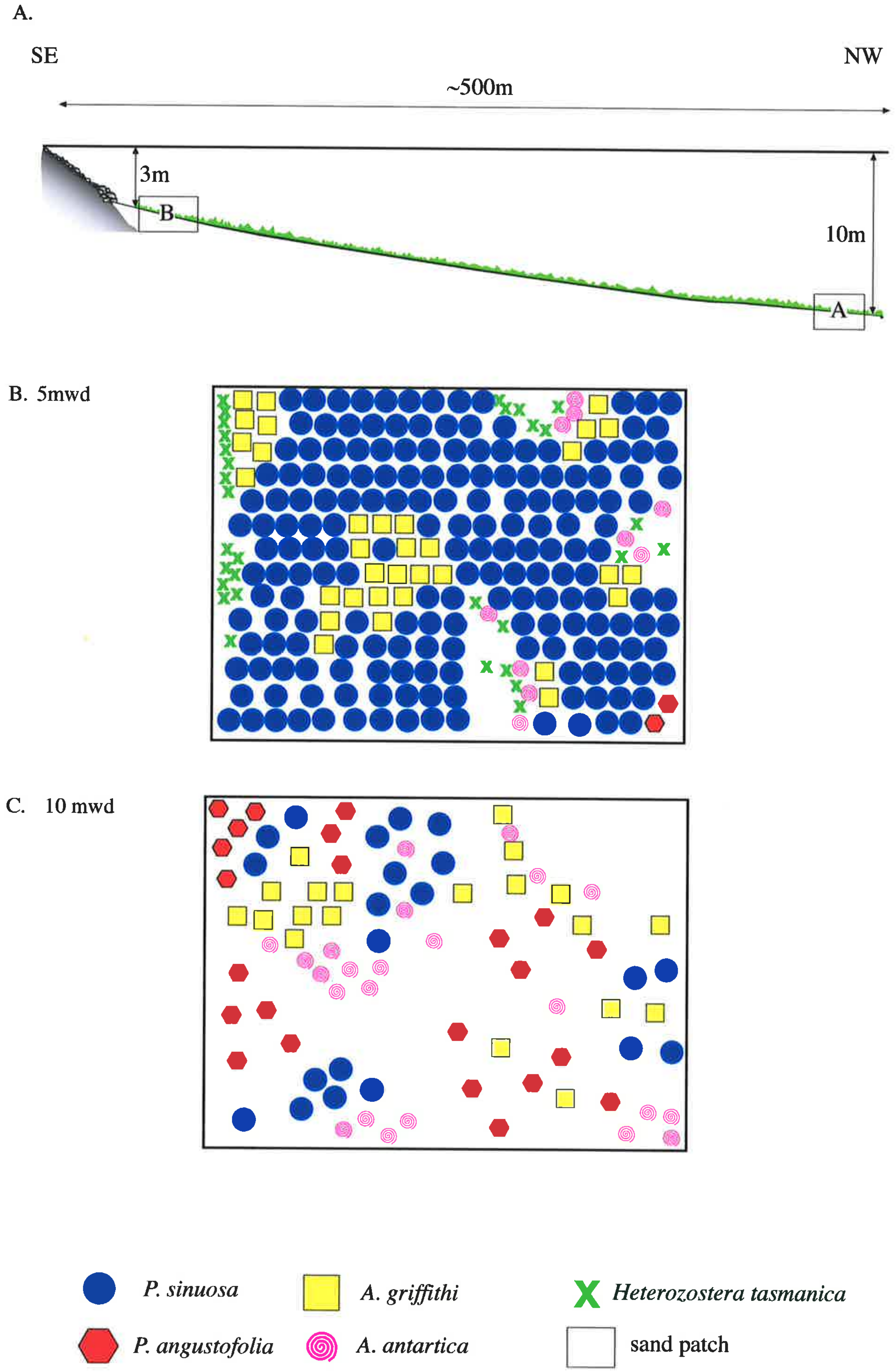


Fig. 5.3 Schematic diagrams of seagrass species distribution at West Island. A. Schematic profile showing rocky shore face and locations of A & B. A. represents distribution and density of seagrass at 5mwd. B. represents distribution and density of seagrass at 10mwd.

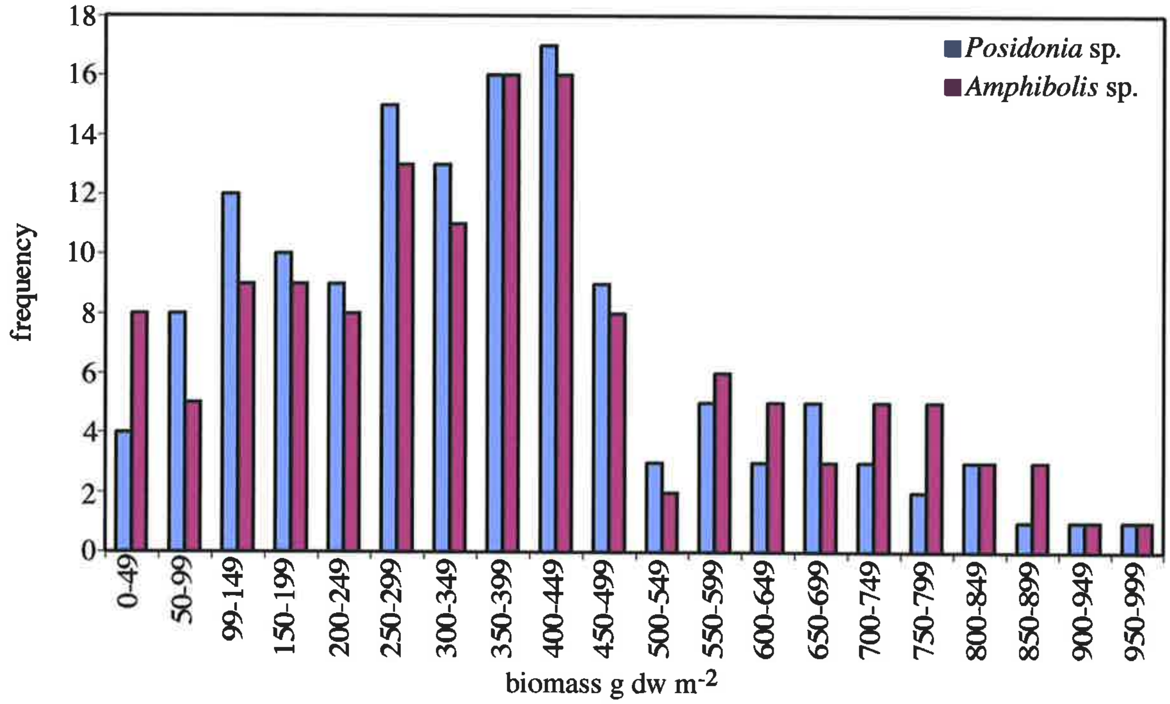


Fig. 5.4 Frequency of ranked seagrass biomass values (g dw m^2) Graph indicates predominance of biomass within 0-449 g dw m^2 and similarity of biomass between *Posidonia* sp. and *Amphibolis* sp..

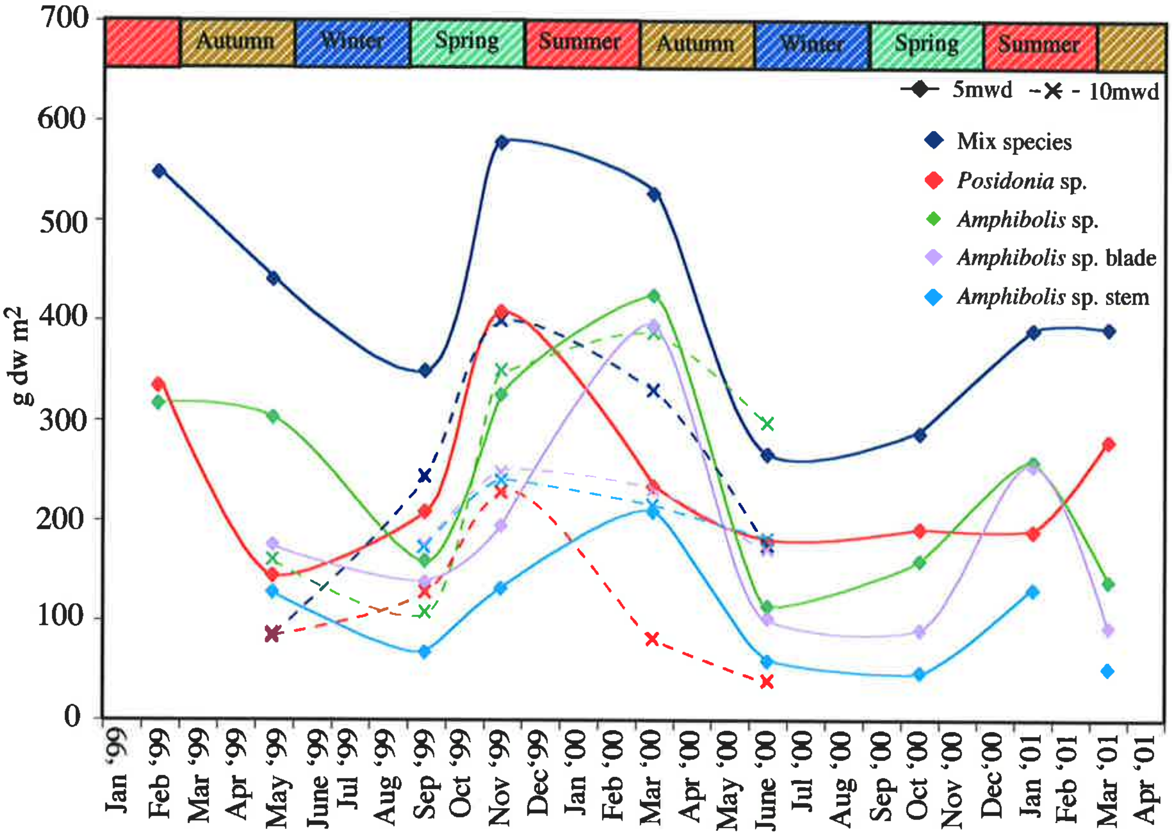


Fig. 5.5. Average seagrass biomass values (g dw m^2) from West Island from 5 & 10mwd, up to a 2 year period. See table 5.5 for s.e.

species level because of the unequal numbers of samples obtained for each species types. Due to the mixed nature of the quadrats the data was examined for the biomass of each genera from each quadrat and as the whole biomass from genera-dominated quadrats.

Results of a 2-way ANOVA indicated significant differences of seagrass biomass between depths ($P \leq 0.001$) and months ($P \leq 0.001$), but showed no interaction term (Table 5.4). Seagrass biomass decreases between the two sites by a factor of approximately two (~420 g/m^2 (5 m mwd) to ~250 g/m^2 (10 m mwd), although this appears to be dependent on the genera and the time of year. According to these results, *Posidonia* sp. is more affected by changes in depth than *Amphibolis* sp. *Amphibolis* sp. showed overall no significant change and, on occasional months, i.e. Nov 1999 and June 2000, appeared to increase in biomass at the deeper site (Table 5.3).

ANOVA results also indicate that there was significant variation in biomass monthly, but Tukey-Kramer HSD does not show any clearly defined patterns (Table 5.4). Variation at this level could be caused by patchiness. It was not until the averaged monthly values were examined graphically did it become clear that biomass was shown to decrease during the autumn and winter and peak during summer (Fig. 5.5). This correlates with temperatures and light levels also recorded. The seasonal pattern was the case for overall quadrat biomass as well as genera and *Amphibolis* components (Fig. 5.5). Inter-annual variation was not significant, according to the ANOVA results, but graphically the winter of 2000 and the summer of 2001 show a minor decline in biomass.

5.3.3 Epiphytic carbonate values

The following information refers to standing stock abundances of calcareous epiphytes attached to the 5 seagrass species found at West Island (Table 5.5). Epiphyte $CaCO_3$ values vary from 2.34 – 605.7 g/m^2 (av. 127.8 ± 8.1 g/m^2) and 20.9 – 766.3 g/kg of seagrass (av. 248.0 ± 10.1). Explanations for the variation in values were tested against the data recorded for seagrass biomass, genera type, species type, depth and seasonality (Table 5.6).

5.3.3.1 Calcareous epiphytes and seagrass biomass

The Kruskall-Wallis test indicates that there was a significant positive correlation between seagrass biomass and $CaCO_3$ g/m^2 ($p<0.001$) but not $CaCO_3$ g/kg of seagrass.

Table 5.4 Summary of 2-way (above dashed line) and 1-way (below dashed line) ANOVA and *Post hoc* Tukey-Kramer HSD results comparing seagrass biomass quantities between depth and among months. The data results, above dashed line, are restricted to May 1999, September 1999, those below are for all months at the shallow site. ***$p \leq 0.001$, ** $p \leq 0.01$, *$0.01 < p \leq 0.05$, ns = not significant ($\alpha = 0.5$).

	Mixed species	*Posidonia* sp.	*Amphibolis* sp.	*Amphibolis* blade	*Amphibolis* stem	*Post hoc* Tukey-Kramer HSD
Depth	***	***	ns	ns	ns	
Month	***	***	*	*	ns	June ≠ Nov, Mar, Sep – Mixed Nov ≠ June, May – *Posidonia* March ≠ Sept – *Amphibolis*
Depth* month	ns	ns	ns	ns	ns	
Month/ year	**	***	ns	**	ns	June 2000 ≠ Nov 1999, Feb 1999 - Mixed Jan 2001 ≠ Nov 1999 ≠ March 1999 ≠ Feb 1999 – *Posidonia* March 2000 ≠ Sep ’99, Mar ’01, Oct ’00 – *Amphibolis* blades

Table 5.5. Average standing stock values of epiphytic $CaCO_3$ from seagrass taxa found at West Island.

	Posidonia			***Amphibolis***			***Amphibolis antarctica***			***Amphibolis griffithii***		
	Total	*angustifolia*	*sinuosa*	Total	Stem	blade	Total	stem	blade	Total	stem	blade
Average (g/m^2)	14.0 (69.5/0.2)	15.6 (45.1/2.0)	12.7 (48.5/0.2)	103.2 (472.6/0.7)	182.1	27.5	162.5 (472.6/16.5)	136.7 (441.0/11.3)	36.7 (67.9/2.2)	96.3 (305.3/2.2)	227.4 (1048.8/16)	18.39 (118.8/0.13)
Average (g/kg)	64.4 (364.9/2.0)	92.1 (195.6/29.6)	55.1 (213.3/2.0)	319.64 (766.3/63.3)	461.5	131.1	337.5 (766.3/143.0)	447.3 (732.3/252.8)	170.1 (259/33.5)	314.9 (714.6/63.3)	475.7 (864.7/182.5)	92.0 (280.3/5.5)
5m (g/m^2)	14.6 (69.5/0.2)	24.8 (45.1/2.0)	13.1 (48.5/0.2)	95.4 (305.3/1.3)	37.2	20.4	84.9 (262.5/16.5)	56.3 (71.1/21.3)	22.6 (54.6/2.2)	96.4 (305.3/2.2)	232.7 (1048.8/16)	18.1 (118.8/0.13)
5m (g/kg)	59.9 (195.6/2.0)	124.2 (195.6/44.7)	50.7 (108.2/2.0)	308.3 (714.6/63.3)	275.7	107.8	233.8 (385.3/143.0)	459.9 (667.0/291.0)	124.1 (229.1/33.5)	310.0 (714.6/63.3)	475.1 (864.8/228.5)	91.5 (280.3/5.5)
10m (g/m^2)	11.1 (55.3/.5)	9.0 (15.2/2.3)	9.78 (17.9/0.5)	135.9 (472.6/0.6)	97.8	31.9	197.4 (472.6/65.8)	174.4 (441.0/17.0)	42.6 (67.9/9.4)	95.1 (213.0/7.1)	117.8 (377.4/42.1)	21.19 (70.6/196.8)
10m (g/kg)	102.5 (364.9/14.2)	69.2 (129.3/29.9)	93.4 (213.3/15.7)	362.3 (766.3/118.8)	279.9	142.9	378.0 (766.3/185.5)	463.3 (732.8/252.8)	189.3 (259/101.3)	356.8 (645.2/118.8)	358.6 (652.4/182.5)	96.58 (196.8/32.7)

Posidonia and *Amphibolis* total data refers to average values of all species within the genera. Total values, in *Amphibolis antarctica* and *A. griffithii* refer to total amount of carbonate from the whole plant. These values are not the addition of stem and blade values because additional data values of whole plants were taken where the sample was deemed too small to be split into the various stem and blade components.

Table 5.6. Average calcareous epiphyte standing stock values from 5 and 10 m mwd sites at West Island from February 1999 to March 2001. Values are from whole quadrats (mixed species) and *Posidonia* and *Amphibolis* genera. **A.** $CaCO_3$ g/m^2. **B.** $CaCO_3$ g/kg of seagrass. Mean ± SE. n = number of quadrats sampled.

A. Time	Overall		*Posidonia* sp.		*Amphibolis* sp.		*Amphibolis* sp. blades		*Amphibolis* sp. stem	
	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
*Overall	131.4 ± 8.3 (n=137)	132.6 ± 9.4 (n=127)	14.6 ± 1.1 (n=114)	12.3 ± 1.2 (n=90)	97.4 ± 7.7 (n=110)	113.2 ± 9.5 (n=98)	17.4 ± 2.3 (n=78)	32.3 ± 5.1 (n=19)	92.3 ± 7.8 (n=78)	146.1 ± 25.1 (n=19)
Feb 1999	198.3 ± 30.1 (n=13)		26.7 ± 6.7 (n=9)		148.8 ± 26.1 (n=11)					
May 1999	195.7 ± 24.7 (n=18)	34.4 ± 7.5 (n=5)	10.9 ± 4.2 (n=14)	25.5 ± 10 (n=4)	143.5 ± 23.9 (n=18)	60.7 ± 37.5 (n=3)	85.6 ± 15.2 (n=18)		487.9 ± 34.3 (n=18)	
Sep 1999	138.1 ± 16 (n=25)	100.9 ± 46.7 (n=7)	12.4 ± 1.9 (n=20)	11.2 ± 2.5 (n=5)	84.2 ± 13.3 (n=23)	79 ± 37.9 (n=3)	147.5 ± 13.8 (n=17)	231.1 ± 14.5 (n=3)	544.6 ± 32 (n=17)	381.3 ± 97.1 (n=3)
Nov 1999	180.8 ± 26 (n=14)	69.3 ± 30.5 (n=6)	21.8 ± 3.9 (n=10)	7.7 ± 0.9 (n=6)	114.4 ± 19 (n=11)	130.9 ± 55.9 (n=4)	61.9 ± 14 (n=11)	39.4 ± 0.7 (n=2)	500.6 ± 67.5 (n=11)	314 ± 131.5 (n=2)
Mar 2000	158.1 ± 27.6 (n=13)	139.5 ± 34 (n=12)	10.9 ± 3.7 (n=9)	6.2 ± 1.7 (n=6)	128.8 ± 28.5 (n=9)	157.4 ± 44.4 (n=9)	64.5 ± 4.8 (n=6)	112.9 ± 15.6 (n=9)	403.3 ± 24.6 (n=6)	456.7 ± 51.9 (n=9)
June 2000	47.5 ± 7.6 (n=13)	120.6 ± 38.1 (n=14)	9.8 ± 1.8 (n=13)	8.1 ± 5.9 (n=3)	40 ± 8.6 (n=9)	159.2 ± 47.3 (n=9)	30.3 ± 14.5 (n=5)	204.3 ± 15.4 (n=5)	362.1 ± 62.8 (n=5)	501 ± 88.7 (n=5)
Oct 2000	79.9 ± 20.4 (n=14)		17 ± 3 (n=13)		59.9 ± 20.7 (n=11)		170.7 ± 23.9 (n=5)		482.6 ± 48.6 (n=5)	
Jan 2001	83.9 ± 20.5 (n=14)		9.1 ± 2.6 (n=13)		69.7 ± 23.8 (n=9)		73.8 ± 9.8 (n=7)		398.5 ± 26.4 (n=7)	
Mar 2001	72.9 ± 14.1 (n=13)		18.2 ± 1.9 (n=13)		54.6 ± 17.2 (n=9)		37.3 ± 9.8 (n=9)		455.1 ± 30.1 (n=9)	

B. Time	Overall		*Posidonia* sp.		*Amphibolis* sp.		*Amphibolis* sp. blades		*Amphibolis* sp. stem	
	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
*Overall	228.5 ± 8.5 (n=136)	271.2 ± 12.6 (n=127)	59.4 ± 4.6 (n=114)	68.1 ± 7.5 (n=90)	316.6 ± 12 (n=110)	338.6 ± 15 (n=98)	89.4 ± 7.3 (n=78)	147.9 ± 16.7 (n=19)	475.3 ± 16.4 (n=78)	441.5 ± 38.5 (n=19)
Feb 1999	253.6 ± 22.6 (n=13)		71.3 ± 9.5 (n=9)		331.6 ± 35.6 (n=11)					
May 1999	307.3 ± 30.2 (n=18)	311.1 ± 50.6 (n=5)	73 ± 30.4 (n=14)	213.4 ± 39.5 (n=4)	351.2 ± 34.3 (n=18)	398.9 ± 124.9 (n=3)	17.8 ± 5.4 (n=18)		125.8 ± 22.1 (n=18)	
Sep 1999	297.3 ± 20.4 (n=25)	211.1 ± 5304 (n=7)	55.7 ± 6.3 (n=20)	79.8 ± 17.8 (n=5)	368.3 ± 25.5 (n=23)	412.6 ± 178.1 (n=3)	25.3 ± 7.3 (n=17)	52.8 ± 7.5 (n=3)	87.9 ± 13.4 (n=17)	121.5 ± 60.1 (n=3)
Nov 1999	235.6 ± 28.4 (n=13)	132 ± 51.7 (n=6)	51.7 ± 7.3 (n=10)	58.5 ± 24.7 (n=6)	295.2 ± 35.1 (n=11)	342.5 ± 96.3 (n=4)	12.6 ± 3.9 (n=11)	10.2 ± 6 (n=2)	101.7 ± 16.9 (n=11)	73.9 ± 17.4 (n=2)
Mar 2000	228.9 ± 27.1 (n=13)	286 ± 44.1 (n=12)	36.9 ± 7.1 (n=9)	67.2 ± 12.7 (n=6)	376.5 ± 58.1 (n=9)	328.3 ± 54.1 (n=9)	28.3 ± 6.4 (n=6)	27.2 ± 6.7 (n=9)	143.2 ± 24.4 (n=6)	153.9 ± 37 (n=9)
June 2000	148 ± 18.2 (n=13)	422.4 ± 50 (n=14)	52.5 ± 10.8 (n=13)	150.7 ± 108.2 (n=3)	288.5 ± 39.2 (n=9)	366.5 ± 54.7 (n=9)	2.5 ± 1.1 (n=5)	37.9 ± 11.2 (n=5)	37.8 ± 13.5 (n=5)	175.6 ± 62.6 (n=5)
Oct 2000	197.7 ± 27.7 (n=14)		83.7 ± 13.4 (n=13)		306.9 ± 30.2 (n=11)		20.2 ± 6.6 (n=5)		49.8 ± 14.3 (n=5)	
Jan 2001	152.5 ± 20.4 (n=14)		44 ± 7.03 (n=13)		250.5 ± 34.3 (n=9)		20.5 ± 4.4 (n=7)		82.4 ± 18.9 (n=7)	
Mar 2001	150.5 ± 19.5 (n=13)		61.4 ± 4.3 (n=13)		269.4 ± 30.2 (n=9)		4.9 ± 2 (n=9)		50.1 ± 16 (n=9)	

Binned biomass values plotted against $CaCO_3$ g/m^2 showed a clear positive relationship ($R^2 = 0.77$; Fig. 5.6A). Individual values of biomass vs $CaCO_3$ g/m^2 were still positive, although the relationship was less clear ($R^2 = 0.44$), indicating that biomass was not the only factor affecting epiphyte abundance (Fig. 5.6C). This was supported by the lack of any relationship between biomass and $CaCO_3$ g/kg of seagrass (Fig. 5.6B). The high value of $CaCO_3$ g/kg of seagrass in the 0-49 bin was in part attributed to limitations of small sample sizes. The positive correlation between biomass and epiphyte abundance was sustained for both mixed seagrass species and individual *Posidonia* species (*P. angustifolia* $r^2 = 0.35$, *P. sinuosa* $r^2 = 0.3$) and *Amphibolis* blades ($r^2 = 0.37$), but was not clear for *Amphibolis* stems ($r^2 = 0.05$).

5.3.3.2 Calcareous epiphytes and seagrass genera and species variation

A series of t-tests was used to assess significant differences between genera (Table 5.7). Significant differences were found between all combinations ($p \leq 0.001$). Significantly less $CaCO_3$ was found attached to *Posidonia* sp. (66.9 ± 5.2 g/kg of seagrass [14.2 ± 1g/m^2]) compared to *Amphibolis* sp. (325 ± 11.8 g/kg of seagrass [105.4 ± 8 g/m^2]). The majority (>80%) of the carbonate on *Amphibolis* sp. was derived from the calcareous epiphytes attached to the stems (468 ± 15.1 g/kg of seagrass [102.9 ± 8.2 g/m^2]), compared to that on the blades (100.9 ± 7.1 g/kg of seagrass [20.3 ± 2.2 g/m^2]). The carbonate on *Amphibolis* sp. blades, however, was still significantly greater than on *Posidonia* sp.

5.3.3.3 Calcareous epiphytes and depth

The data examined to determine changes with depth was restricted to the sampling period of the deep site which was examined monthly. ANOVA results of quadrat $CaCO_3$ g/m^2 indicate that there were significantly lower abundances of carbonate per square metre with increasing depth, although average values show no change (131.4 → 132.6 g/m^2, shallow → deep; Table 5.7, 5.8). There was no significant change of $CaCO_3$ g/kg of seagrass with depth (228.5 → 271.2 g/kg of seagrass, shallow → deep). Individual genera or genera components either showed no change with depth, or, as in the case of *Amphibolis* blades ($CaCO_3$ g/m^2 and g/kg of seagrass) and *Posidonia* ($CaCO_3$ g/kg of seagrass), showed significant increases in carbonate with depth.

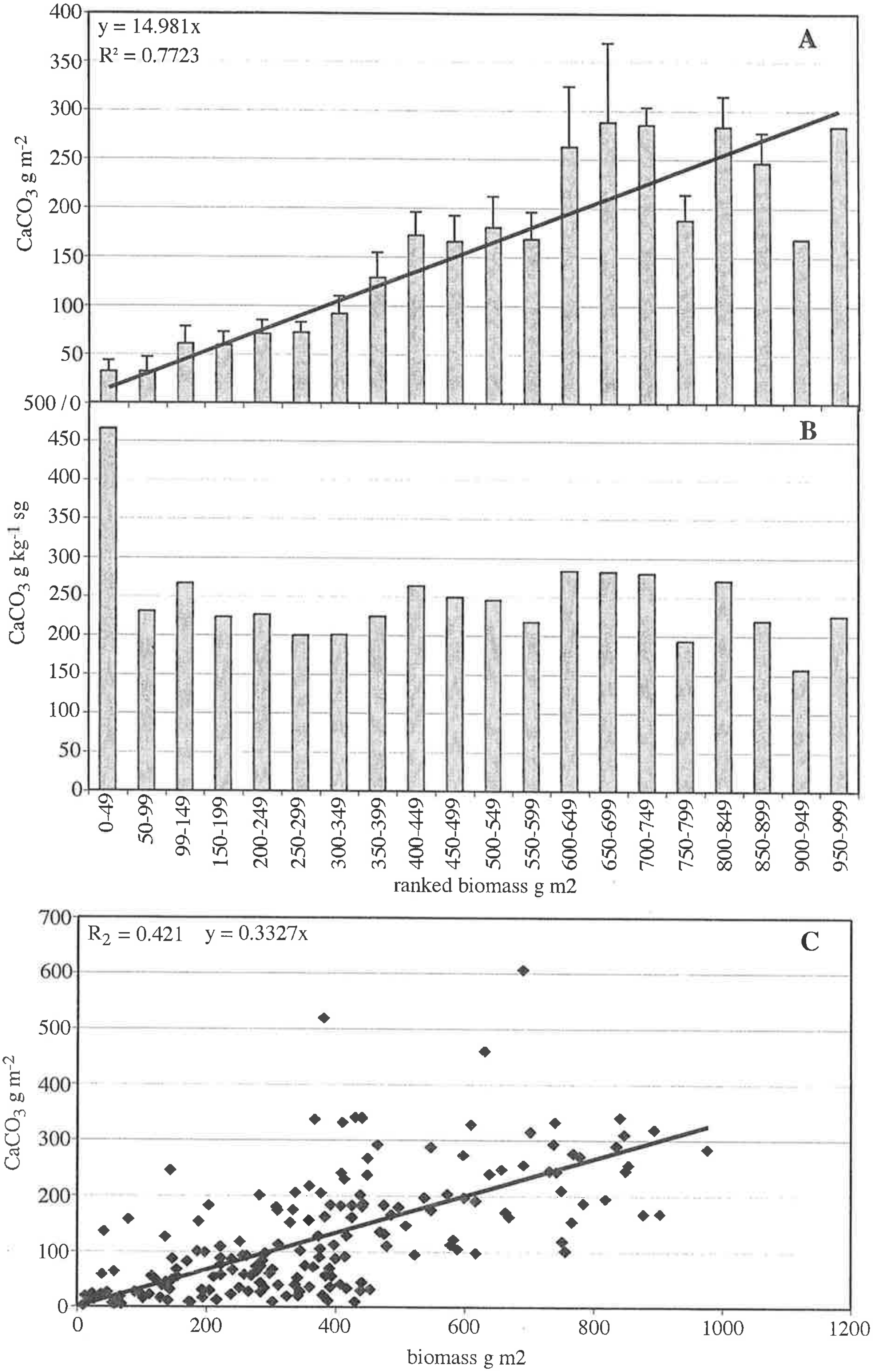


Fig. 5.6. Epiphyte carbonate abundance plotted against seagrass biomass. **A**. Histogram of $CaCO_3$ g m^{-2} quadrat values ranked by 50 g biomass groupings, with line of best fit. **B**. Histogram $CaCO_3$ g kg^{-1} sg quadrat values ranked by 50 g biomass groupings **C**. Scatter plot of $CaCO_3$ g m^{-2} quadrat values

Table 5.7. Summary of 2-way (above dashed line) and 1-way (below dashed line) ANOVA and *Post hoc* Tukey-Kramer HSD results comparing epiphyte standing stock abundance between depth and among months. A. CaCO$_3$ g m^{-2} B. CaCO$_3$ g kg^{-1} sg. Data transformed using $\ln(x+1)$. †denotes data where transformation has failed Levene's test for variance homogeneity: accordingly a more conservative alpha value (i.e. $p=0.01$) has been adopted (Underwood, 1981). The data results, above dashed line, are restricted to May 1999 and September 1999, those below are for all months at the shallow site. ***$p \leq 0.001$, ** $p \leq 0.01$, *$0.01 < p \leq 0.05$, ns = not significant ($\alpha = 0.5$).

A.	Mixed species	*Posidonia* sp.	*Amphibolis* sp.	*Amphibolis* blade	*Amphibolis* stem
Depth	***	Ns	ns	*	Ns
Month	ns	Ns	ns	*	Ns
Depth x month	*	*	ns	*	*
Year	†***	ns	**	ns	ns
Month/year	***	†**	**	***	
B.	Mixed species	*Posidonia* sp.	*Amphibolis* sp.	*Amphibolis* blade	*Amphibolis* stem
Depth	ns	*	ns	***	ns
Month	**	ns	ns	***	ns
Depth x month	***	ns	ns	***	ns
Year	†***	ns	*	**	ns
Month/year	***	*	ns	*	ns

Table 5.8. Results of *post hoc* Tukey-Kramer HSD of epiphyte carbonate (g kg^{-1} sg) monthly variation over a 2 year period from 5mwd.
ns = no significance, sg = significant variation.

	Feb-99	May-99	Sep-99	Nov-99	Mar-00	Jun-00	Oct-00	Jan-01	Mar-01
Feb-99	ns	ns	ns	ns	ns	ns	ns	ns	ns
May-99	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sep-99	ns	ns	ns	ns	ns	ns	ns	ns	ns
Nov-99	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mar-00	ns	ns	ns	ns	ns	ns	ns	ns	ns
Jun-00	ns	sg	sg	ns	ns	ns	ns	ns	ns
Oct-00	ns	ns	ns	ns	ns	ns	ns	ns	ns
Jan-01	sg	sg	sg	ns	ns	ns	ns	ns	ns
Mar-01	ns	sg	sg	ns	ns	ns	ns	ns	ns

5.3.3.4 Calcareous epiphytes and seasonal variation

The seasonal variation of epiphyte $CaCO_3$ g/m^2 follows a similar trend to that of seagrass biomass, i.e. a decrease in winter and a peak at early spring through to summer (Fig. 5.7). This is not unexpected because of the close relationship between seagrass biomass and calcareous epiphyte production as previously discussed (Chapter 4). The trend was reflected across epiphytes on all species and species components, although *Amphibolis* blades tended to vary slightly (Fig. 5.8). Calcareous epiphyte abundance (g/m^2) also decreased overall during the second year of sampling, i.e. June 2000 to April 2001 values were significantly lower than from February 1999 to March 2000 (Fig. 5.7). The decrease in calcareous epiphyte abundance during the second year of sampling was less clear when measured by kg of seagrass, although the decrease was still statistically significant. Calcareous epiphyte abundance per kilogram of seagrass showed increasing production through autumn and winter and decreasing production during spring/summer, i.e. the opposite if $CaCO_3$ g/m^2 pattern. Variability was greatly exaggerated at the greater depth. Again, the overall trend was found, generally, for calcareous epiphytes on all the different seagrass species and components (Fig. 5.7) *Post hoc* Tukey-Kramer HSD did not show any clear distribution pattern for seasonal variation (Table 5.8).

5.4 DISCUSSION

5.4.1 Seagrass

5.4.1.1 Seagrass distribution

Species distribution is controlled by depth, age of the bed of seagrass (maturity), current regime, and sediment stability in an established seagrass bed (Fonseca & Kenworthy 1987, Shepherd & Roberston 1989). The implications of seagrass distribution on calcareous epiphyte abundance are dependent on the relationship between the two organisms, i.e. some seagrass species have greater abundances of calcareous epiphytes associated with them compared to other species (Chapter 4) and hence knowledge of the seagrass species distribution leads to better estimations of calcareous epiphyte abundances over large areas. *A. antarctica* and *H. tasmanica* have been documented as pioneer species (Shepherd & Robertson 1989). This is also true at West Island as shown by their presence at the edge, or in isolation in the middle of sand patches (Fig. 5.3). The dominance of *P. sinuosa* over *P. angustifolia* and *A. griffithii* over *A. antarctica* in 5 m mwd indicates that *P. sinuosa* and *A. griffithii* are the climax species at West Island. This

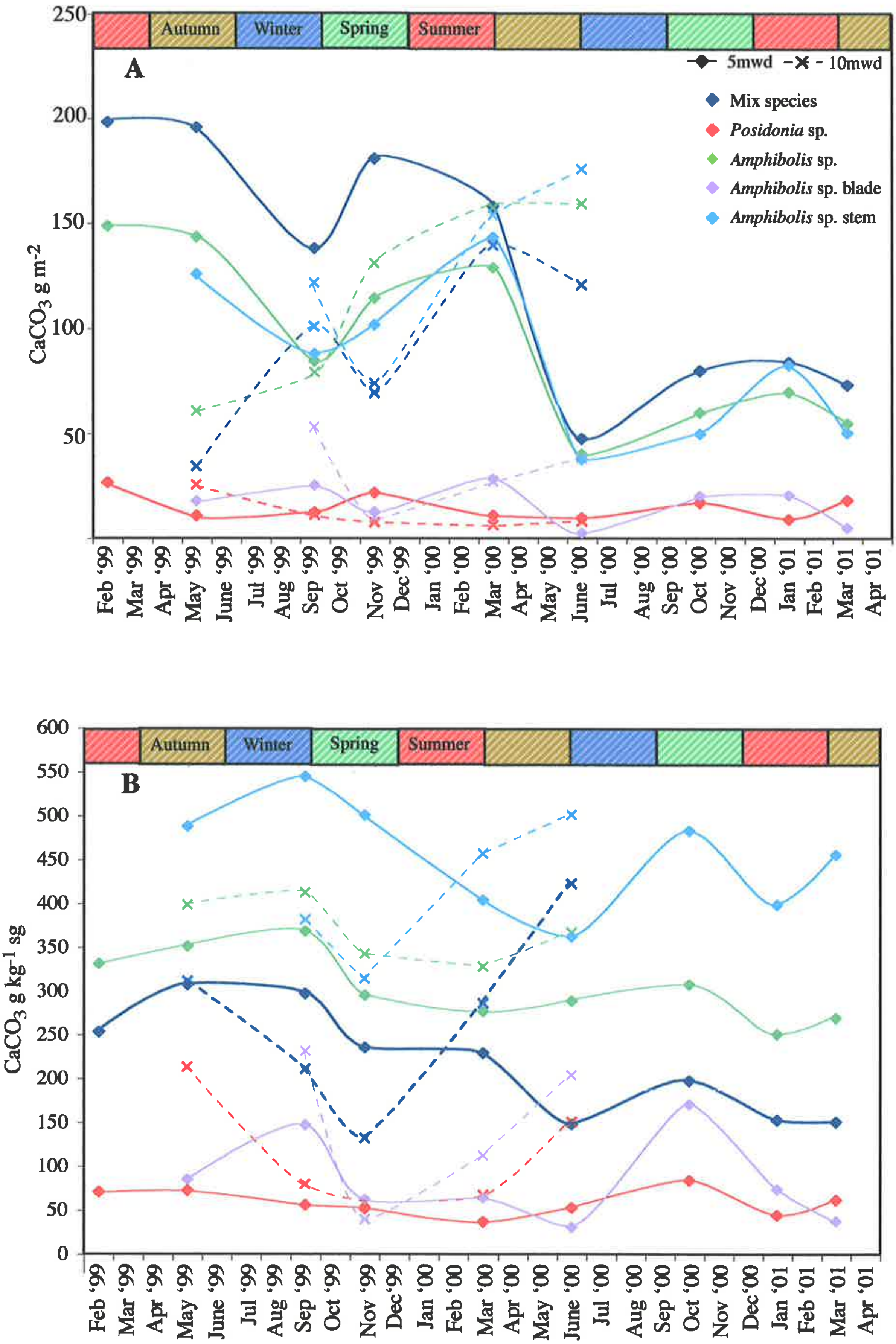


Fig. 5.7 Average calcareous epiphytes standing stock values collected over 2 years and 2 depths at West Island, South Australia. A. CaCO$_{-1}$ g m^{-2}, B. CaCO$_3$ g kg^{-1} sg. See Table 5.6 for s.e.

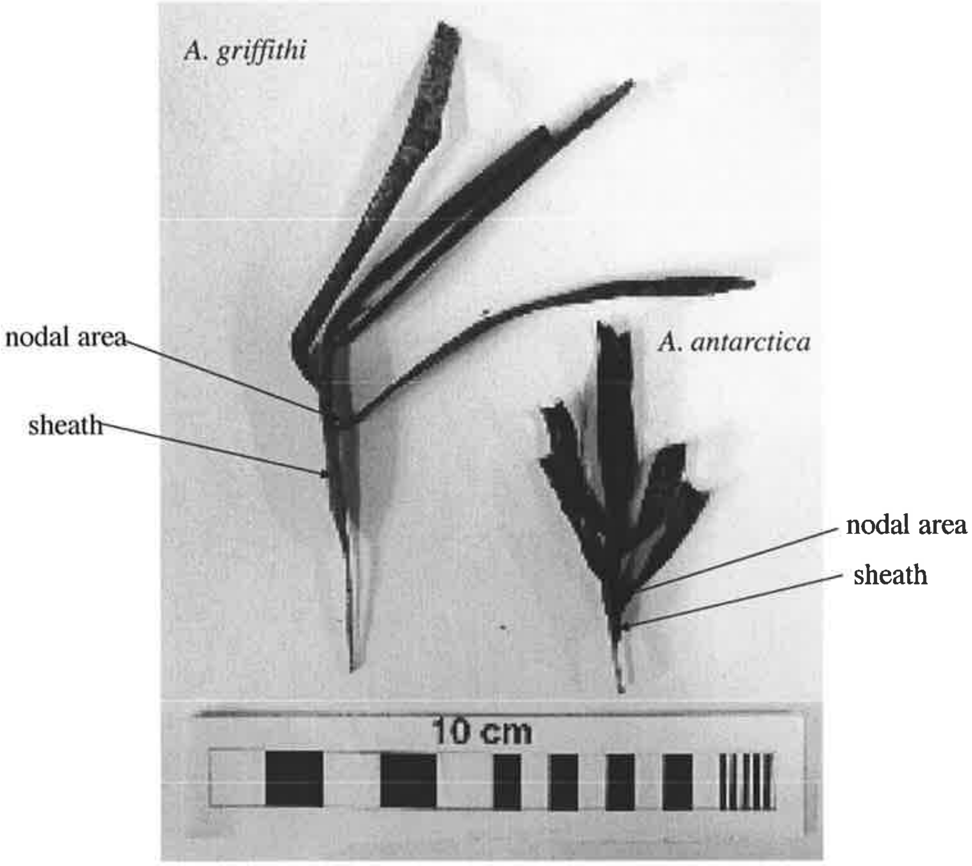


Fig. 5.8. Images of blade clusters of *A. antarctica* and *A. griffithi* demonstrating their significantly different structures,which are believed to explain the different abundances

sequence of species is known as a succession, which is well documented in seagrass (Shepherd & Robertson 1989, Todd & Turner 1994).

The distribution of seagrass in an area can also depend on other factors such as tolerance to strong currents, or to low light levels (Shepherd & Robertson 1989). *P. australis, P. sinuosa* and *A. antarctica* in that order were most susceptible to low light (Masini & Manning 1997,). The relative decrease in dominance of *P. sinuosa* and *A. griffithii* over *P. angustifolia* and *A. antarctica.* with depth, indicates that they are more susceptible to parameters such as light. This distribution indicates that *H. tasmanica* → *P. sinuosa* → *P. angustifolia* and *A. griffithii* → *A. antarctica,* in that order, are least to most tolerant of low light levels at West Island.

5.4.1.2 Seagrass depth

Light appears to be the major controlling factor for the decrease in biomass with depth, with some seagrass speciesmore sensitive than others. This has also been found in many other seagrass studies (eg. Burkholder & Doheny 1968, Backmand & Barilotti 1976, Bulthuis & Woelkerling 1981, Dennison & Alberte 1986, Gordon *et al.* 1994, Hillman *et al.* 1995, Masini *et al.* 1990, Dennison *et al.* 1993, Fitzpatrick & Kirkman 1995, Abal & Dennison 1996, SMCWS 1996, Cambridge & Hocking 1997, Walker *et al.* 1999). Results from this study show that biomass and light decreased exponentially (544→374 gm^2 and 590 →325 μmol photons/m^2/s) over the same depth range, e.g. 5-10 m. It was not possible to determine whether there was a peak of biomass at 2-4 m mwd, as found in Chapter 3, because of the rocky sea bottom of 0-4 m mwd.

5.4.1.3 Seagrass biomass

It may be expected that the seagrass biomass range at West Island would have been more restricted than the range obtained from the 20 other combined sites (Chapter 3). The range in seagrass biomass values, however, was slightly greater at West Island (0 – ~1000 g/m^2) than that of the other combined study sites including West Island (0 – ~900 g/m^2- see Chapter 3; Table 5.9). No correlation between biomass and seagrass species was found, i.e. there was an equal distribution of species throughout the range. Hence the variance at West Island is explained by patchiness, as was concluded in Chapter 3.

Table 5.9. Comparing epiphyte carbonate values from West Island with those from all other sites from this project.

	Min	Max	Average	s.e.
West Island				
$CaCO_3$ g m^{-2}	2.34	605.7	127.8	8.1
$CaCO_3$ g kg^{-1} sg	20.93	766.3	248.0	10.1
All other sites				
$CaCO_3$ g m^{-2}	3.1	655.6	78.7	6.7
$CaCO_3$ g kg^{-1} sg	11.2	767.3	164	6.9

In addition, the average seagrass biomass at West Island was slightly greater than that at the other sites (400 vs. 320 g/m^2). Most frequently, however, the range of seagrass biomass was similar to the other sites, excluding West Island, i.e. 0 – 500 g/m^2. It is suggested that biomass could be limited by nutrients and suitable substrates at the regional scale. It is also speculated that lack of stability in an area (at the metre scale) may restrict biomass in an established seagrass bed such as that at West Island. Instability can be caused by competition between species, sand movement, storm activity or concentrated grazing in patches.

5.4.1.4 Seagrass genera

Another difference found at West Island, in comparison to the other sites (Chapter 3), is the similarity in biomass between genera, i.e. *Amphibolis* and *Posidonia* had similar average biomass values. The biomass difference seen in Chapter 3 may be a function of the different number of samples, as the number of samples collected for each genus was similar at West Island (141 *Posidonia*, 130 *Amphibolis*) compared to the number collected from all the other sites combined (197 *Posidonia*, 73 *Amphibolis*).

5.4.1.5 Seagrass and seasonal variation

Results indicate that seagrass biomass changes monthly and that a seasonal trend can be identified for *Posidonia* spp. Specifically, seagrass biomass is lowest during winter and peaks during summer and autumn. No seasonal trend could be identified for *Amphibolis* spp. This agrees closely with the findings by Kendrick *et al.* (1998a, b) who found lower biomass in winter and higher biomass in summer for *P. coriacea,* but no seasonal trend for *A. griffithii*. Kendrick *et al.* found that this seasonal pattern was reflected in the productivity (abundance) of *P. coriacea*, but the pattern was not as clear for the productivity of *A. griffithii*. The seasonal decrease in productivity during winter has been found in a number of other studies (West & Larkum 1979, Silberstein 1985, Silberstein *et al.* 1986, Walker & McComb 1988, Masini *et al.* 1990, Cambridge & Hocking 1997). The same trend was found during seasonal spot checks at West Island of other primary producers, e.g. *Ecklonia radiata* and Turf algae (Fairhead 2001, Copertino 2002). Yet other studies found little or no change in productivity during the year (Walker & McComb 1988, Masini *et al.* 1990). These latter studies demonstrate that some species e.g. *P. australis*, and *P. sinuosa* can show little or no change in seagrass productivity throughout the year. The results from this study at West Island demonstrated that

Amphibolis sp. showed little change in biomass with seasons at either depth and *Posidonia* sp. appears to be only affected at the deep site - 10 m mwd. This occurs because seagrass species have the ability to utilise stored energy reserves to maintain respiration and growth during period of stress (Masini *et al.* 1990).

A decrease in biomass during winter is related to lower temperatures, reduced light intensity and shorter day lengths. It is not related to lack of nutrients, as demonstrated by the high nutrients available during winter found during this study (Table 5.2). A decrease in biomass during winter may be associated with the decrease of primary productivity in winter. Primary productivity increases in spring due to the onset of warmer weather, longer days and increased light intensity, allowing increased utilisation of the available nutrients. High primary productivity continues through to summer, when it begins to be limited by the lower concentration of nutrients (Table 5.2). Reduced photosynthesis and dieback of the primary producers as temperatures decrease and light becomes attenuated in autumn, result in nutrients being recycled and released back into the water column. The peak of ammonia in summer may be attributed to an increase in the input of guano, as young fledglings practice their flying ability (Paton & Paton 1977). However, an intuitively expected increase in phosphate was not found.

5.4.2 Epiphytic carbonate

The ranges of values for calcareous epiphyte biomass obtained at West Island are almost identical to those from the other 20 study sites (Chapter 4), although average values are slightly higher for West Island (Table 5.9).

5.4.2.1 Calcareous epiphytes and biomass

Data from West Island agrees with the previous findings from the other 20 study sites (Chapter 4). The abundance of calcareous epiphytes is strongly influenced by the seagrass biomass, i.e. the more seagrass the more epiphytes. The explanation for this relationship, as discussed in Chapter 4, is the availability of recruitment space, i.e. if the space is available, calcareous epiphytes will settle on it! The exception to this correlation is the abundance of calcareous epiphytes on *Amphibolis* stems. The lack of an apparent relationship between biomass of *Amphibolis* stems and abundance of calcareous epiphytes was also found by Sim (1991) who gave several potential explanations:

- patchiness of large calcareous epiphytes, i.e. individual shoots in close proximity to each other may have high or low abundances of epiphytes, hence showing no relation to the actual biomass or density of the seagrass. Patchiness of coralline algae was observed at West Island and was demonstrated quantitatively by Sim (1991). Potential causes of patchiness include length of time available for growth, i.e. substrate availability, and variable current velocities within the seagrass (high velocities at the edge of the seagrass bed increasing scouring, low velocities towards the middle of the bed increasing the boundary layer, in turn reducing the exchange of nutrients (Vogel 1981, Koehl 1984 cited in Sim 1991)).
- shoots of different ages collected in the same quadrat will register different calcareous epiphyte productivity. Hence the presence of an abundance of younger plants will increase the biomass of the quadrat, but will have relatively few calcareous epiphytes present.

5.4.2.2 Calcareous epiphytes and genera

Considerably more calcareous epiphytes were found on *Amphibolis* than *Posidonia* at West Island (Fig. 5.7). Other sites studied throughout the year (Chapter 4) also showed that *Amphibolis* (238.5 $CaCO_3$ g/kg of seagrass) had significantly more epiphytic carbonate than *Posidonia* (127.2 $CaCO_3$ g/m^2). The higher abundance was attributed to the longevity of the *Amphibolis* stem (Walker 1985). The reason for the excessive abundance of calcareous epiphytes on *Amphibolis* at West Island, compared to the other sites, is not clear, but may be due to a different calcareous epiphyte faunal assemblage at West Island compared to other sites which produce above 'normal' abundances of carbonate. The different faunal assemblages at the different sites are discussed in Chapter 6.

Amphibolis samples at West Island were split into their various components, i.e. blade and stem. The results showed that up to 80% of the calcareous epiphytes on *Amphibolis* were attached to the stem. This compares well with values of 80% and 88%, found by Curruthers (1994) and Hillman *et al.* (1994) respectively. Lavery *et al.* (2000) also showed that epiphyte 'calcimass' was much higher on *A. griffithii* stems than blades. In contrast, two studies have found calcareous epiphytes to be more abundant on *Amphibolis* blades than stems (Walker & Woelkerling 1988, Sim 1991). Walker & Woelkerling (1988) attributed the higher abundance of calcareous epiphytes on blades to greater surface area of blades available for recruitment; Sim (1991) attributed the difference to local environmental conditions and seasonality of large calcareous epiphytes. This study, as well as those of Curruthers (1994) and Hillman *et al.* (1994), attributes the higher abundance on *Amphibolis* stems to the longer period of time available for the calcareous epiphytes to colonise the stems, compared to the relatively short life of blades. The difference for the findings of the different studies is unclear but may be a result of local controlling factors, e.g. the temperature differences.

Amphibolis stems and blades share similar epiphytic species, in particular geniculate coralline algae (e.g. *Pneophyllum-Fosliella* group) (Ducker *et al.* 1977, den Hartog 1970, Sim 1991, Chapter 6). The finding from this study of additionally high abundance of calcareous epiphytes on *Amphibolis* stems suggests that these organisms are not adapted to the quick turnover rates of the seagrass blades. This in turn indicates that recruitment on to blades is likely to be opportunistic because a favoured attachment site would allow the organisms to reach full maturity, whereas the blades do not.

Amphibolis blades have significantly higher quantities of carbonate than *Posidonia*. This initially seems surprising because of the apparent reduced surface area, over similar life spans, available for epiphyte settlement. There are a number of possible reasons:

1) *Amphibolis* stems provide a local and constant epiphyte source as compared to the *Amphibolis* blades.

The high abundance of calcareous epiphytes and the proximity of the *Amphibolis* stems to the blades may provide a local and continuous source of recruiting epiphytes. The route by which epiphytes can reach new habitat space occurs either by expanding the colony/organism growing edge or by the transportation of the propogules. The importance of conspecific adults in close proximity to newly settled propogules has been noted previously (Keough 1983) and there is evidence that conspecific adults induce settlement of marine invertebrates (Pawlik 1992 and references therein, Rodríguez *et al.* 1993 and references therein). The encrusting cheilostomate bryozoan *Thairopora cincta* was frequently observed during this study to grow directly from *Amphibolis* stems onto the outer sheath of the lower (oldest) blade of a leaf cluster and then to continue on up through the blade cluster. This method of colonisation was not commonly observed for other epiphyte species and in general, the upper (younger) area of *Amphibolis* stems is free of calcareous epiphytes – a phenomenon also found by Sim (1991).

2) The clustering nature of *Amphibolis* blades provides a more sheltered environment for recruitment than do *Posidonia* shoots.

Clustering of *Amphibolis* blades provides nodal areas in which calcareous epiphyte propogules may be trapped (Fig. 5.8). *Posidonia* plants only have this 'nodal' area near the sediment water interface. Experiments to determine if nodal areas do attract propogules were carried out by Harvey & Bourget 1997. Artificial three-dimensional structures in flume experiments showed that polyvinylchloride microparticles (used as a proxy for passive settlement of epiphytes) did not settle in the nodal area (8% of total settlement) They found that calcareous epiphytic propogules, in the field and using the same artificial structure, settled much more frequently in the nodal area (35-80% of total settlement) (Harvey & Bourget 1997).

The influence of the clustering structure of *Amphibolis* blades may be tested by examining the calcareous epiphyte productivity on two *Amphibolis* species that have significantly different cluster structures. *A. antarctica* clusters are loosely arranged and have sheath margins that only overlap in the lower half of the sheath (Womersley 1984 - Fig. 5.8). This provides a relatively large nodal surface area as well as exposing the next youngest blade. *A. griffithii* clusters are tightly grouped and the sheath margins completely overlap (Womersley 1984 - Fig. 5.8). This provides a relatively small nodal area and the next youngest blade is not well exposed until the outer blade is shed. Thus *A. antarctica* provides more surface area for calcareous epiphytes to settle on, using the theory described above. The data from Chapter 4 and from West Island indicate that *A. antarctica* does have higher abundances of calcareous epiphytes than *A. griffithii* (191 and 161.9 $CaCO_3$ g/kg of seagrass *A. antarctica* (averaged sites, West Island respectively) and 89.7 $CaCO_3$ g/kg of seagrass *A. griffithii* (West Island only)).

3) The structure of *Amphibolis* plants is more conducive to calcareous epiphyte recruitment and survival due to the effect on current velocity.

Settlement ability is altered by the hydrodynamic condition (Rodríguez *et al.* 1993) and it has been shown that the thin strap-like leaves, e.g. of *Posidonia,* reduce water movement more efficiently than upright or cylindrical shoots, e.g. of *Amphibolis* (Fonesca *et al.* 1982 and Cambridge 1980 cited in Sim 1991). This would, initially, be thought to increase settlement rates. However, the manner in which the two seagrass species bend also affects the ability of currents to flow through the seagrass bed (Fig. 3.6). The response of *Posidonia* blades to current velocity is to flatten parallel to the current direction forming relatively impermeable dense mats, hence reducing the amount of epiphyte propogules exposed to the surface of the blades. *Amphibolis* blades, on the other hand, remain relatively exposed to calcareous epiphytic recruiting propogules, hence have a greater chance of recruiting to the blade surface. Also, large, relatively inflexible epiphytic colonies (species dependent) would be more prone to damage by the blade-to-blade contact and flexibility of *Posidonia* sp. compared to *Amphibolis* sp. (Hayward 1974; Fig. 1.2).

4) The surface texture of *Amphibolis* blades provides a more favourable site for recruitment than the surface texture of *Posidonia* blades.

Posidonia and *Amphibolis* blades have significantly different surfaces (Fig. 5.9). *Posidonia* blade surfaces are composed of smooth, parallel, regular veins. *Amphibolis* blade surfaces have a rough and pitted texture. Recruitment studies indicate that settlement of crustose coralline algae is higher where the surface is rough (Figueiredo *et al.* 1997, Greig 2000) although many bryozoans have been identified as preferring smooth surfaces on which to settle (Ryland 1976). Hence, the faunal assemblages found on *Posidonia* versus those on *Amphibolis* may indicate whether surface texture contributes to the difference in carbonate abundance. It could be assumed that rough surfaces may be favoured because it is easier to 'grip and stick' to rough surfaces, or alternatively rougher surface may increase the rate at which a biofilm can develop. It is widely documented that settlement and metamorphosis of invertebrate larvae is promoted by the presence of biofilms (microfouling film) (e.g. Pawlik 1992 and references therein, Rodríguez *et al.* 1993 and references therein, Turner & Todd 1993 and references therein, Keough & Raimondi 1995, Scholz & Krumbein 1996).

5) Chemical signatures of plants affect the rate of propagule settlement.

Chemical signatures of plants may affect propogule~~s~~ settlement in one of two ways: i) as a toxin to prevent recruitment, or ii) as a chemical cue for recruitment. Marine algae are known to produce toxins to prevent epiphyte recruitment, e.g. *Dictyopteris divaricata* and *Symphocladia latiuscula* (Pawlik 1992) but there are no known records in the literature of seagrass exuding toxins. Marine invertebrate larval settlement is known to be triggered by certain chemicals (Pawlik 1992 and references therein, Rodríguez *et al.* 1993).

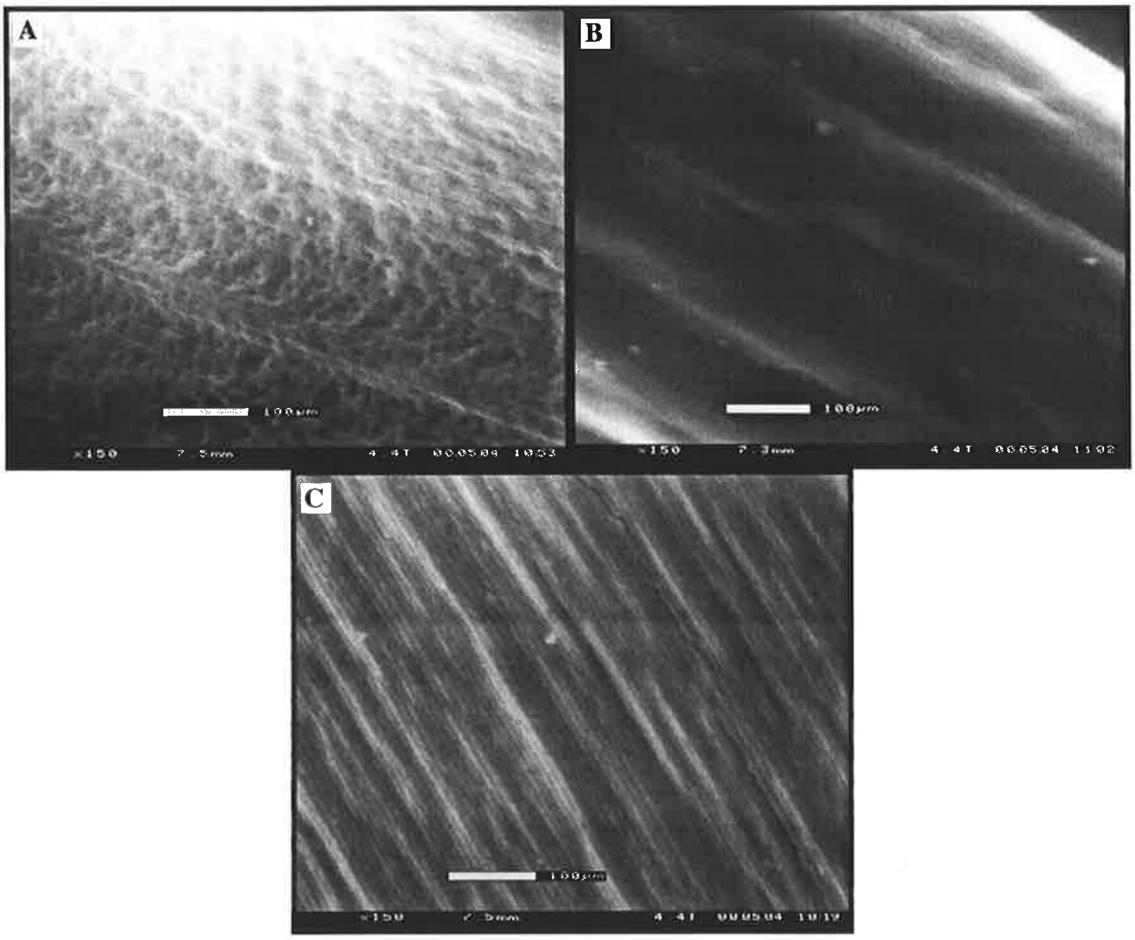


Fig. 5.9. Environmental Scanning electron microscope images of the surfaces of seagrass..
A. *A. antarctica* blade B. *A. antarctica* stem. C. *P. sinuosa* blade. Scale bar on image.

Although there is no evidence that *Amphibolis* sp. produce such chemicals, it seems unlikely that *Amphibolis* would want to attract epiphytes.

The design of *Amphibolis* plants apparently favourable for epiphyte recruitment may explain why, in anthropogenic nutrient rich environments, *Amphibolis* is one of the first species to decline, i.e. increased nutrient results in increased algal epiphyte productivity increasing shading and reducing the ability of the plant to photosynthesise. This pattern has been documented in the Adelaide metropolitan waters of St. Vincent Gulf, South Australia (EPA 1998).

5.4.2.3 Calcareous epiphytes and depth

The decrease in epiphyte $CaCO_3$ g/m^2 coincides with the decrease in seagrass biomass as depth increases. However, the rate of decrease of $CaCO_3$ g/m^2 is not the same ratio as the biomass decrease, indicating other parameters affect the productivity. This is clearly demonstrated by the significant increase in $CaCO_3$ g/kg of seagrass with increased depth, i.e. the amount of epiphytic carbonate on each seagrass plant increases with increased depth. This is similar to the findings discussed in Chapter 4, although the West Island study did not sample below 10 m mwd.

Possible explanations as to why epiphytes increase in abundance with depth, are summarised below:

1) <u>Competition</u> by calcareous epiphytes for space increases with increasing depth because of the decreasing number of plants (lower biomass). This in turn increases the density of calcareous epiphytes on each plant, hence increasing the $CaCO_3$ g/kg of seagrass.

2) <u>Decrease in plant density</u> means that the space between each plant increases. This makes the enviornment less attractive to grazers, thereby increasing the relative abundance of epiphytes with depth. Grazers, including fish and gastropod species, are known to maintain and/or reduce the number of epiphytes (Shepherd *et al.* 1989).

3) <u>Lower light levels</u> reduce the abundance of non-calcareous epiphytes, providing more recruitment space for calcareous epiphytes. Coralline algae are adapted to survive in low light conditions, for example, Jones & Woelkerling (1983) reported that *Hydrolithon farinosum* (Lamouroux) Penrose & Chamberlin 1993, a species found on *A.*

antarctica showed maximum productivity at 12-25 μmol photons/m^2/s. It seems that light levels are not inhibiting for crustose coralline algae at the 'deep' site at West Island as the lowest light level recorded was 100 μmol photons/m^2/s.

4) Reduced current velocities apply with increased depth. The theories about the effects of reduced current velocity on calcareous epiphyte abundance are contradictory. On the one-hand, reduced current velocity may improve settlement and survival rates leading to increased calcareous epiphyte abundance, but on the other-hand, reduced velocity increases the boundary layer between the calcareous epiphytes and the water column, thus reducing the exchange of nutrients, and potentially reducing productivity and abundance (Wheeler 1980 and Gerard 1982 cited in Sim 1991, Fonseca & Kenworthy 1987). Reduced current velocities (i.e. flow) would also be less favourable for filter-feeders as less particulate matter would pass over the surface of the filter-feeders.

The relationship with depth described above was the same for those calcareous epiphytes on *Posidonia* and on *Amphibolis* blades, but different for those associated with *Amphibolis* stems. *Amphibolis* stems showed no significant difference with depth. This relationship supports the theory that light is not a controlling factor on calcareous epiphyte productivity to 10m mwd because the effect would be amplified on *Amphibolis* stems due to their longevity. The significant increase in $CaCO_3$ gm^2 for both *Amphibolis* blade and stems is attributed to the increase in biomass of *Amphibolis* with depth. The only other known study that incorporated various depths (*pers. comm.* Cambridge 2001), showed a decrease in $CaCO_3$ g/m^2 values with depth. The depth range, for the study by Cambridge (2001), was only 0.5-4 m mwd and can not therefore be used as a direct comparison.

5.4.2.4 Calcareous epiphytes and seasonality

Overall values from West Island indicate that there is a decrease in $CaCO_3$ g/m^2 from autumn through winter. This was also reported from seasonal epiphyte studies at an inshore site of approximately 12m mwd at Cockburn Sound Western Australia (SMCWS 1996). However, the findings of SMCWS (1996) at an offshore site at Cockburn Sound, showed an increase in $CaCO_3$ g/m^2 during winter. Studies by Sim (1991) and Lavery *et al.* (1998) also showed an increase in $CaCO_3$ g/m^2 during autumn/winter, for *Amphibolis* blades and *P. coriacea*. The only other known seasonal study of calcareous epiphyte productivity is that of Cambridge (*pers. comm.* 2002) which showed no clear seasonal variation. The increase at the offshore site at Cockburn Sound was attributed to the ability of coralline algae to out-compete filamentous algae in high-energy waters. The higher energy site inshore at Cockburn Sound would have been analogous to the shallow inshore site at West Island due to high wave action, which would have been attenuated at the deeper 10m mwd offshore site. The study by Lavery *et al.* (1998) showed that the time of peak carbonate abundance varied both between sites and with different seagrass species/components, for example at one site the peak carbonate abundance on *A. griffithii* stems was during spring/summer – hence, agreeing with the findings of this study. Contradictory to the SMCWS (1996) study, the present research showed that calcareous epiphyte abundance decreased at both depths during winter. The most likely control in calcareous epiphyte abundance at both sites of this study was decreasing seagrass biomass, representing decreased recruitment space during autumn/winter. The close correlation between seagrass biomass and calcareous epiphyte abundance was identical to that found in other areas of this study (Chapter 4). The relationship between seagrass biomass and calcareous epiphyte $CaCO_3$ g/m^2 is further reinforced by the finding of a significant decrease in abundance in both, from 1999 to 2001.

Significant monthly variation was found for epiphyte $CaCO_3$ g/kg of seagrasss, but the *post hoc* Tukey did not indicate a clear seasonal pattern. Graphically the results imply that calcareous epiphyte abundance on an individual plant increases during autumn/winter and decreases during spring/summer. An *in situ* study by Yates & Halley (1999) from the Florida Keys measured calcification rates (independent of biomass) using measurements of geochemical changes over a seagrass bed, and concluded that calcification rates were higher in winter, hence agreeing with the findings of this study. The other studies that found increased abundances of epiphytes during autumn/winter (i.e. Sim 1991, SMCWS 1996, Lavery *et al.* 1998) do not give data independent of biomass, but also do not indicate the relationship of carbonate abundance with seagrass biomass at the study sites. The theory, put forward by Sim (1991) to explain the increase in abundance during winter was that it was due to the slower turnover rates of the seagrass blades, in particular *A. antarctica.* This study supports the theory that calcareous epiphyte abundances per plant are greater during autumn/winter.

These results are contradictory to settlement plate studies and artificial seagrass units that predominantly show decreasing settlement rates in winter (e.g. Keough 1983, Silberstein 1985, Todd & Turner 1986, EPA 1998, Harbison & Wiltshire 1992, Turner & Todd 1993). The faunal assemblages of settlement plates and artificial seagrass units are similar to seagrass, but the surfaces are not ideal analogies as they provide a relatively inert, stable substrate compared to the organic flexible substrate of seagrass. The flexible nature allows distribution through the water column, thus exposing the epiphytes to light and nutrients which enhances growth (Silberstein 1985). Hence, any direct comparison should be viewed with caution.

Keough (1983) distinguished four types of recruitment patterns from settlement plates i) year round settlement, ii) seasonal peaks, iii) regular recruitments at the same time each year, and iv) irregular and intense peaks of recruitment. These patterns can be directly linked to:

1) Life history

Larval abundance is influenced by the adult reproductive cycle (Roughgarden *et al.* 1988) and hydrographic patterns conditions and larval mortality (Rodríguez *et al.* 1993 and references therein). The number of propogules may be lower in winter than in summer (Turner & Todd 1993) and Borowitzka *et al.* (1990) noted that there was a clear increase in epiphyte species in spring on *A. griffithii* in Western Australia, but knowledge about the life histories of epiphytic taxa is limited. A summary of current knowledge about the 5 main calcareous epiphytic taxa follows:

Coralline algae: Studies of the crustose coralline *Pneophyllum– Fosliella* complex, which is common on seagrass species in southern Australia, have indicated that temperature and light have the greatest effects on the growth rates (Bressan & Tomini 1982, Jones & Woelkerling 1983). Jones & Woelkerling (1983) found that *Fosliella cruciata* (a common species on *A. antarctica*) does not germinate in temperatures at and below 10°C and that above this, increased photon light flux significantly increases the growth rates and production of conceptacles of the plants (26-33 days). Bressan & Tomini (1982) concluded that growth was slowest under winter and spring conditions.

Bryozoans: According to Ström (1977) bryozoans exhibit year round reproduction or to biomodal reproduction in summer and autumn, or peak production in autumn. Most temperate species have a breeding optimum in early autumn. Short lived and shallow species, as found on seagrass, have brief but intensive periods of reproduction (Ryland 1970, Eggleston 1972). Brown *et al.* (2000a, b) reported that *Lanceopora smeatoni*, epiphytic to *P. sinuosa* sheaths at West Island, had an annual life cycle, with small colonies first identified during winter, completing the cycle the following autumn.

Serpulids & spirorbids: Serpulids and spirorbids ~~are~~ reproduce all year round, although the abundance varies between years (Chalmer 1982, Keough 1983, Todd & Turner 1986). Several species were treated together by Todd & Turner (1986). Spirorbids are negatively phototaxic, i.e. they choose to settle in areas of lower light. Hence during summer the number of spirorbids may be relatively reduced in the upper canopy of the seagrass and concentrated towards the base of the plants (Dirnberger 1993, Hamamoto & Mukai 1999, Saunders & Connell 2001).

Foraminifers: No studies on the ecology of temperate benthic marine foraminifers have been reported, although it is suggested reproduction occurs all year round, with different species peaking at certain periods during the year (*pers. comm.* Qianyu Li & Brian McGowran 2001).

It appears from the above that there would be calcareous epiphyte propogules available all year around, but the volumes are not known. It is likely that there is a succession of calcareous epiphyte propogules throughout the year, i.e. peak propagule production of one species may coincide with the low period for another and as the production of that species decreases, so another increases. Thus, as Ólafsson *et al.* (1994) concluded from the literature, larval supply is generally not limiting and other factors determine the pattern of species distribution and abundance observed.

2) Settlement rates

Settlement of epiphytic propogules occurs either passively, actively or a combination of both. Passive settlement is considered to be the dominant method when hydrodynamic conditions do not allow active settlement (Harvey & Bourget 1997). Some species of bryozoans, e.g. *Membranipora membranacea* are known to have the ability to move actively against moderate currents to their selected place of settlement (Abelson 1997). In addition biofilms are believed to be an important cue for active settlement (Keough &

Raimondi 1995, Scholz & Krumbein 1996). Biofilms form by the adsorption and growth of microorganisms at interfaces (Scheer 1945, Neu 1994). There is some evidence to suggest that low wave energy enhances the buildup of biofilms (Yallop & Paterson 1994).

3) Mortality rates

Post-settlement mortality rates are usually high, e.g. the non-calcareous bryozoan *Alcyonidium hirsutum* was reported to have a survival rate of 0-1% in these shallow environments (Hunt & Scheibling 1997). Causes of mortality include delay of metamorphosis, biological disturbance (grazing), physical disturbance, physiological stress, competition, developmental abnormalities, insufficient energy reserves, disease and parasitism (Hunt & Scheibling 1997). No known studies have specifically identified changes in mortality rate with season.

4) Growth rates

There are few studies focussing on measuring changes in growth rate with temperature. Intuitively growth rates decrease in winter due to a decrease in metabolism and food source. Some species of bryozoans show increased growth rates, but reduction in zooid size in warmer temperatures (Menon 1972, Best & Thorpe 1994, Sanderson & Thorpe 1996, O'Dea & Okamura 1999 and references therein, 2000).

This study indicates that the abundance of calcareous epiphyte propagules available for recruitment, and the success of that recruitment, is not hindered by factors associated with winter. It may be that there is a slight increase or decrease in the propagules and recruitment success rate, but it is not significant.

Increase in calcareous epiphyte abundance on each plant during autumn and winter supports the theory of the importance of recruitment space for epiphytes. During winter when biomass, and hence recruitment space, is reduced the number of calcareous epiphytes recruiting per surface area increases. Hence an increase in $CaCO_3$ g/kg of seagrass, but decrease in $CaCO_3$ g/m^2 results. In spring, however, when seagrass productivity increases and hence recruitment space increases, the actual abundance on each blade is relatively reduced. At this time the calcareous epiphyte propagules recruit successfully, but only until seagrass productivity falls off again during autumn/winter.

This implies that the rate of seagrass productivity during spring is greater than the recruitment rate of calcareous epiphytes. This has important ramifications for the seagrass plants because it is at this time of year that they build up their stores for when climates are not so favourable. If calcareous epiphyte recruitment were also increased during this time of year, then the photosynthetic capabilities of the seagrass would be inhibited due to surface coverage.

5.5 SUMMARY & CONCLUSIONS

The following findings from West Island all correlate with the data from the other South Australian sites. (Chapter 4): biomass range, $CaCO_3$ range, high abundance of calcareous epiphytes associated with *Amphibolis*, positive correlation of $CaCO_3$ and seagrass biomass, decrease in seagrass biomass with depth and calcareous epiphyte abundance increase with depth to 10m mwd.

The study at West Island, additionally, identified that 80% of the epiphytic $CaCO_3$ is associated with *Amphibolis* stems and that *Amphibolis* blades have significantly greater abundances of calcareous epiphytes associated with them than do *Posidonia*. The reason for the increased abundance of calcareous epiphytes on *Amphibolis* blades was attributed to the morphological structure of *Amphibolis* blades and their proximity to conspecific adults. It appears that *Amphibolis* is more susceptible to calcareous epiphyte recruitment than *Posidonia*. This may explain why *Amphibolis* plants are one of the first species to recede when, due to anthropogenic nutrient input, non-calcareous algal epiphytes increase.

The decline in $CaCO_3$ during autumn/winter is attributed to the simultaneous decrease in seagrass biomass, hence reducing recruitment space. The independent measure of $CaCO_3$ g/kg of seagrass, however, showed a greater abundance of calcareous epiphytes in autumn/winter and less in spring/summer. This is also attributed to the availability of recruitment space, in that an increase in seagrass productivity in spring also increases the amount of substrate available for recruitment, effectively diluting the abundance of epiphytes on each unit surface area. This relationship implies that the epiphyte propagule availability and settlement rate does not vary significantly throughout the year.

CHAPTER 6

CALCAREOUS EPIPHYTES

6.1 INTRODUCTION

There are no known reports of studies quantitatively or qualitatively examining the ratios of calcareous epiphyte taxa. This chapter addresses questions about the epiphytes themselves:

- what are they;
- what is the relative importance of the taxa and species in terms of carbonate abundance and frequency of occurrence;
- and is it possible to ascertain information about the particular environment or seagrass species from calcareous epiphyte species/faunal assemblages or morphological type?

The methods used to examine the calcareous epiphytes in order to answer the above questions are described in chapter 2. In total, 1544 individual blades and stems of seagrasses were examined, comprising:

- 333 from *Posidonia sinuosa*;
- 179 from *P. australis*;
- 130 from *P. angustifolia*;
- 58 from *Amphibolis antarctica* stems;
- 435 from *A. antarctica* blades,
- 53 from *A. griffithii* stems; and
- 356 from *A. griffithii* blades.

The faunal assemblages were examined at all sites that were also sampled for epiphytic $CaCO_3$ abundance (Fig. 2.1, 6.1), i.e. 23 sites.

6.2 INTER-TAXA RELATIONSHIPS

The relationship between the calcareous epiphyte taxa and their surrounding environments was examined using the ratios of each taxa and the standing stock abundances, compared to geographical location, seagrass species, water depth, salinity, temperature and nutrient concentrations. The overall relative importance of epiphytic taxa was:

- coralline algae (53.6%);
- foraminifers (17.4%);
- bryozoans (16.4%);
- spirorbids (8.0%)

- bivalves (0.3%);
- serpulids (0.2%);
- ostracods & others (<0.1%).

6.2.1 Geographical distribution

Examination of the different ratios of taxa from the different sites reveals that coralline algae has the highest ratio at nearly every site, in particular at Cape Jaffa (Fig. 6.1, Table 6.1). The exceptions to this are Semaphore, that was dominated by foraminifers, Cowlers Landing that also had a higher % of foramanifers and Chinaman Creek (3) where the dominant taxa is bryozoans. Bryozoans were present in significant quantities (defined as >5%) at all sites except Cape Jaffa, Pt Moorowie and Streaky Bay. Foraminifers were present in significant quantities at all sites except Cape Jaffa, Chinaman Creek (2) and West Island (shallow and deep). Fifteen out of the 23 sites also had significant quantities of spirorbids, e.g. Marino Rocks, which consisted of 35% spirorbids.

Extrapolation of the % ratio data (Fig.6.2) to the actual abundances of carbonate from each taxa (Table 6.2, Fig. 6.3) showed that coralline algae ~~was~~ were still dominant, in particular at Normanville (256 g/m^2, 262 g/kg of seagrass). The deep site at West Island had the greatest abundance of carbonate from bryozoans (46.6 g/m^2, 71.8 g/kg of seagrass), although Cape Hardy bryozoans had higher abundances per plant (80.1 g/kg of seagrass). Streaky Bay had the highest abundance of foramanifers (74.5 g/m^2), but Semaphore had high densities of foramanifers on each plant (284.1 g/kg of seagrass). Moonta Bay had the highest abundance of spirorbids (30.4 g/m^2, 40.5 g/kg of seagrass).

Coralline algae showed the only geographical trend, decreasing northward up the Spencer Gulf (Fig. 6.3. Table 6.2). This trend is not, however, reflected in examination of relative carbonate abundances on the individual seagrass types (Fig. ~~6.3~~ 6.1, 6.2). Significant differences of carbonate at different sites on different seagrass types were shown, but no clear geographic relationship was determined.

6.2.2 Seagrass species

All seagrass species are dominated by coralline algae (38.2 - 67.8%; Table 6.2, Fig. 6.3), although the dominance on *Ampbibolis antarctica* blades was less pronounced. *Amphibolis* stems, however, show the highest proportion of coralline algae, (av. 65.3%) and bryozoans (av. 30.8%) but they have few other calcareous epiphytes present (Fig. 6.3). *Posidonia*

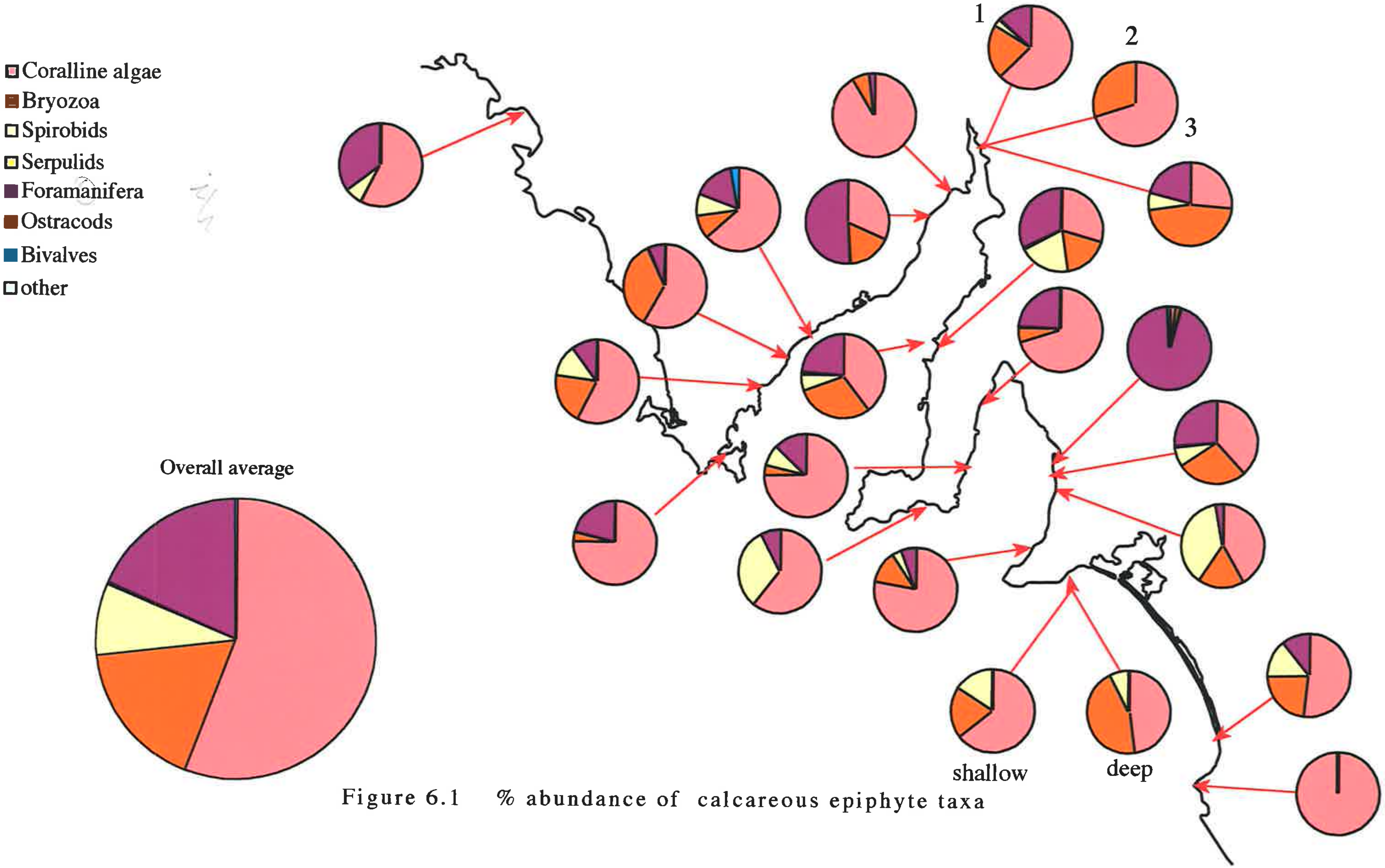


Figure 6.1 % abundance of calcareous epiphyte taxa

Table 6.1. Calcareous epiphyte components from each site, sampled from west to east. Percentage values (%) are ratios of the relative abundance of each taxa from each site. Carbonate values are the actual amounts of carbonate derived from each taxa ($CaCO_3$ columns are: **A** = g/m^2 and **B** = g/kg/sg). West Island (shallow site) derived from samples collected in February, May and September, 1999. Σ = total % estimation. n = total number of blades and stems analysed for each site

Site	Coralline algae			Bryozoans			Spirobids			Serpulids			Foraminifers			Ostracods			Bivalves			Other			Σ	N
	%	A	B	%	A	B	%	A	B	%	A	B	%	A	B	%	A	B	%	A	B	%	A	B		
StBy03/1999	55.1	123.3	144.8	0.4	0.8	1.0	6.2	13.8	16.2	0.1	0.2	0.2	33.3	74.5	87.5	0	0	0	0.42	0.9	1.1	0	0	0	95.3	96
PtLi03/1999	69.4	30.5	88.8	3.2	1.4	4.1	0.2	0.1	0.2	0	0	0	18.6	8.2	23.8	0.01	0	0	0.17	0.1	0.2	0	0	0	91.6	29
Tum03/1999	56.6	76.2	143.8	19.6	26.3	49.7	11.6	15.7	29.6	0.1	0.1	0.2	9.3	12.5	23.7	0	0	0	0	0	0	0.61	0.8	1.5	97.9	29
CaHa10/1999	54.9	62.1	138.4	31.8	36.0	80.1	0.3	0.3	0.6	0.1	0.2	0.3	6.3	7.1	15.8	0.04	0	0.1	0.14	0.2	0.3	0	0	0	93.6	72
Dut10/1999	60.8	8.8	94.9	8.3	1.2	12.9	8.9	1.3	13.9	0	0	0	14.9	2.2	23.2	0	0	0	3.13	0.5	4.9	0	0	0	95.9	20
Cow06/1999	30.0	11.3	56.1	15.4	5.8	28.9	0	0	0	0.2	0.1	0.5	48.4	18.3	90.5	0.01	0	0	0.09	0	0.2	0	0	0	94.2	30
Why03/1999	85.8	8.8	40.7	6.0	0.6	2.8	0	0	0	0	0	0	2.4	0.3	1.2	0	0	0	0	0	0	0	0	0	94.3	30
ChCk11/2000.1	62.7	23.4	92.0	21.3	7.9	31.3	2.4	0.9	3.6	0.8	0.3	1.1	12.8	4.8	18.9	0.01	0	0	0.09	0	0.1	0	0	0	100.1	29
ChCk11/2000.2	65.5	8.1	18.2	28.3	3.5	7.9	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	93.9	30
ChCk11/2000.3	26.2	6.2	27.3	43.9	10.3	45.7	7.1	1.7	7.4	0	0	0	19.9	4.7	20.7	0.01	0	0	0.09	0	0.1	0	0	0	97.2	30
Moo04/1999	27.6	44.9	59.9	15.9	25.9	34.5	18.6	30.4	40.5	0.7	1.1	1.4	29.6	48.2	64.3	0.16	0.3	0.4	0.20	0.3	0.4	0	0	0	92.7	126
Tip10/1999	41.9	7.0	63.0	31.6	5.3	47.5	7.1	1.2	10.7	1.1	0.2	1.6	24.6	4.1	36.9	0	0	0	0	0	0	0	0	0	106.2	33
PtMo04/1999	56.7	39.3	84.6	0	0	0	29.3	20.3	43.8	0	0	0	7.3	5.0	10.8	0	0	0	0	0	0	0	0	0	93.2	41
Stan04/1999	72.7	21.2	79.7	3.8	1.1	4.2	7.9	2.3	8.6	0	0	0	12.3	3.6	13.5	0.01	0	0	0	0	0	0	0	0	96.7	27
Ard04/1999	66.8	111.9	171.2	5.7	9.5	14.6	0.5	0.9	1.4	0.1	0.1	0.2	22.1	37.1	56.7	0.01	0	0	0.44	0.7	1.1	0	0	0	95.	86
Sem05/2000T1	2.2	0.3	7.2	1.7	0.3	5.6	0.2	0	0.6	0.3	0.1	1.1	87.5	13.0	284.1	0	0	0	1.22	0.2	3.9	0	0	0	93.22	25
Tor05/2000	40.7	5.8	33.1	29.3	4.1	23.8	7.8	1.1	6.3	1.0	0.1	0.8	28.4	4.0	23.2	0.01	0	0	0.02	0	0	0	0	0	107.1	30
Mar01/1999	39.1	12.1	29.1	17.0	5.3	12.6	35.1	10.9	26.1	0	0	0	3.2	1.0	2.4	0	0	0	0	0	0	0	0	0	94.4	117
Norm05/1999	70.2	256.0	262.2	10.7	39.0	40.0	3.3	12.2	12.5	0	0.1	0.1	5.5	20.1	20.5	0	0	0	0	0	0	0	0	0	89.8	171
WI shallow	59.5	78.1	136.4	18.6	24.5	42.8	14.2	18.6	32.5	0.2	0.2	0.4	0.4	0.5	0.8	0	0	0	0	0	0	0	0	0	92.8	356
WI9/1999deep	41.9	49.0	75.4	39.9	46.6	71.8	6.5	7.6	11.7	0.1	0.1	0.2	0.4	0.4	0.7	0	0	0	0.00	0	0	0	0	0	88.7	65
King11/1999	58.7	20.9	61.8	24.5	8.7	25.8	16.5	5.9	17.4	0	0	0	12.4	4.4	13.1	0	0	0	0.08	0	0.1	0	0	0	112.2	30
CaJa11/1999	87.5	49.3	94.5	0.4	0.2	0.5	0	0	0	0	0	0	0.3	0.2	0.4	0	0	0	0	0	0	0	0	0	88.3	25

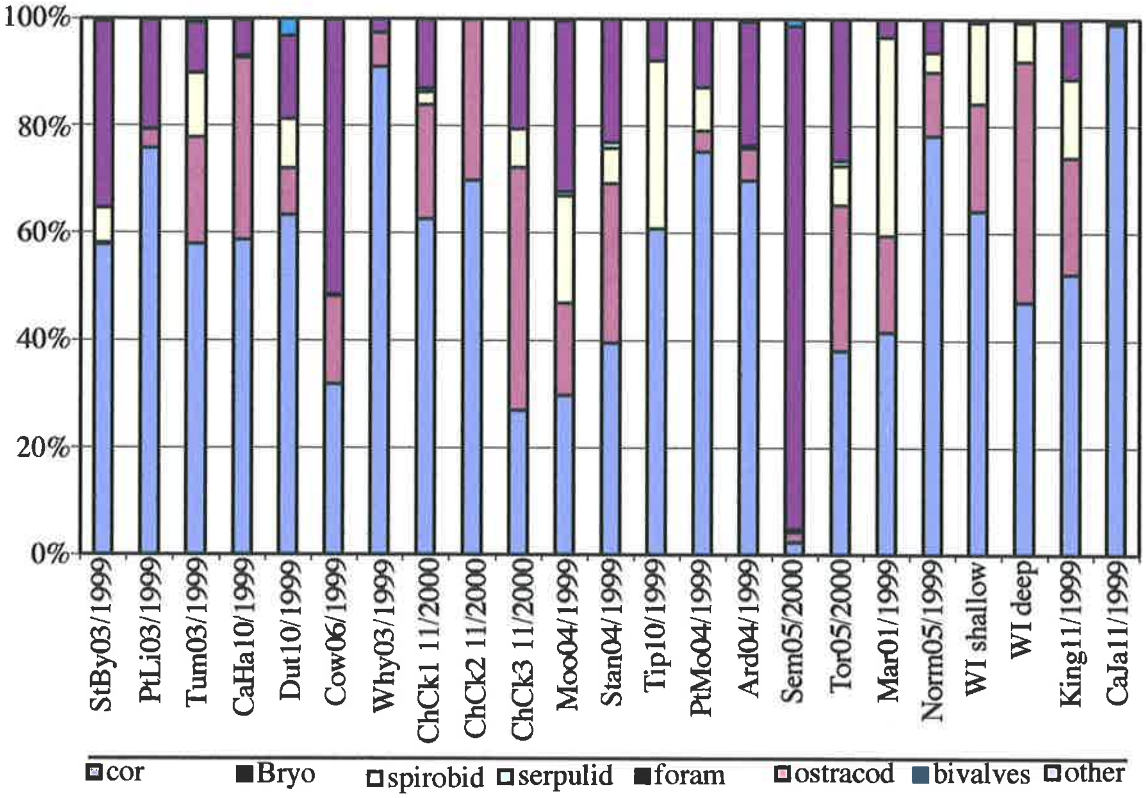


Fig. 6.2 (A) Relative % abundance of different epiphyte taxa at each site, mixed s.eagrass species.

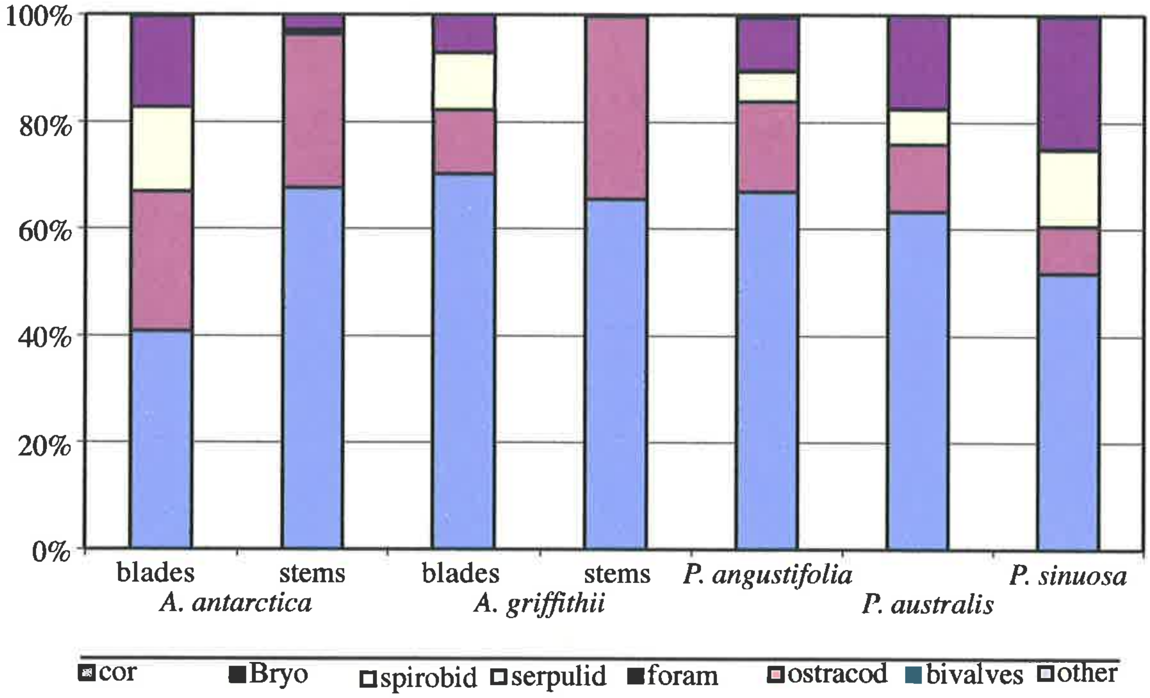


Fig. 6.2. (B) Relative % abundance of different epiphyte taxa from each seagrass species, combined site data

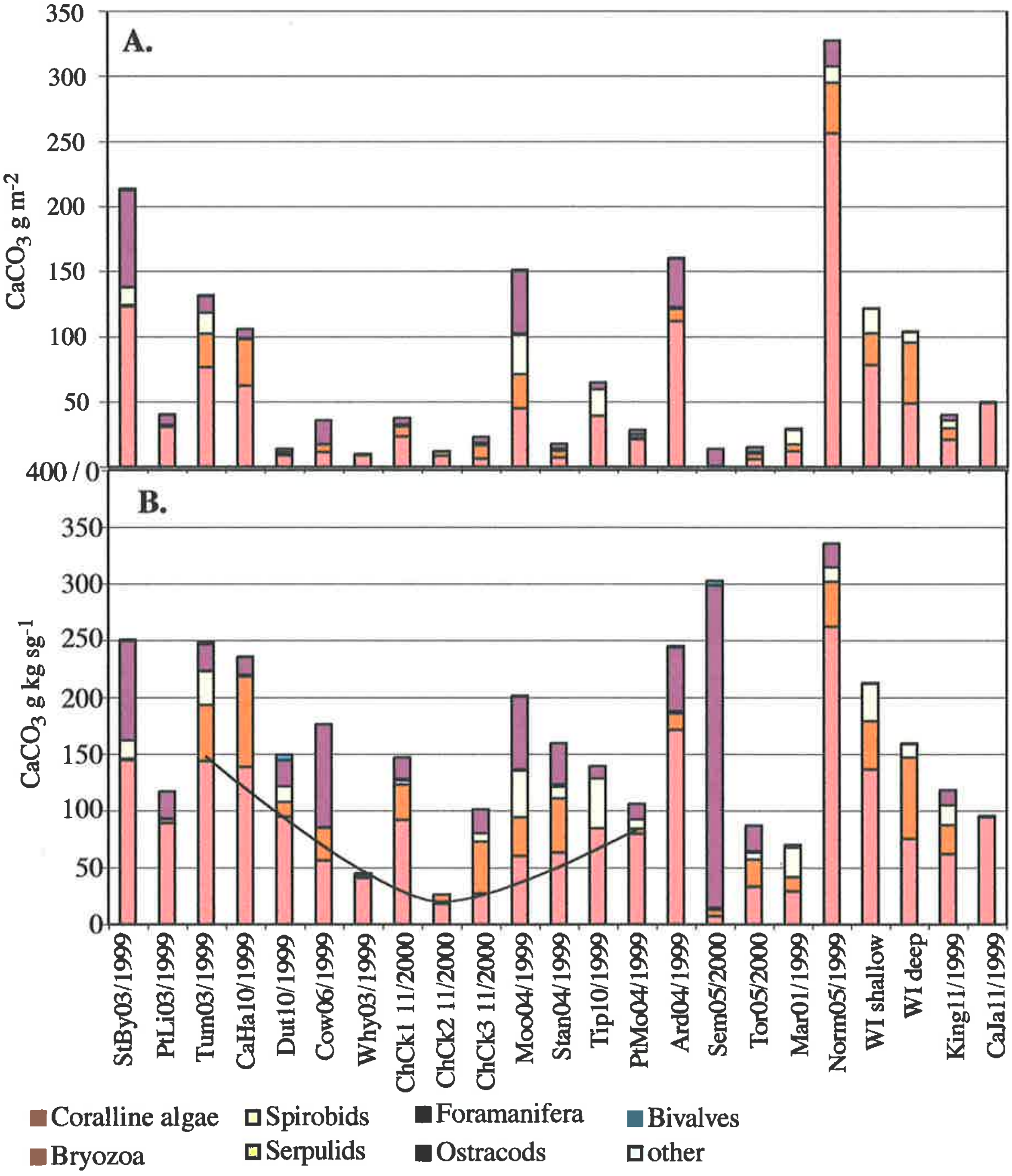


Fig. 6.3. Calcareous epiphyte taxa components of standing stock CaCO$_3$/g m2 (**A**) and g/kg/s (**B**) at each site sampled from mixed seagrass species.

Table 6.2. Percentage of epiphyte taxa on different seagrass species and their various components. Σ total %, n = number of samples.

Seagrass species	Coralline algae	Bryozoans	Spirobids	Serpulids	Foraminifers	Ostracods	Bivalves	Other	Σ	N
A. antarctica blade	38.2	24.3	14.7	0.1	15.9	0.03	0.22	0.00	93.5	425
A. antarctica stem	66.0	27.9	0.5	0.4	2.7	0.03	0.01	0.00	97.6	54
A. griffithii blade	67.8	9.8	7.6	0.1	4.8	0.00	0.00	0.00	90.5	357
A. griffithii stem	64.5	33.6	0.1	0.1	0.1	0.00	0.00	0.00	98.4	53
P. angustifolia	63.0	15.9	5.3	0.2	9.3	0.00	0.52	0.00	94.1	120
P. australis	60.4	12.0	6.4	0.1	16.7	0.00	0.01	0.00	95.6	179
P. sinuosa	50.4	8.5	14.1	0.2	24.1	0.00	0.14	0.04	97.4	334

sinuosa has a relatively high abundance of spirorbids and foraminifers in comparison to the other *Posidonia* species (Table 6.2 & Fig. 6.3).

Significant variations in the ratios of calcareous epiphyte taxa on the different seagrass species were found using 1-way ANOVA and *post hoc* Tukey-Kramer HSD (Table 6.3). All runs failed Levene's test of homogeneity of variance and transformation of data did not improve the heterogeneity, hence a more conservative alpha value (i.e. $p = 0.01$) was adopted (Underwood 1981). ANOVA determined that there was a significant difference in the relative abundances of coralline algae, bryozoans, spirorbids, foraminiferas ($p \leq 0.001$) and spirorbids ($p \leq 0.01$) between different seagrass species, but no significant difference for serpulids, ostracods, bivalves and 'other' calcareous epiphyte taxa. *Post hoc* Tukey indicated that coralline algae was significantly lower on *A. antarctica* blades, bryozoans were significantly higher on *Amphibolis* stems, spirorbids were significantly higher on *A. antarctica* blades & *P. sinuosa* and that foraminiferas were significantly higher on *P. sinuosa*, but low on *A. antarctica* stems, *A. griffithii* stems and blades.

It was not possible to run 2-way ANOVA's to determine if there was an interaction term between seagrass species and site as not all seagrasses were found at all sites making the data unorthogonal, hence site and seagrass species variations are determined separately as above.

6.2.3 Other parameters

No significant difference was found for taxon abundance with depth, water temperature and salinity using ANOVA. Regression analysis showed negligible R^2 value relationships, but the following trends are still worthy of note; coralline algae decreased with increasing depth, salinity and temperature. Bryozoans increased with increasing depth, salinity and temperature and foraminiferas showed no change with any change in all parameters.

The number of water analyses was limited, hence it is not possible to statistically analyse the nutrient data. The result from Semaphore (Table 3.7), however, showed an apparent correlation between high nutrient values, high foraminifer abundance and low coralline algae abundance. This site also correlates with the lowest seagrass biomass, but highest calcareous epiphyte abundance (g/kg of seagrass; Tables 3.2, 6.1).

Table 6.3. Results of 1-way ANOVA of epiphyte taxa ratio variation associated with different seagrass species, with site. Locations named represent the site(s) of the most significantly high (↑) or low (↓) taxa abundance present. An alpha value of $p = 0.01$ was used to compensate for the failure of Levene's test for variance homogeneity. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, ns = not significant.

Seagrass species	Coralline algae	Bryozoans	Spirobids	Serpulids	Foraminifers	Ostracods	Bivalves	Other	No.sites
P. sinuosa	*** ↓Semaphore	***	*** ↑WI shallow	*** ↑Tipparra ↑Chinaman(2)	*** ↑↑Semaphore ↑Streaky Bay ↑Cowlers	ns	*** ↑Semaphore	ns	15
P. angustifolia	***	*** ↑Marino	** ↑Marino	*** ↑Torrens	*** ↑Torrens	ns	ns	ns	6
P. australis	*** ↓Moonta ↓Chinaman(3)	*** ↑Chinaman(1-3)	*** ↑Port Moorowie	ns	*** ↑Moonta	ns	ns	ns	9
A. antarctica blades	*** ↓Marino	*** ↑West Island, shallow	*** ↑Marino	Ns	*** ↑Streaky Bay	ns	ns	ns	9
A. antarctica stems	**	***	ns	ns	ns	*** ↑Ardrossan	*** ↑Ardrossan	ns	9
A. griffithii blades	*** ↓West Island, shallow	*** ↑West Island, shallow	ns	*** ↑Streaky Bay	***	ns	***	ns	6
A. griffithii stems	ns	ns	ns	ns	ns	ns	ns	ns	6

6.2.4 Inter-taxa summary

Coralline algae were the most commonly distributed taxon between seagrass species and sites. Bryozoans, foraminifers and spirorbids were nearly always present. There were significant differences in the ratios of the taxa between sites, but there was no clear trend in geographical positions (Fig. 6.1).

There were significant differences in the ratio of calcareous epiphyte taxa between seagrass species (Fig. 6.3). Specifically: - i) coralline algae was low on *A. antarctica* blades, ii) bryozoans were high on *A. antarctica* stems, iii) spirorbids were high on A. *antarctica* blades and *P. sinuosa,* and iv) foraminifers were high on *P. sinuosa,* but low on *Amphibolis* stems and *A. griffithii* blades (Fig. 6.4, Table 6.4).

There were no significant differences in taxa abundance with water depth, salinity and temperature, although trends of decreasing abundance of coralline algae and increasing abundance of bryozoans with increasing depth, salinity and temperature should not be ignored. There was insufficient data to determine whether there is a correlation between taxa abundance and nutrient concentrations, however, at Semaphore high nutrient values correlated with high abundances of foraminifers and negligible coralline algae.

6.3 INTRA-TAXON ANALYSIS

Examination within taxa was carried out to determine:

1) dominant occurring species type;
2) important carbonate producing species;
3) whether there are specific individuals or assemblages that are associated with specific seagrass species;
4) whether there are specific individuals or assemblages that are associated with specific environmental conditions;
5) number of species/different seagrass species "stems"; and
6) number of individuals (or individual colonies) present/different seagrass species.

6.3.1 Coralline algae (see CDs for additional data)

Coralline algae produce 38.2 to 67.8% of all epiphytic carbonate, depending on the seagrass species (Fig. 6.3, Table 6.4). Coralline algae occurred on 1523 of 1544 blades and stems analysed. The majority (68.8%) was of the 'encrusting sheet' type coralline algae (type 2), 20.9% of the erect filamentous form (type 3), 7.8% of the erect narrowly segmented form

Table 6.4 Average abundance of $CaCO_3$ g kg^{-1} sg from each coralline algae type on each seagrass species/components. Mean ± s.e. (number of occurrences)

Seagrass	Type 1	Type 2	Type 3	Type 4	Type 5
A. antarctica blade	0.6	67.0	31.7	0.4	0
A. antarctica stem	0.0	18.8	36.0	42.6	5.6
A. griffithii blade	3.4	88.8	26.5	1.5	0.0
A. griffithii stem	9.6	25.9	0.1	12.0	0.0
P. angustifolia	0.6	42.1	21.6	0.2	0.0
P. australis	0.0	59.5	15.2	24.0	0.0
P. sinuosa	0.8	19.5	15.5	3.8	0.0
Average	3.4 ± 1.3 (12)	42.7 ± 5.5 (62)	21.9 ± 4.1 (37)	14.5 ± 5.9 (37)	6.0 ± 0.9 (3)

(type 4), 2.3% of the thick encrusting form (type 1) and 0.3% of erect broadly segmented forms (type 5) (Table 2.7). The abundance of $CaCO_3$ produced from coralline algae ranges from <0.01 to 232g/kg of seagrass. Type 2 coralline algae, not only had the most frequent occurrence, but also greatest amount of carbonate per g/kg of seagrass (Table 6.4). This finding was the same on all seagrass species/components, except *A. antarctica* stems where type 3 and 4 coralline algae were in greater abundance (Table 6.4).

The effects of geographical variation and other parameters were examined, but only for 'type 2' coralline algae on *Posidonia sinuosa*, as it was the most frequently found species and hence was more likely to indicate any distributions. The results do not show any relationship with geographical location, water depth or nutrient concentration. There is a generally decreasing trend of abundance with increasing temperature and salinity, however, the trend was not statistical significant ($r^2 = 0.15$ salinity and $r^2 = 0.17$ temperature).

6.3.2 **Bryozoans** (see CDs for additional data)

Bryozoans occurred at all sites and on all seagrass species (Tables 6.1, 6.2, Figs 6.1-6.4). They produce 8.5 to 33.6% of all epiphytic carbonate, depending on the seagrass species. Bryozoans were present on 916 from the 1544 blades and stems analysed. Attached directly to seagrass were 61 different species (Table 6.5, Fig. 1.5), plus an additional 44 species that were found in close association with seagrass – i.e. found on calcareous epiphyte algae or in the loose "sediment" that separated from the blades (Table 6.6). The 61 epiphytic species included 47 different genera (including 4 unknowns) from 30 families (including 1 unknown) of which 10 were cyclostomes and the rest cheilostomes. Those species found directly on seagrass were examined further for distribution and assemblage patterns. The most frequently occurring bryozoan was the cheilostome *Heterooecium* sp. (Figure 6.5), which was present at 19 of the 23 sites and occurred on all seagrass species, except on *A. griffithii* stems (Table 6.5). The next most commonly occurring genus was another cheilostome were *Thairopora* sp. (Fig. 6.5; 15 sites on all seagrass species) , closely followed by the cyclostomes *Diaperocecia australis* (14 sites, all but *A. antarctica* stem), *Crisia acropora*, *Disporella pristis* and *Favosipora* sp. (11 sites each; Fig. 6.5). Eighteen of the species identified were only found at one location each. The most common morphotype of bryozoan was the 'encrusting robust sheet' type; 22 of the 61 species were classified within this group (Table 6.5, Fig. 6.5). The second most abundant morphotype was the 'encrusting delicate sheet' type (Fig. 1.5); 17 species were classified within this group. The most common erect bryozoan

Table 6.5. Bryozoan species found attached to seagrass

SEM		genera and species	family	suborder	comments
001ti, 001ai, 001aiii, 001(100)TIV	BR 001	Parasmittina unispinosa	Smittinidae	Ascophora	
002(050)HIV	BR 002	Thairopora sp. a	Thalamoporellidae	Anasca	small cryptocyst
003BI	BR 003	Celleporaria cristata	Lepraliellidae	Ascophora	
004BI	BR 004	Celleporina costata	Celleporidae	Ascophora	
005AD-I, 005AD-IV, 005AD-V	BR 005	Caberea boryi	Candidae	Anasca	
006II, 006CII	BR 006	Mesonea radians?	Crisinidae	Cyclostomata	
007BI-CRAP	BR 007	sp 1	Phidoloporidae	Ascophora	
008GI,008ACII	BR 008	Heterooecium sp.	Tendridae	Anasca	Electridae
010I, 010OI	BR 010	Catenicella elegans	Catenicellidae	Ascophora	Vittaticella?
011AI	BR 011	Diaperoecia?? australis	Diaperoeciidae	Cyclostomata	
014bi,014ov	BR 014	Electra pilosa	Electridae	Anasca	
018ci	BR 018	Emma rotunda	Candidae	Anasca	
020aii, 020aiv, 020aiii	BR 020	Iodictyum?	Phidoloporidae	Ascophora	
021aii,021abi, 021abii	BR 021	Smittina papilifera	Smittinidae	Ascophora	ancestrula
022ciii,022ci,022civ, 022cv	BR 022	Pterocella alata	Catenicellidae	Ascophora	
re-do	BR 024	Crisia ?acropora	Crisiidae	Cyclostomata	
026ri,026riii	BR 026	Hesychoxenia praelonga	Thalamoporellidae	Anasca	uncalcified?
028(033)ei, 28(128)aciii, 28(033)tv, 28(074)miii	BR 028	Rhynchozoon sp.A	Phidoloporidae	Ascophora	was sp 5, family - Bitectiporidae
031div, 031di	BR 031	Chaperia cervicornis?	Chaperiidae	Anasca	
032aa-1, 032(045)x-I, 032(117)aa-I, 032(117)aa-iii	BR 032	Tubulipora? ?pulchra	Tubuliporidae	Cyclostomata	was sp 18
0360ii, 036Oiii	BR 036	Thairopora cincta?	Tendridae	Anasca	
037(108)si, 037(108)siii, 037(108)sviii	BR 037	Canda ?arachnoides	Candidae	Anasca	C. ?arachnoides
042(139)(2)I, 042(139)acii	BR 042	Smittina maplestoni	Smittinidae	Ascophora	
052(112)ui, 052hii	BR 052	Celleporaria sp c	Lepraliellidae	Ascophora	
054Ii, 54liiii	BR 054	Adeonellopsis ?sulcata	Adeonidae	Ascophora	
056li, 056aa-I, 056(132)aa-1, 056(096)aa-v	BR 056	Disporella pristis	Lichenoporidae	Cyclostomata	was sp 9
062(156)ae-ii, 062(156)aei	BR 062	Arachnopusia unicornis	Arachnopuiidae	Ascophora	
063(080)v-I, 063(080)v-ii, 063(080)v-v	BR 063	Mychoplectra pocula	Electridae	Anasca	
064(73)mi, 064(73)mii, 063(94)Oiv	BR 064	Micropora coriacea	Microporidae	Anasca	
076mi, 076mii	BR 076	Vitrius insignis (Hincks, 1881)	Lacernidae	Ascophora	was sp 3

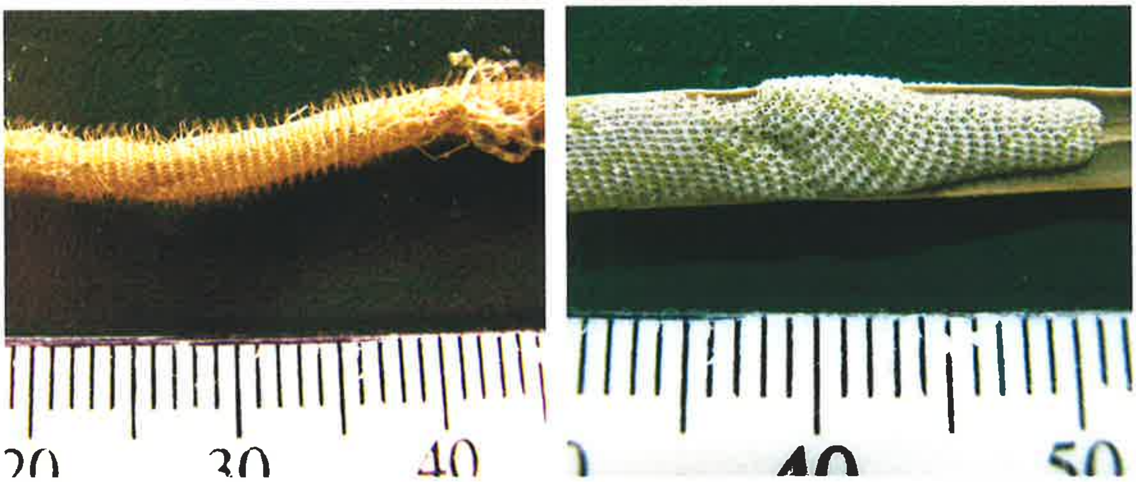
078ni, 078niii	BR 078	Emma sp	Candidae	Anasca	
081(135)abi,abiii,abvi	BR 081	Celleporaria sp d	Lepraliellidae	Ascophora	
083ni, nii	BR 083	Claviporella sp.	Catenicellidae	Ascophora	
084ni, nii	BR 084	Lanceopora? ?obliqua	Lanceoporidae	Ascophora	was sp 19
086niii	BR 086	Hippothoa sp.	Hippothoidae	Ascophora	
087ov,087oiii,087oiv	BR 087	Celleporella delta	Hippothoidae	Ascophora	
088OII, 088Oiii	BR 088	Adeonellopsis? Sp.	Adeonidae	Ascophora	
093oi	BR 093	Fenestrulina sp.a	Microporellidae	Ascophora	ancestrula
103rii, 103riv	BR 103	Scrupocellaria sp.	Scrupocellariidae	Anasca	
104si, 104sii	BR 104	Jellyella sp.	Membraniporidae	Anasca	
107v-ii	BR 107	sp 1	?	Anasca	
111	BR 111	Disporella sp.	Lichenoporidae	Cyclostomata	was sp 11
115(120)v-ii	BR 115	Mucropetralia	Petraliellidae	Ascophora	=BR120, was sp 4
116v-I, 116aa-iii	BR 116	Favosipora?	Densiporidae?	Cyclostomata	was sp 13
119(131)z-I, 119v-ii, 1199131)z-iv	BR 119	Celleporaria sp a	Lepraliellidae	Ascophora	
121v-ii, 121v-vii	BR 121	Dimetopia	Bugulidae	Anasca	
122(166)ah-ii, 122(166)ah-iii	BR 122	Beania quadricornuta	Beaniidae	Anasca	
123x-I, 123x-iii	BR 123	Celleporaria sp b	Lepraliellidae	Ascophora	
124x-I, 124x-ii	BR 124	Cornucopina ?grandis	Bugulidae	Anasca	C. ?tuba
127y-I, 127y-vi	BR 127	Celleporaria sp e	Cellaridae	Anasca	
130z-I, 130z-iv	BR 130	Tubulipora sp. a	Tubuliporidae	Cyclostomata	was sp 15
134abii, 134abix	BR 134	Osthimosia sp. b [or Lagenicella]	Celleporidae	Ascophora	
136aai, 136aaii	BR 136	Tublipora sp.b	Lichenoporidae	Cyclostomata	was sp 16
138aci	BR 138	sp 7	Crisiidae?	Cyclostomata	was sp 17
141aci, 141aciii	BR 141	Microporella ?ciliata	Microporellidae	Ascophora	M. ?orientalis
142aei & 142aeii combined, 142acii	BR 142	Notoplites sp.	Candidae	Anasca	
149ae-I, 149ae-vi	BR 149	Scrupocellaria pusilla	Scrupocellariidae	Anasca	
150ad-I, 150ad-v	BR 150	Aetea sp.	Aeteidae	Anasca	
154ad-iii, 154ad-ii	BR 154	Rhynchozoon sp.B	Phidoloporidae?	Ascophora	was sp 6, Bitectiporidae
165ag-I, 165ag-ii - redo?	BR 165	Cellaria sp	Cellaridae	Anasca	
168ah-I, 168ah-iv	BR 168	sp 2	Flustridae	Anasca	

Table 6.6. Bryozoan species found in close association with seagrass

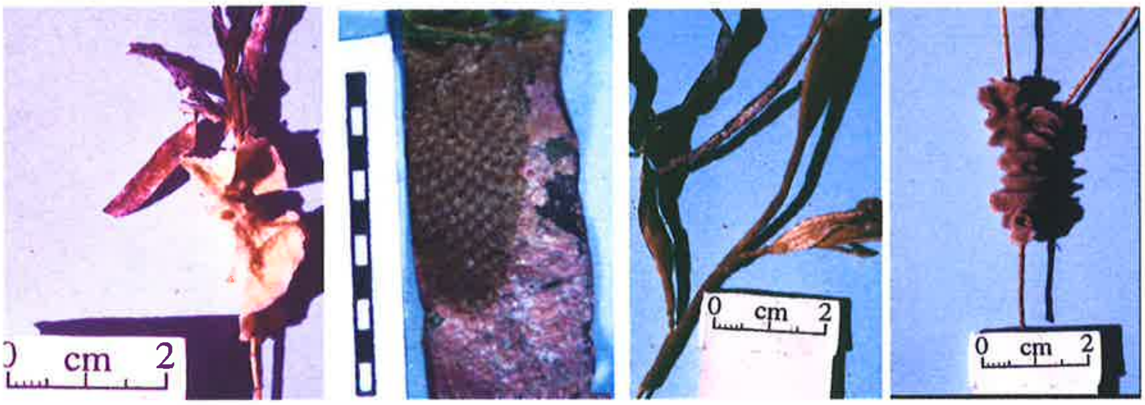
	genera and species	family	suborder	comments
BR 013	Orthoscuticella elegans	Catenicellidae	Ascophora	O. margaritacea?
BR 019	Amathia biseriata	?Vesiculariidae	Ctenostomata	
BR 023	sp 6	Cribrilinidae?	Cribrimorpha	
BR 025	Calloporina ?canaliculata	Microporellidae	Ascophora	
BR 027	Scruparia sp.	Scrupariidae	Anasca	
BR 029	Thairopora sp. b	Thalamoporellidae	Anasca	
BR 030	Membranipora membranacea	Membraniporidae	Anasca	
BR 033	Rhynchozoon sp. C	Phidoloporidae	Ascophora	
BR 034	?Caberea ?helicina	Candidae	Anasca	
BR 035	Didymosella larvalis	Didymosellidae	Ascophora	
BR 038	Costaticella?	Catenicellidae	Ascophora	
BR 039	Claviporella aurita	Catenicellidae	Ascophora	
BR 040	Orthoscuticella margaritacea	Catenicellidae	Ascophora	O. elegans?
BR 041	Gigantopora biturrita	Gigantoporidae	Ascophora	
BR 043	??Amphiblestrum sp.	Calloporidae	Anasca	
BR 047	Thairopora sp. c	Thalamoporellidae	Anasca	
BR 048	Bugula ?neritina	Bugulidae	Anasca	
BR 049	Reteporella sp.	Phidoloporidae	Ascophora	
BR 051	Arachnopusia? Sp. b	Arachnopuiidae	Ascophora	
BR 053	Galeopsis or Osthimosia	Celleporidae	Ascophora	
BR 057	Amphiblestrum or Chaperia or Amastigia?		Anasca	
BR 061	Stylopoma	Schizoporellidae	Ascophora	Fenestrulina?
BR 066	Lanceopora smeatoni	Lanceoporidae	Ascophora	
BR 067	sp 4	?	Anasca	uncalcified?
BR 068	Cyclicopora?	Cyclicoporidae	Ascophora	
BR 069	Cellaria pilosa	Cellaridae	Ascophora	
BR 085	Hincksinoflustra denticulata	Electridae	Anasca	?Electra
BR 089	Buffonellodes sp.	Buffonellodidae	Ascophora	
BR 090	Osthimosia sp.a[or Celleporaria]	Celleporidae	Ascophora	

BR 091	Beania magellanica	Beaniidae	Anasca	
BR 092	Thairopora sp. d	Thalamoporellidae	Anasca	
BR 101	Celleporaria bispinata	Lepraliellidae	Ascophora	
BR 102	Tricellaria sp.	Candidae	Anasca	
BR 105	Triphyllozoon sp.	Phidoloporidae	Ascophora	
BR 106	Triphyllozoon ?moniliferum	Phidoloporidae	Ascophora	
BR 110	Porina ?gracilis	Porinidae	Ascophora	
BR 113	Smittoidea unicornis	Smittinidae	Ascophora	
BR 137	sp 3	Phidoloporidae	Ascophora	was sp 21
BR 151	Aetea ?anguina	Aeteidae	Anasca	A. ?australis
BR 153	Smittoidea sp.	Smittinidae	Ascophora	T. ?sinuatum
BR 159	Cryptosula sp	Cryptosulidae	Ascophora	
BR 160	Crepidacantha kirkpatricki	Crepidacanthidae	Ascophora	
BR 162	Arachnopusia? Sp. a	Arachnopuiidae	Ascophora	
BR 164	Fenestrulina sp.b	Microporellidae	Ascophora	

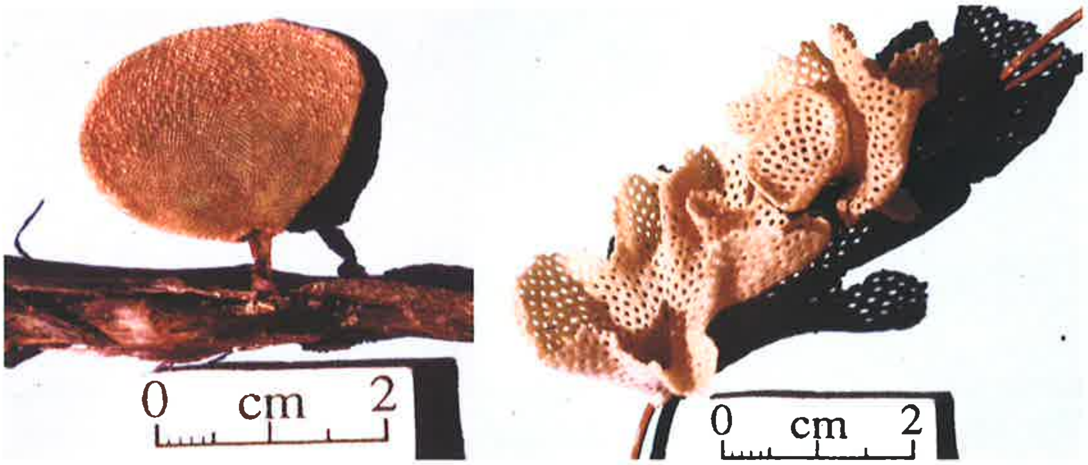
BR number refers to SEM catalogue



(a) *Thairopora* sp. (b) *Heterooecium* sp.



(c) *Celleporaria* sp. (d) *Heteroecium* sp. (e) *Thairopora* sp. (f) *Celleporaria cristata*



(g) *Parmularia reniformis* (h) *Sertella* sp.

Fig. 6.5. Some of the common bryozoans that can use seagrass as their substrate.
(g) has used the sheath area of *Posidonia* for attachment and then adopted an erect growth habit; encrusting sheet-like (d) has used as a substrate a coralline algae that is itself encrusting *Posidonia*; (a), (c), (f) and (h) are attached to *Amphibolis* stems, with (a) adopting a complete encirclement of the stem whilst the others are erect; (b) is attached as an encrusting sheet to an *Amphibolis* blade whilst (e) has encrusted (smothered) both stems and blades.

was the 'delicate branching' type (8 species; Fig. 6.5) and then 'articulated zooidal' type (Fig. 1.4d; 6 species).

Electra pilosa had the greatest amount of carbonate per unit area (89.3 g $CaCO_3/m^2$) compared to other epiphytic bryozoan species. This quantity was recorded from *A. antarctica* stems at West Island deep site. The next largest carbonate abundance from bryozoans, per unit area, were *Diaperoecia australis* generating 78.8 g $CaCO_3/m^2$ and *Mychoplectra pocula* producing 68.9 g $CaCO_3/m^2$. The greatest carbonate abundance from bryozoan species on an individual plant was from *Thairopora cincta* (Fig. 6.5) that was recorded to generate 66.6 g $CaCO_3$/kg of seagrass on *A. griffithii* stems at the West Island shallow site. The next largest carbonate producing bryozoans per individual seagrass plants were *Iodictyum* sp., generating 65.9 g/kg of seagrass (Fig. 1.7b) and *Mychopletra pocula* generating 65.3 g/kg of seagrass.

When bryozoan carbonate abundances were averaged from all sites (Table 6.7), the most important species in terms of carbonate productivity per plant in South Australia was the erect fenestrate *Iodictyum* sp. (21% of all carbonate generated from bryozoan epiphytes), followed by the erect arborescent *Celleporaria* sp. (8%), the encrusting robust sheet *Thairopora cincta* (6.9%) and *Mychopletra pocula* (6.3%). The most common species *Heterooecium* sp. only contributed 1.2% of the total carbonate produced by bryozoans and, 18 species contributed a combined value of less then 1%. The most important carbonate producing bryozoans per unit area were similar species to that per kg of seagrass; *Iodictyum* sp (14.8%), *Thairopora cincta* (13.6%) and *Mychopletra pocula* (10.1%).

The most important carbonate producing morphotype was 'erect fenestrate', which produced on average 26.7 g/m^2 or 44.1 g/kg of seagrass (Table 6.7). This morphotype, however, was relatively uncommon amongst the epiphytic bryozoans, in comparison to the other morphologies, with only 1 epiphytic species recorded falling in to the 'erect fenestrate' category, i.e. *Iodictyum* sp. The 'erect arborescent' and 'encrusting delicate sheet' bryozoans were the next most important epiphytic bryozoan morphology in terms of carbonate production (Table 6.7).

The number of species/genera and morphological types found at each site was analysed to determine whether species diversity was related to particular environments. It was also analysed to see if there was any correlation with geographic location, nutrient concentration, temperature, salinity and sediment composition. West Island (shallow site) has the highest

Table 6.7. Number of epiphytic bryozoans on seagrass samples, grouped according to their morphological type (from Bone and James 1993). Average carbonate production is shown as weight per m^2 of seagrass and per kg of seagrass sampled. found.

Habit	Form	No. of epiphyte species	Av. $CaCO_3$ g/m^2	Av. $CaCO_3$ g/kg of seagrass
Erect	Fenestrate	1	26.7	44.1
	Foliose	1	0.8	3.5
	Flat robust branching	2	7.3	11.4
	Delicate branching	8	1.4	2.0
Erect flexible	Articulated branching	2	1.2	1.1
	Articulated zooidal	6	3.1	2.7
Encrusting	Robust sheet	22	2.0	2.1
	Delicate sheet	17	7.2	5.2
	Delicate branching	2	1.1	2.0

Table 6.8. The distribution, on the different seagrass species and seagrass components, of bryozoan morphotypes and the number of species occurring within each morphotype.

Bryozoan morphotype	*Amphibolis antarctica* blade	*A. antarctica* stem	*A. griffithii* blade	*A. griffithii* stem	*Posidonia angustifolia*	*P. australis*	*P. sinuosa*
1.Erect Fenestrate	0	1	0	0	0	0	0
2. Erect Foliose	1	1	0	0	0	1	2
3. Erect Flat robust branching	0	2	0	1	0	0	0
4. Erect Delicate branching	4	1	1	3	1	3	3
5. Erect Articulated branching	1	2	1	1	1	0	1
6. Erect Articulated zooidal	0	1	0	4	2	0	3
7. Encrusting Robust sheet	9	10	8	12	7	5	10
8. Encusting Delicate sheet	7	7	6	7	4	4	12
9. Encrusting Delicate branching	1	1	1	0	1	2	2
No. species	23	26	17	28	16	15	33
No. species unique to species	1	5	1	8	0	0	8
No. of diff morphologies	6	9	5	6	6	5	7

Table 6.9. The distribution, on the different seagrass species and seagrass components, of bryozoan morphotypes and the number of species occurring within each morphotype.

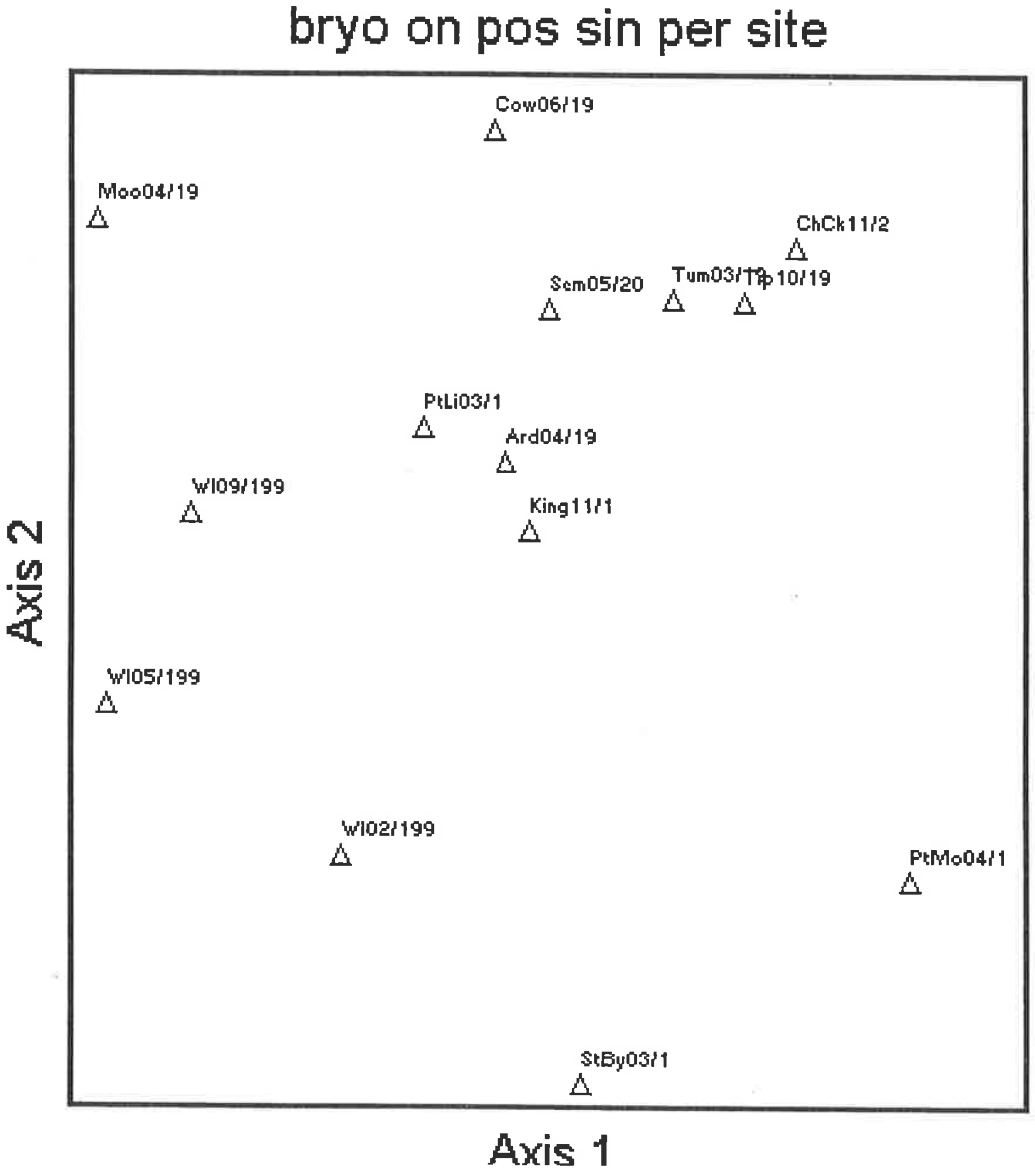
Bryozoan morphotype	*Amphibolis antarctica* blade	*A. antarctica* stem	*A. griffithii* blade	*A. griffithii* stem	*Posidonia angustifolia*	*P. australis*	*P. sinuosa*
1.Erect Fenestrate	0	1	0	0	0	0	0
2. Erect Foliose	1	1	0	0	0	1	2
3. Erect Flat robust branching	0	2	0	1	0	0	0
4. Erect Delicate branching	4	1	1	3	1	3	3
5. Erect Articulated branching	1	2	1	1	1	0	1
6. Erect Articulated zooidal	0	1	0	4	2	0	3
7. Encrusting Robust sheet	9	10	8	12	7	5	10
8. Encusting Delicate sheet	7	7	6	7	4	4	12
9. Encrusting Delicate branching	1	1	1	0	1	2	2
No. species	23	26	17	28	16	15	33
No. species unique to species	1	5	1	8	0	0	8
No. of diff morphologies	6	9	5	6	6	5	7

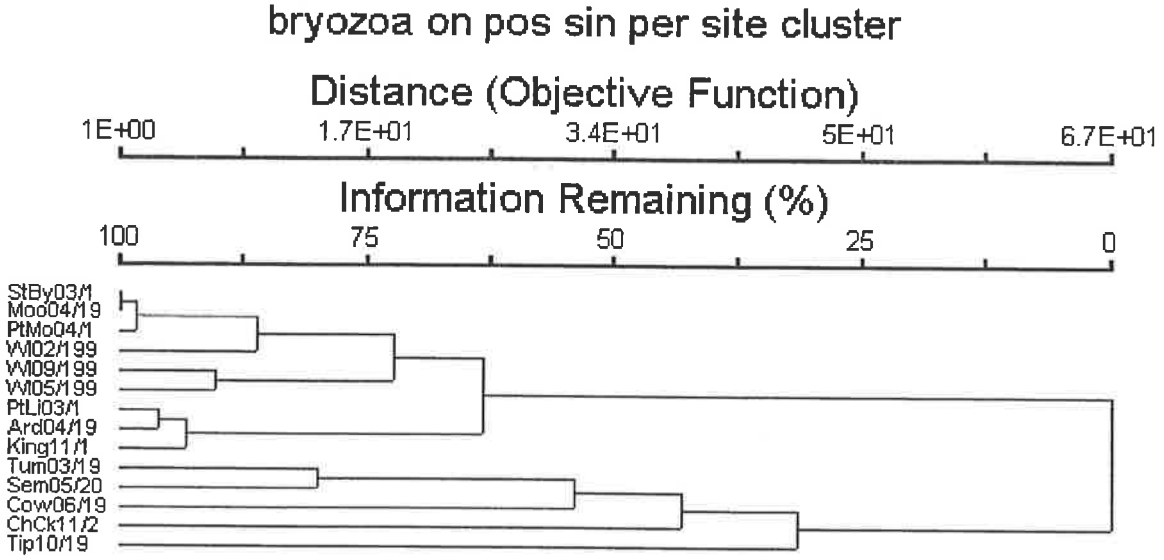
bryozoan diversity of all sites sampled (30 species). Other sites with moderately high bryozoan species diversity included Tiparra Reef (21 species), Cape Hardy (18 species) and West Island deep site (17 species). Cluster analysis of the sample sites with presence/absence data of epiphytic bryozoans produced 3 groups largely based on the diversity of bryozoan species at each site (Table. 6.8). There was, however, no apparent correlation with geographic distribution either with longitude or latitude. Cluster analysis of the bryozoan species at the different sites also indicates that there is also no apparent correlation of bryozoan genera or morphological type with geographic location. Regression analysis of species diversity at each site versus depth, salinity, temperature, nutrient concentration and sediment composition revealed only a weak correlation with depth and water temperature. Species diversity decreased with increasing temperature (best fit with linear regression $r^2 = 0.18$), but increased with increasing depth (best fit with power regression $r^2 = 0.25$. Statistically these values are not significant; nonetheless, the trends were apparent.

Determination of whether certain bryozoan species/genera or morphological types adhere specifically or preferably to specific seagrass species or components of seagrass species further clarifies relationships to specific environments and may have ramifications for identifying the presence of specific seagrass species or specific seagrass morphologies in the rock record. The results indicate that *P. sinuosa* has the highest diversity of bryozoans and *P. australis* has the lowest although this data may be biased by the sample size of each species (Table 6.8). Twenty-three species occurred only on one seagrass species or seagrass component, predominantly *P. sinuosa* and *A. griffithii* stem (Table 6.8). The 'unique' species only occurred at a maximum of 2 sites and hence may reflect local environmental conditions rather than specific relationship to that particular seagrass species.

Of all the bryozoan species recorded, 13 were only found on *P.* seagrass and an additional 8 species were only found on seagrasses with blades (*Posidonia* and *Amphibolis* blades; Table 6.9). Eleven species were only found on *Amphibolis* stems and four species of bryozoan were found on all seagrass species/components of seagrass (Table 6.8). Cluster analysis of bryozoan species presence/absence data on particular seagrass species produces two groups; i) *Amphibolis* stems and ii) *Amphibolis* blades and *Posidonia,* i.e. there appears to be a relationship between the morphological component, of seagrass i.e. stem vs blade, and its bryozoan epiphyte assemblage. The bladed group can further be divided into *Posidonia* and *Amphibolis* suggesting that there are also different bryozoan assemblage found on different fauna.

Fig. 6.6. MDS plot distribution of bryozoa on *Posidonia sinuosa* per site





There does not appear to be any one type of bryozoan morphotype that is more attributed to a particular seagrass type than another. *A. antarctica* stems have the greatest diversity of bryozoan morphotypes, with all 9 morphotypes being found (Table 6.8). All seagrass species and components, however, accommodate a variety of different morphotypes (Table 6.7). It is difficult to statistically attribute typical bryozoan morphotypes to different seagrass species and their components, because of the uneven distribution of species found on each seagrass type and the non-orthogonal sample size of the seagrass species examined. Cluster analysis, however, of the frequency of morphotypes found on the different seagrass types indicate two groups; i) *Amphibolis* stems and *P. sinuosa* and ii) which can be divided in to two further subgroups; a) *A. antarctica* blades and *P. australis* and b) *A. griffithii* blades and *P. angustifolia*. The first group reflects the greater diversity of bryozoa morphotypes, the second group the less diverse, but also the less sampled group.

It has been established that there are differences in the bryozoan assemblages on different seagrass types and species, consequently it is important to examine the data from each seagrass species to ascertain correlations of diversity and species type with geographic position and environmental parameters such as temperature/depth. The results of this analysis are described below.

Posidonia sinuosa

Thirty-three bryozoan species were found on *P. sinuosa*, of which 8 species were unique to the seagrass species. Three of the unique species were found at more than two different locations, the remainder were only found at one. There were no bryozoan species that occurred at all sites where *P. sinuosa* was found. The most common species was *Heterooecium* sp. (9 occurrences out of 12 sites), *Diaperoecia australis* (8 occurrences) and *Tubulipora pulchra* (7 occurrences). Cluster analysis of presence/absence data produced two groups based on bryozoan diversity. The first group (grp1) comprises sites with relatively low species diversity, but no apparent geographical relation. The sites constituting the second group (grp 2) have relatively high bryozoan diversity and all occur within the Spencer Gulf, but do not show increasing or decreasing diversity trends within the gulf. There is no correlation with morphological structures of the bryozoans. Regression analysis of species diversity with environmental parameters indicates weak relationships with depth (positive correlation $r^2 = 0.3$), salinity (negative correlation $r^2 = 0.29$), water temperature (positive correlation $r^2 = 0.29$). Bryozoans on *P. sinuosa* produced wide ranges of $CaCO_3$ abundance. The single most abundant carbonate producing bryozoan at any one location was *Heterooecium* sp. that generated 20.7 g $CaCO_3$/kg of seagrass at Cowlers Landing. The most important bryozoans, however, in terms of carbonate abundance of carbonate averaged over the entire study region were *Thairopora* sp. a and *Parasmittina unispinosa*, producing 6.3 and 5.5 g $CaCO_3$ kg of seagrass respectively.

Posidonia angustifolia

The most common bryozoan species on *P. angustifolia* was *Thairopora* sp, found at 4 of the 5 sites sampled, followed by *Heterooecium* sp. found at 3 sites. Cluster analysis produced 3 groups; i) Dutton and West Island; ii) Marino, Normanville and Cape Jaffa; and iii) Torrens. The Torrens site was distinctive because of the high diversity of species (12 species), compared to the other sites that had a maximum of 4 species. The sites were largely divided by the number of species present and do not indicate geographical trends. Regression analysis indicated a weakly significant correlation ($r^2 = 0.23$) between increased depth and increased species diversity. The data available does not adequately allow further correlations to be proven or disproven. The greatest average abundance of carbonate produced from bryozoans on *P. angustifolia* was from *Tubulipora pulchra* (8.7 g $CaCO_3$/kg of seagrass), followed by *Thairopora* sp. a (6.4 g $CaCO_3$/kg of seagrass). *T. pulchra* also produced the single most abundant amount of carbonate from any bryozoan on *P. angustifolia* (17.5 g $CaCO_3$/kg of seagrass) at the Torrens site.

Posidonia australis

The most common bryozoan species on *P. australis* was *Heterooecium* sp. and *Hesychoxenia praelonga*, occurring at 7 of the 8 locations. Three of these locations are from the Chinaman Creek region where the bryozoan species on *P. australis* were significantly different enough to be separated on the presence/absence cluster analysis dendogram (Figure 6.6). Cluster analysis shows no correlation to geographic location. Regression analysis indicated a weak correlation of increasing diversity with increasing depth ($r^2 = 2.5$), and a good correlation with increasing temperature ($r^2 = 0.63$) and increasing salinity ($r^2 = 0.46$). The most important bryozoans in terms of carbonate abundance on *P. australis* were *Scrupocellaria pusilla* and an unidentified species 7 (av. 8.7 g $CaCO_3$/kg of seagrass each), followed by *Caberea boryi* (av. 6.7 g $CaCO_3$/kg of seagrass). The single largest amount of carbonate produced from a single bryozoan was from *S. pusilla* at Chinaman Creek (site 3) producing 17.4 g $CaCO_3$/kg of seagrass.

Amphibolis antarctica blades

There were no bryozoans that were found at all sites on *A. antarctica* blades, but the most common species are *Thairopora* sp. (6 sites out of 9), *Heterooecium* sp. (5 sites), and

Disporella pristis (5 sites). Clustering showed West Island (9/99deep) as an isolated site, otherwise cluster analysis and regression showed no correlation with geographic location or environmental parameters. The most important carbonate-producing species was *Thairopora* sp. *a*, producing on average 6.9 g $CaCO_3$/kg of seagrass and a maximum of 15.6 g $CaCO_3$/kg of seagrass at Normanville. Other important abundances of carbonate were derived from *Rhynchozoon* sp. a and *Chaperia cervicornis* (4.5 and 3.7 g $CaCO_3$/kg of seagrass, respectively).

Amphibolis antarctica stems

A. antarctica blades and stems share 10 bryozoan species, although finding the species on the blades does not necessarily mean finding it on the stem as well, and vice versa, although this was frequently the case. No species were found at all sites, but the most common species was *Mychoplectra pocula* (6 out of 8 sites), *Catenicella elegans* (4 sites) and *Crisia acropora* (4 sites). Cluster analysis defines two groups split by species diversity, group 1 having the higher species diversity. There were no trends with geographical location and regression analysis showed no correlation with any of the environmental parameters measured. Carbonate abundance from bryozoans was high on *A. antarctica* stems with 5 species (*Iodictyum* sp., *Adeonellopsis sulcata, Thairopora cincta, Celleporaria* sp. d, *Adeonellopsis* sp. and *Celleporaria cristata),* with all of these producing, on average, over 10g $CaCO_3$/kg of seagrass at each site where they occurred. The abundance of carbonate both on average and at an isolated site, was from *Iodictyum* sp., producing on average 44 g $CaCO_3$/kg of seagrass, with a peak abundance of 65.9 g $CaCO_3$/kg of seagrass. Several other species were also important in terms of carbonate producers because of their relatively common distribution through the study region, e.g. *Electra pilosa* and *Mychoplectra pocula.*

Amphibolis griffithii blades & stems

Only 3 sites were found which had *A. griffithii* and hence, statistical analysis was not suitable. The number of different bryozoans species on *A. griffithii* blades at West Island was the greatest (6-13 species) and Marino and Normanville had 1 & 3 species, respectively. No species were found consistently across all three sites, except for *Mychoplectra pocula.* The highest average abundance of carbonate produced by bryozoans was 2.1 g $CaCO_3$/kg of seagrass from *Tublipora pulchra* and *Disporella* sp., the latter also producing the greatest individual abundance at one site of 5.4 g $CaCO_3$/kg of seagrass. The diversity of bryozoans on *A. griffithii* stems was high at West Island where 13-21 species were found. Eight out of 26 species were found on both stems and blades of *A. griffithii*. Only two species of bryozoans produced on average over 10g $CaCO_3$/kg of seagrass, namely *Thairopora cincta* and *Mychoplectra pocula* (31.1 and 23.7 g $CaCO_3$/kg of seagrass, respectively).

6.3.3 **Foraminifers** (see CDs for additional data)

Foraminifers occurred at all sites and on all seagrass species and generated 0.1 to 33.6% of all epiphytic carbonate (Fig. 6.3, Table 6.4). Foraminifers were present on 939 samples out of the 1544 blades and stems analysed. The number of epiphytic foraminifer species found was 30, from 18 genera, plus an additional 23 species that were found in close association (Table 6.10). The majority of the species were recognised to be 'clinging' to the seagrass via filamentous attachments (Fig. 1.7c), followed by the adhesive and encrusting type. The only species that was categorised as 'encrusting' was *Nubecularia* sp. (Fig. 6.7), although some discorbids show evidence for a calcareous lamina (Fig. 6.7).

The maximum abundances of carbonate recorded from epiphytic foraminifers is 27.6 g $CaCO_3/m^2$ or 238.2 g $CaCO_3$/kg of seagrass (average 1g $CaCO_3/m^2$ or 4 g $CaCO_3$/kg of seagrass). Of this, 45% was derived from *Discorbis dimidiatus* and 33% from *Nubecularia* sp. *D. dimidiatus* was found on all seagrass species examined and also was the only species to occur at every site sampled. The second most commonly distributed species was *Elphidium* sp. (*E. crispum* and *E. silvestrii* combined) and was found at 22 sites (including 3 seasons from West Island). All but 4 species of foraminifers were found at more then one site. *P. sinuosa* and *P. australis* appear to be the favoured substrate for high foraminifer abundances (Table 6.1, Figs 6.1-4) although 1-way ANOVA indicate the abundances are not significantly different between seagrass species. Semaphore had the highest abundance of carbonate from foraminifers (31%). The next sites with the most abundant foraminifers were Moonta Bay (18%) and Streaky Bay (9.8%). Abundance of carbonate from foraminifers does not appear to have geographical correlation, nor does it have any significant correlation with depth, salinity and temperature. Nutrient data is inadequate to identify any relationships, but the correlation between extremely high nutrient levels, and high $CaCO_3$ abundance of foraminifers from Semaphore should not be overlooked (Table 3.7).

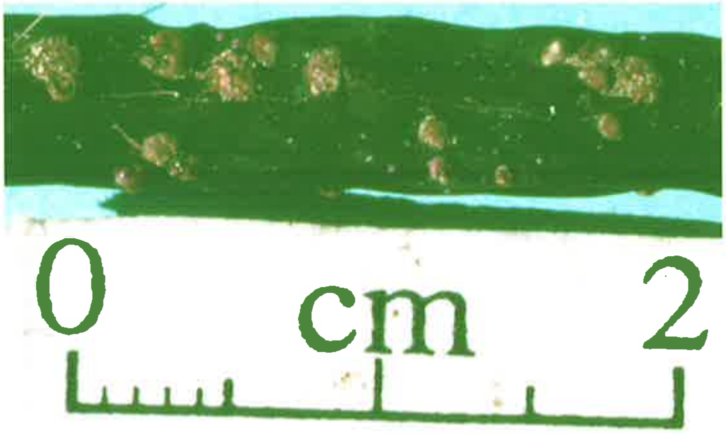
Cluster analysis of the sites using the presence/absence data of foraminifer species produces two distinct groups that had no clear geographical distribution, whether from east to west or within gulfs. Cluster analysis of the presence/absence data of foraminifer species from different sites also produces two main groups, predominantly clustered by the frequency of occurrence on the different seagrass species/ components. Group 1 consists of those species that occur on 3 or more of the different seagrass species and those in group 2 occur on two or

Table 6.10. Foraminifers identified, either securely or loosely attached, to seagrasses.

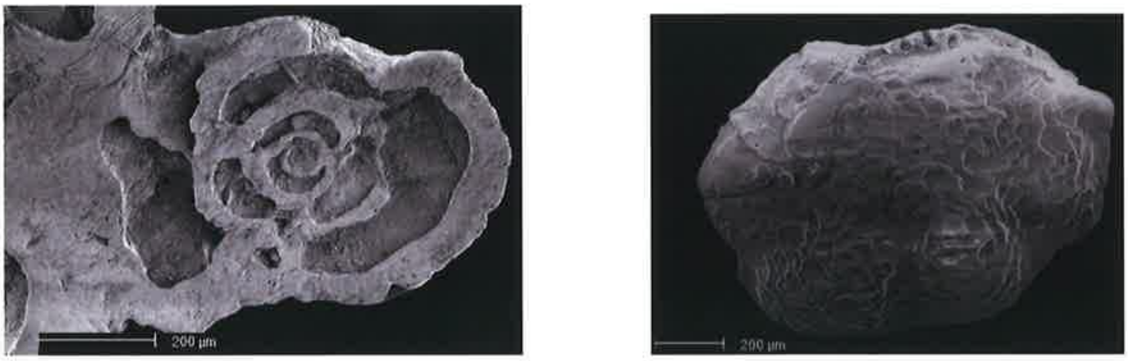
	genera/species	family	finder	super group	SEM images	supergroups	morphotype
FOR 01	Discorbis dimidiatus	Discorbidae Ehrenberg 1838			01AI,01cii,01aiv,01ii	discorbids	ii
FOR 02	Discopulvinulina sp.	Discorbinellidae			02ai, 02civ	discorbids	ii
FOR 03	Acervulina inhaerens	Acervulinidae Schultze 1854	Schulze 1854		03ai, 3aii,3i	planorbulinids	ii
FOR 04	Planorbulina mediterranensis	Planorbulinidae Schwager 1877	d'Orbigny, 1826		3di	planorbulinids	ii
FOR 07	Triloculina striatotrigonula	Hauerinidae Schwager 1876			07iii	miliolids	I
FOR 08	Nubecularia lucifuga	Nubeculariidae Jones 1875	DeFrance, 1820		08dbii,08dai	miliolids	iii
For 09	Nubecularia? Sp	Nubeculariidae Jones 1875			08ai, 08dci	miliolids	iii
FOR 10	Triloculina inflata	Hauerinidae	d'Orbigny		10fi	miliolids	ii
FOR 11	Triloculina oblonga	Hauerinidae	Montagu, 1803		11III	miliolids	I
FOR 12	Peneroplis pertusus	Peneroplidae Schultze 1854	Forskal, 1775	Miliolona	12di	miliolids	I
FOR 14	Scutuloris parri	Hauerinidae	Collins		14ai	miliolids	I
FOR 16	Spiroculina antillarium	Spiroloculinidae Wiesner	d'Orbigny, 1839	Miliolona	16ci, 16-42cii	miliolids	I
FOR 17	Bolivina striatula	Bolivinidae Glaessner 1937	Cushman	Rotaliina	17iii	buliminids	I
FOR 18	Miliolinella labiosa	Hauerinidae	d'Orbigny, 1839	Miliolona	18a-1, 18ii	miliolids	I
FOR 18	Miliolinella subrounda	Hauerinidae	Montagu, 1803	Miliolona	18-4, 18a1	miliolids	I
FOR 19	Spiroculina tricosta	Spiroloculinidae		Miliolona	19ai	miliolids	I
FOR 21	Quinqueloculina boueana	Hauerinidae	d'Orbigny	Miliolona	21i	miliolids	I
FOR 21	Quinqueloculina sp.C	Hauerinidae		Miliolona	21ai	miliolids	I
FOR 24	Globerina sp.	Globigerinidae Carpenter, Parker and Jones 1862			24ai	planktonics	planktonic
FOR 26	Vertebralina striata	Fischerinidae Millett 1898	d'Orbigny, 1826	Miliolona	26di, 26diii	cornuspirids	I
FOR 27	Elphidium articulatum = E. excavatum	Elphidiidae Galloway 1933	d'Orbigny &Terqueum sensu lato	Rotaliina	27ai	elphidiids	I
FOR 29	Planulina biconcavus	Planulinidae Bermúdez 1952	Jones & Parker, 1862		29ai	discorbids	I
For 30	Oolina globosa	Lagenidae Reuss 1862	Montague, 1803		30aii	lagenids	I
FOR 30	Oolina sp.	Lagenidae			30ai	lagenids	I
FOR 33	Quinqueloculina seminulina	Hauerinidae	Linne, 1767	Miliolona	33ii	miliolids	I
FOR 33	Quinqueloculina sp. A	Hauerinidae		Miliolona	33cii	miliolids	I
FOR 34	Quinqueloculina cf. cultrata	Hauerinidae	Brady	Miliolona	34ai	miliolids	

FOR 35	Annulopatellina annularis	Annulopatellinidae Loeblich and Tappan 1964	Parker & Jones, 1860		35ai, 35fi, 35fii	discorbids	ii
FOR 36	Elphidium crispum	Elphidiidae	Linne, 1758	Rotaliina	36II	discorbids	I
FOR 36	Elphidium silvestrii	Elphidiidae		Rotaliina	36i	elphidiids	I
FOR 38	Elphidium fichtellianum	Elphidiidae	d'Orbigny	Rotaliina	38cii, 36civ	elphidiids	I
FOR 40	Discorbis sp.	Discorbidae			40i, 40iii	elphidiids	ii
FOR 41	Rosalina sp.	Discorbidae			41i	discorbids	ii
FOR 43	Bolivina pseudoplicata	Bolivinidae	Heron-Allen & Earland	Rotaliina	43cii	discorbids	I?
FOR 44	Annulopatellina sp.	Annulopatellinidae			44ci, 44iii	buliminids	ii
FOR 45	Quinqueloculina sp D	Hauerinidae		Miliolona	45ci	miliolids	I
FOR 46	Quinqueloculina bradyana	Hauerinidae	Cushman, 1910	Miliolona	46i	miliolids	I
FOR 46	Quinqueloculina subpolygona	Hauerinidae	Parr, 1945	Miliolona	46ci	miliolids	I
FOR 48	Discorbina sp.	Discorbidae Ehrenberg 1838			48ci	discorbids	ii
FOR 50	Acervulina sp. B	Acervulinidae Schultze 1854			50ci	planorbulinids	ii
FOR 53	unknown				53ci		I?
FOR 54	Fissurina marginata	Spirillinidae	Walker & Boys, 1784		54ci	lagenids	I?
FOR 55	Fissurina lucida	Spirillinidae	Williamson, 1848		55ii	lagenids	I?
FOR 55	Fissurina marginatoperforata	Spirillinidae Reuss and Fritsch 1861	Seguenza, 1880		55ci	lagenids	I?
FOR 56	Cornuspira sp.	Cornuspiridae Schultze 1854		Miliolina	56ci	cornuspirids	I
FOR 57	Renssella spinulosa	Reussellidae Cushman 1933	Reuss		57cii	buliminids	I?
FOR 60	Pileolina zealandica	Glabratellidae Loeblich and Tappan 1964			60i, 60ii	discorbids	ii
FOR 61	Penerolplis planatus	Peneroplidae Schultze 1854	Fixgrwk & Moll, 1978	Miliolona	61di	miliolids	I?
FOR 62	Bolivinella folium	Bolivinidae Jones 1875	Parker & Jones, 1860	Rotaliina	62fi	buliminids	I
FOR 63	unknown	Saccamina			63iii	textulariids (or agglutinated	I
FOR 64	Textularia pseudogramen	Textulariidae Ehrenberg 1838	Chapman & Parr, 1937		64i	textulariids (or agglutinated	ii
FOR 65	Haplophragmoides australensis	Haplophragmoididae Maync 1952	Albani, 1978		65i	textulariids (or agglutinated	ii
FOR 66	Rectobolivina sp.	Siphogenerinoididae Saidova 1981			66i	buliminids	?

Elphidium sp.

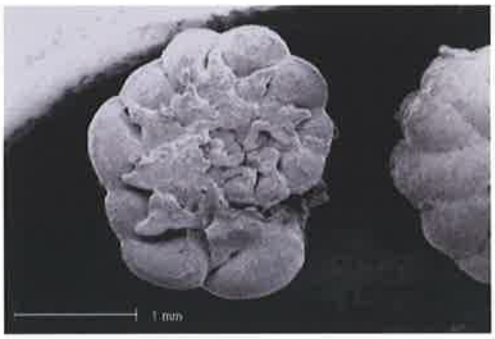


Discorbis sp.

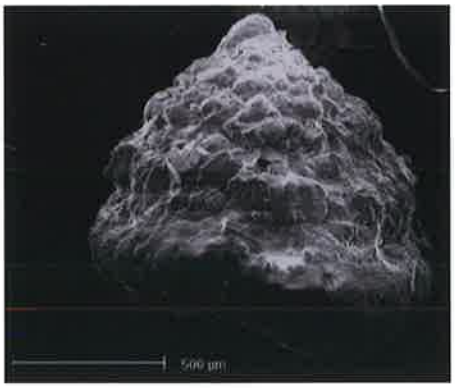


Nubecularia lucifuga

Discorbis dimidiatus



Discorbis sp.



Unidentified foraminifer

Peneropolis sp.

Fig. 6.7. Various foraminifers that can either attach securely or loosely to seagrasses. Colour images show secure attachment to *Posidonia*. *Nubecularia* is almost always attached.

less. Stansbury and Ardrossan had the greatest species diversity (12 foraminifer species), followed by Tumby Bay, Cowlers Landing and Chinaman Creek (1), which each had 11 species. The grouping shows no relationship with temperature, salinity, depth, nutrient concentration or sediment composition.

Cluster analysis of the seagrass species/components using presence/absence of foraminifers species reveals that no seagrass genera, species or component had a unique foraminifer assemblage, although some species were only found on certain species as already described. The most similar assemblage was found on *A. griffithii* blades and stems. There was also no clear correlation between foraminifer assemblages and morphological structure of the plant, i.e. both stems and blades as well as *Posidonia* and *Amphibolis* were found in the same groups. Cluster analysis of the presence/absence of foraminifera species on the different seagrass components produces two main groups. Group 2 consists of the, apparently, more specialised foraminifers which are either found on stems or blades only, or on certain species only – as described above.

The most frequently occurring foraminifera species, in terms of their distribution on different seagrass species are *Discorbis dimidiatus, Nubecularia lucifuga, Nubecularia* sp., and *Elphidium* sp (*E. crispum* & *E. silvestrii* combined), which occur on all seagrass species and compoenents. *Spiroculina antillarium* and an unidentified species of the family Saccamina were only found on *Posidonia* blades. *Quinqueloculina bradyana* and *Q. subpolygona* were only found on *Amphibolis* blades. In addition *Quinquelocuina seminulin* and *another Quinqueloculina* (sp. a) were only found on bladed seagrass (i.e. not on *Amphibolis* stems). *Miliolinella labiosa* and *Elphidium articulatum* were only found on *Amphibolis* stems. *Elphidium fichtellianum* was only found on *Amphibolis antarctica* blades, *Triloculina striatotrigonula* and *Quinquelocuina* sp. D were only found on *A. antarctica* stems, and *Bolivinella folium* was only found on *P. sinuosa*, but each only occurred at one site.

6.3.4 Ostracods (see CDs for additional data)

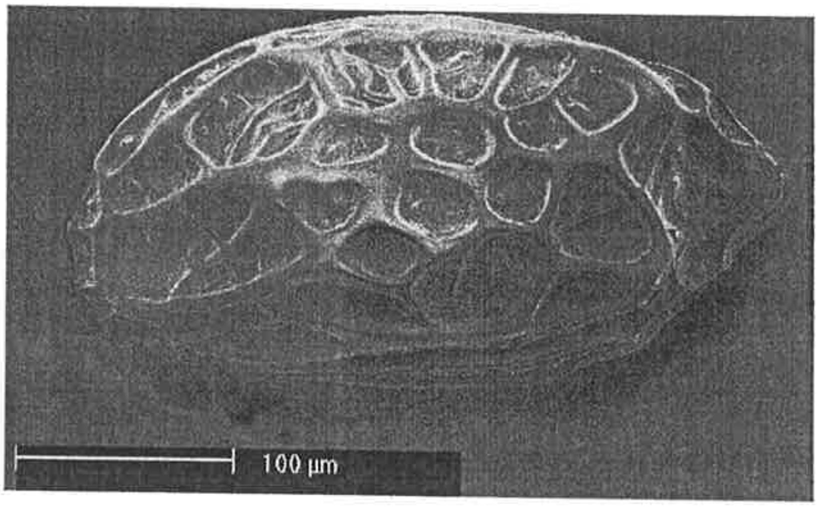
Ostracods occurred on 48 samples from 1544 blades and stems analysed. Fourteen ostracod species (Table 6.11) were found at 15 sites on all seagrass species and components examined. An additional 38 (Table 6.12) were picked from the sediment that detached from the seagrass. Ostracods were insignificant in terms of their contribution to the epiphytic sediment produced (<0.04%; Figs 6.1-4), but particular species may be useful as environmental indictors. *Xestolibris* (Fig. 6.8) was the most common genera found at most sites and on most seagrass

Table 6.11. Ostracods found attached to seagrass.

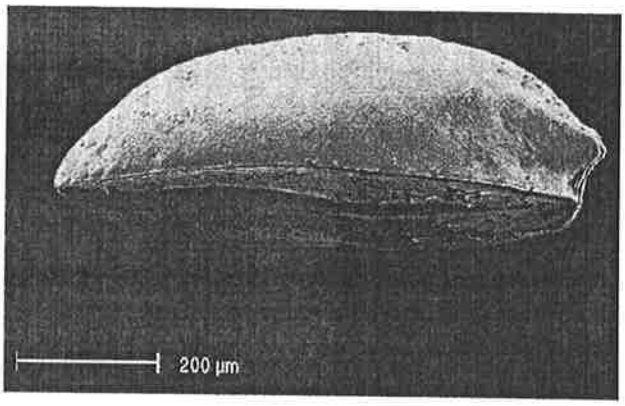
spec id	species	SEM
Ost 01	Leptocythere sp.	ost01b
Ost 03	Xextoleberis trigrina	ost03di, 03iii, 03bi
Ost 07	Paradoxostoma sp. A	ost07i, 07ii
Ost 10	Loxochoncha australis	ost10i 10ii
Ost 13	Paradoxostoma albaniense	ost13-I
Ost 15	Paranesidea sp. A	ost15i, 15fi
Ost 17	Paranesidea romi	ost17i, 17ii
OSt 18	Austroparadoxostoma ventromarginale	Ost18vi, 18di, 18diii, 18i, 18div
Ost 20	Unid B	ost20di
Ost 25	Xstolebris sp. A	ost25i
ost 27	Parakrithella australis	ost27di
ost 30	Paradoxostoma ?horrochensis	ost30i
ost 34	Hemicytherura hartmanni	ost34i
ost 39	Xestoleberis saxumchinensis	ost39iv, 39iii

Table 6.12. Ostracods found in the sediment that was adhering to seagrass samples.

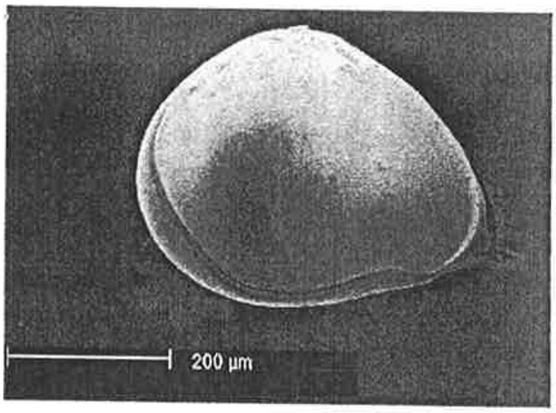
spec id	species	SEM
OSt 18	Austroparadoxostoma ventromarginale	0st18vi, 18di, 18diii, 18i, 18div
Ost 01	Leptocythere sp.	ost01b
Ost 03	Xextoleberis trigrina	ost03di, 03iii, 03bi
Ost 07	Paradoxostoma sp. A	ost07i, 07ii
Ost 10	Loxochoncha australis	ost10i 10ii
Ost 13	Paradoxostoma albaniense	ost13-I
Ost 15	Paranesidea sp. A	ost15i, 15fi
Ost 17	Paranesidea romi	ost17i, 17ii
Ost 20	Unid B	ost20di
Ost 25	Xstolebris sp. A	ost25i
ost 27	Parakrithella australis	ost27di
ost 30	Paradoxostoma ?horrochensis	ost30i
ost 34	Hemicytherura hartmanni	ost34i
ost 39	Xestoleberis saxumchinensis	ost39iv, 39iii
Ost 02	Trachyleberis (Ponticoccytheresis) militaris	
Ost 04	unid A	
Ost 06	Leptocythere gravecostata	
Ost 08	Cytherellea sp. A	
Ost 09	Callistocythere bucethomi	
Ost 11	Parabrithella australis	
Ost 12	Callistocythere dorsotuberculata paucicostata	
Ost 14	Papillatabairdia elongata	
OSt 19	Loxoconcha cf. trita	
ost 22	Xestolebris cedunaensis	
ost 23	Psropontocypris sp. A	
ost 24	Cytherella sp. B	
ost 29	Trachyleberis (“Ponticocythereis”) jervisbayensis	
ost 31	Loxoconchella pulchra	
ost 32	Loxoconcha sp.	
ost 33	Polycope sp. A	
ost 35	Keijcyoidea keiji	
ost 36	Cytherrella ?dromedaria	
ost 37	Cytherella sp. C	
ost 38	Cytherelloidea goodbeachensistherella	
Ost 40	Mutilus pumilus	
Ost 43	?Xestolebris sp. B	
ost 44	Cytherella sp. D	
ost 45	Foreoleberis brevirostris	
ost 48	?McKenzjeartia portjacksonensis	
ost 49	Propontocypris ?onslowensis	
ost 50	unid c	
ost 51	unid d	
ost 52	Aurila jonesi	
ost 53	unid e	
ost 54	Microcytherura ?peterroyi	
ost 55	Callistocythere keiji	
ost 56	? Tasmomocypris dietmarkeyseri	
ost 57	Semicytherura cryptifera	
ost 58	unid f	
ost 59	Cytherella sp. E	
ost 60	?Propontcypris albaniensis	
ost 61	Cytheralison cosmetica	



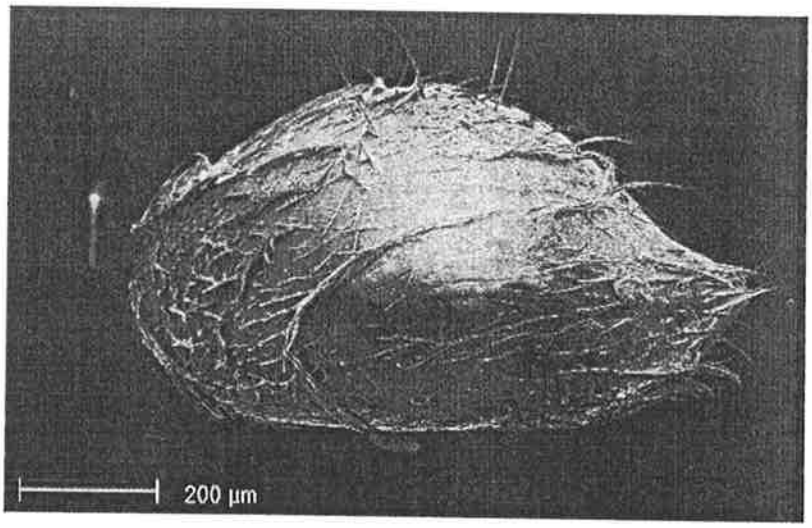
Hemicytherura hartmanni



Austroparadoxostoma ventromarginale



Xestrolobris sp. A



Paranesidea sp. A

Fig. 6.8. Ostraocods commonly associated with seagrasses.

species, although it was not clear whether they physically attached to the blades or not. *Austroporadoxostoma ventromarginale* (Fig. 6.8), an unidentified species, *Paranesidea* sp. a, *Hemicytherura hartmanni* (Fig. 6.8), and *Mutilus pumilus* all showed close relationships with the seagrass. *A. ventromarginale* has a flat base making it suitable for the seagrass substrate. *H. hartmanni* and *Paranesidea* sp. a were commonly found and, on occasion, were found attached to the seagrass via filamentous threads protruding from the posterior end of the ostracod (Fig. 6.8). Most of the other species were only observed entangled in amongst algae, sponges, ascidians and the agglutinated sediment of some species of foraminifer. No ostracod species showed specific relationship with any seagrass species type. There were not enough ostracods sampled to warrant statistical analysis of parameters controlling distribution.

6.3.5 **Serpulids and spirorbids** (see CDs for additional data)

Spirorbids occurred on 741 of the 1544 blades and stems examined and serpulids were found on 73 of the blades and stems. Eleven spirorbid (Fig. 1.7e) and two serpulid (Fig. 1.7d) distinct tube shapes were defined for identification purposes (Table 2.9). Serpulids did not produce significant quantities of carbonate compared to the other epiphytic genera (Table 6.3). Spirorbids produce significant abundances (>5%) on all by *Amphibolis* stems. Spirorbids were most abundant on *A. antarctica* blades and *P. sinuosa* (14% each).

Cluster analysis indicated that species of spirorbid had no particular association with certain seagrass species or components. The low diversity of spirorbids on *A. griffithii* stems and blades may reflect the lower number of samples examined. Clustering of sites with presence/absence of spirorbid species shows no correlation with geographic position, temperature, salinity, depth, and nutrient concentration.

6.3.6 **Bivalves** (see CDs for additional data)

Bivalves occurred on 47 of 1544 blades and stems examined. Five species were found, although it was not possible to identify all the species because most are in their juvenile/spat form. The bivalves identified attach themselves to the seagrass via byssal filaments. Out of the bivalves an unidentified species, sp. 2, was the most common, followed by *Electoma georgina*, which was commonly found in more saline conditions.

6.3.7 **Other epiphytes** (see CDs for additional data)

The only other calcareous epiphyte worthy of note was an organism that was preliminar~~y~~rily identified as an egg case. SEMs reveal a series of calcareous plates overlapping each other (similar to coccolith plates) in multiple mounds. They are covered by an organic sheet, which binds them to the surface. On occasion they were found in such abundance that they covered significant portions of the blades.

6.4 BIODIVERSITY AND RELATIVE ABUNDANCES

Coralline algae, the dominant calcareous epiphyte in terms of both frequency and abundance (53.6%), were not significantly species-rich (8 genera) in comparison to foraminifers and bryozoans (30 species and 61 species respectively). The latter, combined, produced a significant quantity of the $CaCO_3$ (~30%) produced. The remainder percentage of carbonate producing epiphytes consisted of spirorbids (8%, 11 morphological types recognised), bivalves (0.3%, 5 species), serpulids (2 morphological types recognised) and ostracods (<0.1%, 14 species). There are no known directly comparable studies. Table 6.12 summarises some data that are relevant to this project.

Sim (1991) identified coralline algae species, comparable to this study, growing on *A. antarctica*. Sim (1991) also identified that articulated coralline species were the dominant type of coralline algae, which was also the findings for this study from *Amphibolis* sp. plants. Encrusting corallines were, however, dominant in terms of abundance and frequency. Bryozoan species-richness on seagrass is also similar in other studies ranging from 36 to 90 species (Hayward 1974). The low number of species (6) found by Lethridge *et al.* (1988), is probably due to their small sample size. No known study identifies epiphyte foraminifer or ostracod species-richness, but the number of spirorbids and bivalves found during this study was similar to the findings of Lethridge *et al.* (1988) (1 spirorbid) and Jernakoff & Nielsen (1998) (5 bivalves).

Species richness in seagrass beds is comparably higher to those of surrounding sandy sea-floor environments. It is possible, therefore, to differentiate seagrass bed areas from non-seagrass areas. Identification of seagrass areas from other environmental habitats such as rock beds can also be done by species assemblage differences. However, it is more complex to try and identify seagrass areas from other ecologically-rich niches in similar conditions which also leave no trace, or very little trace, of their original substrate, e.g. algal beds, sponge beds, etc.

The significance of species richness is several fold. The presence of seagrass increases species richness. Consequently, examples within the rock record of high species richness may indicate the presence of something else other than bare sand, i.e. it may have been an area of seagrass. The particular morphology of the species is important as seagrass supplies a

Table 6.13. Species richness in other studies.

author	Phylum	No. sp.	seagrass type	location	notes
Gautier 1962 *in* Hayward 1974	bryozoans	72			
Harmelin 1973, *in* Hayward 1974	bryozoans	90			
Hayward (1974)	bryozoans	36	*P. oceanica*	Chios, Agean Sea	encrusting predominant, number of erect as well. 1 species specific
Ducker *et al* (1977)	invertebrates	20	*Amphibolis antarctica*	at Wilsons Promontory, Victoria	116 algal species
Harlin (1980)	invertebrates	178	*Amphibolis, cymodocea, Diplanthera, Enhalus, Halophila, Posidonia, Syringodium, Thalassia, Phyllospadix* and *Zostera*	different parts of the world	summary paper included gastropods, amphipods, isopods which would not fall under the definition of an epiphyte for this study
Lethridge, Borowitzka & Benjamin 1988	algae bryozoans hydroids spirobids gastropod	161 8 6 1 1	*Amphibolis* stems 140, blades 21 stems 6, blades 2 stems 2, blades 4 stems 1, blades 1 stems 1		
Borowitzka *et al* 1990	sessile invertebrates	40. –	*Amphibolis griffithii*	Penguin Island, Seven Mile beach, Two Peoples bay –W.A	number of species greater on stems

greater surface area for colonisation/settlement, e.g. encrusters. Nevertheless, other environments that would basically be bare sand can still be highly enriched with organisms, e.g. rhodolith pavements, boulder encrusters, kelp environments, coral reefs etc., but it is the species assemblage that supplies the clues. It has been shown by several studies that species richness is much higher within seagrass beds than the surrounding area. However, it is possible to identify seagrass regions rather than kelp beds faunas or other ecosytsems from the assemblage of calcareous epiphytes preserved. It is fairly obvious that seagrass beds are significantly different from coral reefs for example, although coral reefs also have coralline algae and even bryozoans in high quantities, but there is a difference in the assemblage reflecting the structural difference in the substrate.

There are numerous other studies that have presented data on epiphytes, but these have often not differentiated between calcareous and non-calcareous species. Some of those that definitely include calcareous epiphytes are:

- Borowitzka & Benjamin (1988); 140 species found, but most rare – the coralline algae are usually the dominant algal epiphytes – *Metagoniolithon, Haliptylon, Hypnea, Polysiphonia, Champia, Gloiosaccion, Laurencia;*
- Holmes (1997); bryozoans made the greatest (61% and 81%) contribution to species richness at several islands (Green Island and Cape Tribulation);
- Trautman & Borowitzka (1999); there are approximately 3 times as many epiphytic algal species as invertebrate species.

Others are less specific in the composition of the species, i.e. are they calcareous? Many of them, however, could well include calcareous epiphytes:

- Kendrick *et a.l* (1988) described 66 species of macroalgae on stems of *Amphibolis antarctica* at Shark Bay, W.A.
- Ducker *et al.* (1977) identified 116 species of epiphytic algae on *Amphibolis antarctica* at Wilsons Promontory, Victoria – also recognised 20 species of epiphytic invertebrates.
- Lavery *et al.* (2000); 97 taxa of epiphyte algae, of which 92 found on *Amphibolis griffithii* (25 uniquely), 71 on *Posidonia coriacea* (4 uniquely), and 34 *Heterozostera.*
- Ballantine & Humm (1975 *in* Harlin 1980); 66 species of benthic algae on *T. testuinum, H. wrightii, Syringodium filiforme* and *Halophilia engelmannii* combined.
- Ducker *et al.* (1977); 105 algal species on *Amphibolis antarctica* and *A. griffithii.*
- Harlin (1980) summarises previous epiphyte findings: microalgae 152 species, macroalgae 366 species, 178 invertebrate epiphytes. These from *Amphibolis cymodocea, Diplanthera, Enhalus, Halophila, Posidonia, Syringodium, Thalassia, Phyllospadix* and *Zostera* from different parts of the world and different environment. The invertebrates

listed included gastropods, amphipods and isopods which would not fall under the definition of an epiphyte for this study.

- Jernakoff & Nielsen (1998); *Posidonia* 45 algal species epiphytes. *Amphibolis* 83 species – 67 on leaves, 80 on stem. Amphipod grazers 25 species on *Posidonia*, 40 on *Amphibolis*. Six suspension feeding amphipods on *Posidonia*, 9 on *Amphibolis*. 14 and 30 gastropod species on *Posidonia* and *Amphibolis* respectively. Five bivalve species found on each seagrass. Perth coastal waters, Western Australia.
- Lavery & Vanderklift (2000); Macroalgae, Success Bank, W.A. 91 tax on *Amphibolis griffithii* and 70 on *Posidonia coricea.*

6.4.1 Coralline algae (8 genera or 5 morphological groups)

The high ratio of coralline algae compared to other epiphyte taxa found in this study tends to agree with other studies around the world (e.g. Land 1970 – Discovery Bay; Patriquin 1972 - Barbados, Jamaica; Bosence 1989 – Florida Bay; Frankovich & Zieman 1994 – Florida Bay; Lord 1998 – Success Bank, W.A.) who, in some circumstances, have only considered coralline algae in their calculations of sediment abundance from epiphytes (e.g. Sim 1991). Coralline algae were dominant on all seagrass species and components, although they were significantly lower on *A. antarctica* blades. This may be a function of the life-span rates of the blades or the actual structure of the blades.

The dominance of coralline algae raises the question as to why are coralline algae so successful? Coralline algae have been noted as the primary colonisers of stems and blades of *Amphibolis* as well as on other species (van den Ende & Haage 1963 cited in Borowitzka *et al.* 1990; Humm 1964 cited in Borowitzka *et al.* 1990; Bramwell & Woelkerling 1984; Borowitzka *et al.* 1990) – although so also are the bryozoans *Thairopora mamillaris, Pyripora polita* and *Electra flagellum* (Borowitzka *et al.* 1990).

Is adaptation to seagrasses and rapid turnover rates a possible explanation? Coralline algae seem to be particularly good at recruiting but do not appear to favour any particular substrate type. Even though identification was morphological only, some genera such as *Jania* were recognised, i.e. the geniculate forms, and they are also known to attach to different substrates. This indicates that geniculate coralline algae are not adapted, as such, to recruiting on seagrass. This was also shown by the large quantities of coralline algae found on *Amphibolis* stems, which suggests that quick turnover rates of blades is not necessarily preferential. It is not as easy to ascertain the relationship between non-geniculate coralline algae and their substrates, as species identification was not practical. Hence it is impossible to determine whether the species are isolated to seagrass or whether their life spans actually exceed that of seagrass, indicating their use of seagrass as a substrate is purely opportunistic. In the case of the genticulate species, it would appear that seagrass would not be an ideal substrate. This suggests that passive, rather then active, recruitment operates.

The non-geniculate type coralline algae seem to be found in more abundance than geniculate types. Findings by Patriquin (1972) also found that the encrusting (*Melobesia*-like) algae make up the bulk of the calcareous material on *Thalassia* in Barbados. This has ramifications for both recruitment patterns and sediment deposition. The abundance of non-geniculate coralline algae may be a function of slower growth rate and longer life span. Alternatively, it maybe that non-geniculates have fast recruitment and metamorphosis, hence survive better, or that they are preferentially adapted to colonise on seagrass blades. If the latter were true, then this would be apparent on the different seagrass components, i.e. R vs K strategists.

Borowtizka *et al.* (1990) stated that "crustose coralline algae seem to act, at least in some part, as pioneer plants, possibly providing a suitable substratum for other epiphytes. For example, the geniculate coralline alga *Metagoniolithon stelliferum* has been reported to settle and grow only on these coralline algae (Ducker 1979, Ducker & Knox 1984) — although further studies have shown that the geniculate coralline algae will settle on coralline algal-free artificial seagrass. This could be due to a different biofilm production on the artificial seagrass, however."

Comparison of coralline algae types (encrusting/erect) on *Amphibolis* blades and *Amphibolis* stems indicates a preference for encrusting types on blades and for erect types on stems. However, this apparent difference does not allow for the number of ~~colonies~~ thalli, nor on stems does it allow for the loss by breakage, which is more likely to occur with erect colonies. thalli

Recruitment studies indicate that settlement of crustose coralline algae is higher where the surface is rough (Figueiredo *et al.* 1997, Greig 2000. All seagrass species are dominated by coralline algae (38.2 - 67.8%), although coralline algae are less dominant for *A. antarctica* blades. But *Amphibolis* blades have the greater abundance of epiphytes on them.

So why are coralline algae more successful at recruiting if they do not show specialised adaptive mechanisms? Possibilities include:

i) number of spores produced, i.e. vast quantities due to quick reproduction and/or short life-cycle;

ii) effective and efficient methods of recruitment, with passive action used;

iii) low post-recruitment mortality; i.e. quick metamorphosis and excellent ability to adhere to their substrate (geniculates are particularly low-lying, which makes them less susceptible to breakage, but they may be disadvantaged by the amount of room they need to colonise, rather than erects which are not limited by space (as shown by those on stems). Encrusters may appear to be more abundant because of the large surface area upon which they recruit and then spread, compared to erect types (or to other taxa).

iv) rapid growth rates/good competitors; expand rapidly, utilising as much of the substrate as possible.

The dominance of coralline algae has ramifications in the deposition and accumulation of carbonate sediments compared to the other calcareous epiphytic taxa. Break down of geniculate and non-geniculate coralline algae would go down two pathways. Geniculate niches? coralline algae are susceptible to abrasion whilst they are living, so that even before the plant dies, it sheds blades, and pieces may be broken off. Geniculate coralline algae are made up of calcareous segments interspersed with a non-calcareous organic segments, which, on disaggregation, separate the segments.

Non-geniculate coralline algae do not break down so readily (they were the most difficult of all the calcareous epiphytes to remove during the separation process (Chapter 4 & 5). Examination of seagrass washed up on shore shows that it is predominantly encrusting coralline algae that are present. This is partly a consequence of the attachment mechanism, which allows it to remain attached during the transport of the seagrass to the shore. Hence encrusting coralline algae probably enter the sediment budget whilst still attached to seagrass. If they are retained on the seagrass blades, they may become rapidly buried. It is possible, however, that as the seagrass breaks down it produces an acidic environment, which would destroy the carbonate. However, it is more likely that the exchange with the surrounding water (which is weakly alkaline) will render this process negligible to non-existent. Whatever mechanism prevails, when the encrusting coralline algae finally detach from the blades, they are likely to be broken down into unrecognisable particles - i.e. to disaggegrate. This does not bode well for their recognition in the sedimentary record. Lowenstam (1955) suggested that "the disaggregation of corallines may prevent recognition of perhaps quite significant contributions". Nelson & Ginsburg (1986) also suggested that the encrusting coralline algae (*Melobesia membranacea* and *Fosliella farinose)* would disintegrate rapidly when seagrass blades are broken or shed. Walter & Burton (1990 cited in Frankovich & Zieman 1994) found that the dissolution of red algal substrates ranged from 10–50% in iron-poor, organic-rich and actively bioturbated sediments in Florida Bay. Findings by the latter author that although *Melobesia membranacea* and *Fosliella farinose* predominate amongst carbonate-producing organisms, this does not match the composition of the accumulating sediment, which is mostly aragonite.

6.4.2 Bryozoans

Sixty one different species of bryozoans were found attached to seagrasses, plus an additional 44 species were found in close association with seagrass, e.g. using epiphytic calcareous algae as a substrate. Bryozoans are good recruiters but poor competitors for space (Butler 1991). Sim (1991) showed that the number of epiphyte species increases with increasing seagrass height, with coralline algae most abundant on the upper 30% of the stem, whilst bryozoans, e.g. *Celleporina* sp., are most abundant near the base.

6.4.3 Foraminifers

Thirty different species of foraminifers from 18 genera were found attached to seagrasses, plus an additional 23 species were found in close association with seagrass. Foraminifers showed the highest diversity of species occurring as epiphytes.

6.4.4 Spirorbids

Spirorbids are indicated to be of secondary importance as seagrass calcareous epiphytes (Land 1970, Bosence 1989).

6.5 SUMMARY OF BIODIVERSITY AND RELATIVE ABUNDANCE

The findings from this study indicate that although coralline algae have a low species-richness, in terms of productivity, they are the most important. Bryozoans had the highest species richness, but were not so important in terms of carbonate production. In terms of tools for indicating paleoenviroments, bryozoans would be more useful than coralline algae due to the likelihood of massive break down to fine mud particles of the coralline algae.

CHAPTER 7

CALCAREOUS EPIPHYTIC PRODUCTIVITY AND GEOLOGICAL IMPLICATIONS

7.1 INTRODUCTION

Seagrass communities, unlike their terrestrial counterparts, are dominated by a diverse encrusting fauna and flora, which includes major animal and plant phyla, albeit invertebrates in the case of the fauna (Pawlik 1992). A recent survey/identifying researchers'/managers' perception of what constitutes a healthy seagrass ecosystem, showed that they placed a high emphasis on the abundance of non-calcareous and calcareous epiphytes. A further study showed that the volume of calcareous epiphytes present did not show significant variation between healthy and unhealthy seagrass ecosystems (Wood & Lavery 2000). Not in reference list.

This chapter aims to describe and quantify calcareous epiphyte productivity in South Australia. South Australia has 9,612 km^2 seagrass (Edyvane 1999a & b) and is proximal to the largest E-W trending cool-water carbonate platform (James 1997). These two factors make it an ideal study region to test the hypothesis that calcareous epiphytes on seagrass are a significant source of carbonate sediment in the shallow water of such regimes.

The extrapolation of the information gained from chapters 3-5 (which determined the controls on epiphyte distribution and quantity) has allowed the estimation of the productivity rates and the abundance of epiphytic carbonate produced throughout South Australia. Productivity of the epiphytes is calculated from standing stock values and turnover/productivity rates of seagrass. It was not part of this project to determine turnover rates of the seagrass at the sites sampled, so conservative rates from other studies have been used.

7.2 CARBONATE STANDING STOCK

Table 7.1 summarises the standing stock values of $CaCO_3$ g/m^2 and g/kg of seagrass found from the 23 sites sampled along the South Australian coastline. The main parameters controlling calcareous epiphyte abundance include seagrass biomass, seagrass genera, depth and seasonality. Biomass ratios have been determined to predict standing stock abundance using the gradient of y=28x seagrass biomass to $CaCO_3$ g/m^2 and y=29x $\sum$ biomass to $CaCO_3$ g/m^2. *Amphibolis* commonly has 3.5 times more $CaCO_3$ g/kg of seagrass, i.e. calcareous epiphytes associated with it) than does *Posidonia* (Table 7.2). Additionally, the *Amphibolis*

Table 7.1. Average epiphyte productivity from sites along the South Australian coastline. Number in brackets indicates s.e.. No value in the brackets indicates that only one sample was available.

	Total Average		*P. angustifolia*		*P. australis*		*P. sinuosa*		*A. antarctica* blades		*A. griffithii* blades		*A. antarctica* stems		*A. griffithii* stems	
	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}	g m^{-2} yr^{-1}	g kg^{-1} sg yr^{-1}
Ardrossan	456.5 (54.2)	1093.8 (89.6)					121.2 (15.2)	398 (64.6)	277.8 (57.3)	718.6 (100.5)	202.6 (26.9)		41.9 (9.6)	153 (19.4)		
Cape Hardy	258.2 (20.6)	1760.5 (397.8)					10.77 (5.4)	237.8 (37.8)	94.6 (11.6)	519.4 (52.79)			23.3 (4.7)	114.9 (9.1)		
Cape Jaffa	197.2 (34.0)	378.1 (36.5)	197.2 (34)	378.1 (36.5)												
Chinaman Creek (1)	120.9 (19.3)	547.5 (43.3)			109 (35.9)	435.6 (60.9)	125.8 (24.2)	542.6 (45.7)								
Chinaman Creek (2)	57 (14.6)	141.3 (45.7)			43.4 (5.7)	97.4 (13.8)	220.3	667.6								
Chinaman Creek (3)	82.5 (8.5)	364.6 (17.2)			82.5 (8.5)	364.6 (17.2)										
Cowlers	132 (11.6)	654.5 (44.4)					132 (11.6)	654.5 (44.4)								
Dutton	49.3 (10.9)	541.1 (120.1)	40.6 (10.8)	421.4 (56.9)												
Kingston	124.9 (16.9)	368.6 (41.1)					124.9 (16.9)	368.6 (41.1)								
Marino	71.4 (20)	307.6 (109.2)					59	149.7								
Moonta	261.2 (28)	561.2 (194.7)			220.6 (106.4)	1099 (637.9)										
Normanville	521.4 (50.6)	692.8 (55.7)	48.5 (24.2)	308.9 (84.7)												
Port Lincoln	153.8 (15.7)	447.7 (52)			139.6 (13.9)	384.4 (33.2)	239 (33.7)	827.7 (65.6)								
Port Moorowie	242.6 (33.4)	522.7 (38.7)			126.4	299.8	235.2 (46.2)	521.9 (39.9)								

Semaphore	58.5 (10.8)	1089 (340.4)	58.5 (10.8)	1089 (340.4)												
Stansbury	102.3 (11.6)	383.8 (27.9)			102.3 (11.6)	383.8 (27.9)										
Streaky Bay	661.2 (198.1)	1235.6 (221.3)			96.5 (20.5)	401.6 (28.4)	192.1 (52.8)	560.4 (31.1)	305.4 (131.1)	722.1 (143.2)			30 (6.9)	95 (12.1)		
Tiparra	51.5 (6.6)	815.4 (92)	35.5 (5.4)	384.8 (20.2)									1			
Torrens	49.5 (4.3)	285.2 (13.9)	49.5 (4.3)	285.1 (13.9)												
Tumby	455.3 (94.5)	902 (112.6)					450.6 (94.9)	892.9 (113)								
Whyalla	36.1 (4.3)	166 (12.7)			36.1 (4.3)	166 (12.7)										
WI01/01	160.9 (34.1)	861.9 (215.7)					32 (9.1)	154.1 (25.4)	150.3	536.8		340.9 (45.2)	38	158.4	41.7 (11.2)	206.1 (13.4)
WI02/99	402.7 (55.4)	885.5 (114.8)	135.1	364.2			88.2 (26.1)	235.4 (33.9)			94.3 (24.1)					
WI03/00	322.9 (57.7)	839.1 (100.2)					38 (12.8)	129 (25)				322.6 (24.1)			71.6 (12.2)	201.6 (12.3)
WI03/00deep	295.6 (80)	911.5 (108.7)	31.3 (7.9)	278.6 (53.1)					208 (32.3)	599.8 (54.18)	141.6 (31.8)	536 (140.7)	102.3 (38.9)	187.3 (26.5)	56.7 (9.7)	261.2 (37.4)
WI03/01	147.2 (16.2)	659.3 (76.9)					63.7 (6.8)	215 (14.9)			78.4 (39.9)	186.4 (47.7)			25.1 (8)	227.5 (15.1)
WI05/19	308.6 (34.2)	1200.4 (192.8)					38.3 (14.7)	255.3 (106.5)			24.3 (10)	427.9 (75.9)			62.9 (11.1)	244 (17.1)
WI05/99deep	98.3 (25.1)	1164.1 (133.5)					89.3 (35.1)	746.8 (138.4)			89 (26.8)					
WI06/00	99.7 (11.1)	651.1 (80.2)	77.7	581.1			30.7 (5.5)	150.8 (19.5)	11.1	167.3		147.5 (93.3)	7.1	145.5	21.9 (7.8)	189.9 (38.9)
WI06/00deep	197.3 (50)	1157.6 (117.3)					28.3 (20.7)	527.4 (378.6)	148.8 (49.6)	1080 (65.74)	13 (7.2)	789.1	92 (40)	278.1 (44.8)	71.2	140
WI09/9910	327.32 (39.7)	1530.4 (119.6)	55.8	387.2			42.8 (6.9)	184.8 (20.7)	150 (122.9)	626.2 (112.2)	353.1	752.6 (77.1)	55.4 (48.7)	255.3 (78.1)	42.4 (5.9)	274.6 (16.4)
WI09/99	220.1 (82.5)	915.8 (217.3)	31.5 (13)	251.6 (102.1)			51.1 (5.3)	320.9 (66.9)	263.9 (37.7)	1155 (72.28)	123.4 (39.6)		60.7 (30)	190.7 (48.6)		p212

WI10/00	182.1 (36.5)	977 (148)	82.4 (75.4)	420.6 (264.1)			55.1 (7.3)	235.3 (19.3)				853.5 (119.3)			24.9 (7.1)	241.3 (24.3)
WI11/99	370.9 (44)	982.9 (138.5)					76.3 (13.5)	180.8 (25.4)			101.1 (33)	309.4 (69.9)			50.9 (8.5)	244.6 (36.8)
WI11/99deep	122.5 (56.5)	432.9 (168.9)	32.6	104.5			25.9 (3.8)	224.7 (103)			63.1 (19.7)	196.9 (3.4)			37 (8.8)	157 (65.8)

Table 7.2. Summary of the standing stock values obtained along the South Australian coastline. Values are averaged site values. N = number of sites where species found. Sg = seagrass.

		Mean	**Std. Error**	**N**	**Minimum**	**Maximum**
$CaCO_3$ g/m^2						
Total		**94.7**	**21.8**	**23**	**10.3**	**364.6**
A. antarctica	Whole	106.5	32.7	10	2.6	324.7
	Blade	39.8	8.4	5	18.9	61.1
	Stem	88.5	22.5	5	46.5	174.5
A. griffithii	Whole	184.8	88.0	3	95	360.8
	Blade	19.15	2.1	2	17.1	21.2
	Stem	100.1	7	2	93.1	107.1
Amphibolis sp.		218.0	100.4	10	3.1	1061.9
P. angustifolia		19.6	5.5	8	9	56.3
P. australis		30.4	5.2	9	10.3	63
P. sinuosa		42.8	9.9	12	3.1	128.7
Posidonia sp.		32.1	5.8	23	3.1	128.7
Other		37.7	10.2	10	4.2	113.1
$CaCO_3$ g/kg/sg						
total kg		**165.2**	**18.4**	**23**	**27.82**	**373.5**
A. antarctica	Whole	224.5	32.8	10	65.8	378.1
	Blade	135	15.9	5	97.8	185.2
	Stem	315.1	48.9	5	189.9	442.5
A. griffithii	Whole	344.9	14.6	3	315.8	362.1
	Blade	92.8	3.9	2	88.9	96.6
	Stem	459.6	19.5	2	440.1	479
Amphibolis sp.		458.9	132.6	10	132.9	1148.5
P. angustifolia		126.2	27.3	8	69.2	311.1
P. australis		115.3	27.1	9	27.8	314
P. sinuosa		138.4	19.4	12	42.8	255.1
Posidonia sp.		129.5	15.8	23	27.8	314

components are markedly different, with 3.4x ($CaCO_3$ g/kg of seagrass) more calcareous epiphytes associated with the stems than with the blades (Tables 3.4, 7.2). Calcareous epiphyte abundance is also affected by water depth, but further studies are required to obtain accurate rates of change with depth. It is only possible to say, at this stage, that calcareous epiphytes increase in abundance from a depth of 2 to 10 mwd (Table 5.6). Calcareous epiphyte abundance decreases significantly during winter, but without further studies using ASUs, the % rate of decrease in winter cannot be calculated. Consequently, the $CaCO_3$ g/kg of seagrass values have been taken as remaining constant throughout the year.

7.3 SEAGRASS PRODUCTIVITY / TURNOVER RATES

It was not part of this project to determine seagrass productivity results in the study area. Hence, the results of other studies have been used to estimate turnover rates for South Australia (Table 7.3). The values selected are conservative, so it was decided that for this study, there would be no difference in the turnover rates used within genera. *Amphibolis* sp. stems are biennial, hence a turnover rate of 0.5/yr was used (Walker 1985, Coupland 1997).

Estimations of the number of *Amphibolis* crops per year is derived from the knowledge that if e.g. *A. griffithi* has a growth rate of 0.038 blade clusters/day, then it takes 26.3 days for a full new blade or ~14 blades per year. Each blade cluster consists of ~4 blades, hence that is a cluster turnover of 3.5/yr. Carruthers (1999) showed that there was no difference in leaf production at different heights within the canopy, hence this turnover rate can be used for the whole plant. The lower value obtained by this study is probably due to a slightly different method used to obtain the values.

It appears that the plant physiology of the blades changes during their life-span: in early life they are buoyant, to enable growth closer to the light, but at blade maturation and just after death, the blades become negatively buoyant, resulting in the leaf litter being present in or adjacent to the beds. The mature blades will also be weighed down by epiphytes which may increase the negative buoyancy. It appears that *Amphibolis* blades become very buoyant before death and *Posidonia* blades post death, potentially explaining the tendency for large deposits of *Posidonia* blades being washed up on beaches in comparison to few *Amphibolis* blades.

Table 7.3. Summary of the range of turnover rates (crops/yr^{-}) from W.A and N.S.W. and the rates adopted for this project.

Seagrass Species	Range - crop turnover/yr^{-}	Values used for this study
P. australis	2.8 → 6.4	3.5
P. sinuosa	3.7 → 5.2	3.5
P. angustifolia	-	3.5
A. antarctica blades	5.2 → 5.6	5
A. antarctica stem	-	0.5
A. griffithii blades	3.5 → 5.4	5
A. griffithii stem	-	0.5

7.4 CALCAREOUS EPIPHYTE PRODUCTIVITY RATES

Table 7.4 shows the average values of quadrat productivity values of each species. The data includes the West Island information. Contradictory to the standing stock values obtained, the blades of *A. antarctica* are the most important substrate in terms of epiphyte productivity and *Amphibolis* stems are the least important. There is not a high variance in productivity of epiphytes on different species of *Posidonia*, although the abundance of epiphytes on *P. sinuosa* is slightly greater. *A. griffithii* blades are low in comparison to *A. antarctica* blades, but this may be due to the predominance of the samples being obtained from West Island.

Kruskall-Wallace analysis of variance indicated that there is significant variation between species (Chi = 57.8 $CaCO_3$ g/m^2, 108.1 $CaCO_3$ g/kg of seagrass), $Chi_{crit, 0.05}$ = 14.6). Nemenyi *post hoc* analysis show that comparisons vary depending on whether $CaCO_3$ is measured per/ m^2 or per/kg seagrass (Table 7.5). However, generally *P. sinuosa* = *P. australis* ≠ *P. angustifolia* = *A. griffithii* blades ≠ *A. antarctica* blades ≠ *A. antarctica* stem = *A. griffithii* stem.

Examining the productivity of each site is relatively complex in mixed seagrass beds as each species has its own turnover rate. Hence to determine site productivity rates it is necessary to calculate productivity of the individual species and then compile the data for each quadrat. Frequently there were species additional to the 5 main *Posidonia* and *Amphibolis* species, including *Heterozostera tasmanica*, *Halophila* sp. and *Caulpera* sp. Turnover rates of *H. tasmanica* are only available for blades, and as the blades and stem area were not separated in the laboratory analyses, it is not possible to determine accurate productivity. No turnover rates are known for the other species and hence these other species are grouped together as 'other'. 'Other' also includes the sediment that became dislodged during the laboratory separation process and consequently the seagrass species from which it originated is unknown. As the group 'other' has a mixed origin and therefore mixed turnover rate it was deemed that a turnover rate of 3 crops/yr would be acceptable, if perhaps conservative, as it is unlikely that any of the host plants have a lower turnover rate.

Average epiphyte productivity over all the sites is 210 ± 26 g/m^2/yr or 750 ± 65 g/kg of seagrass/yr$^-$. Table 7.1 depicts the average productivity results from each site indicating that the distribution is similar to that of the standing stock distribution (Table 7.2). The most noticeable difference is the importance of productivity per/kg of seagrass at Cape Hardy, although productivity/m^2 remains low. This is attributed to the dominance of *A. antarctica* at this particular site. Semaphore shows similar distribution to Cape Hardy although only

Table 7.4. Calcareous epiphyte productivity values (g/m^2/yr$^-$ and g/kg/sg/yr) of the 5 predominant species in this study, averaged from individual quadrat productivity values from each site. sg = seagrass.

		Mean	Std. Error	N	Minimum	Maximum
<u>$CaCO_3$ g/m^2/yr</u>						
P. angustifolia		79.1	10.7	67	6.2	565.1
P. australis		88.6	7.5	75	10.7	424.7
P. sinuosa		106.3	10.6	198	0.7	1227.4
A. antarctica	Blade	202.6	26.9	35	11.1	741.7
	Stem	50.4	8.3	35	6.7	218.5
A. griffithii	Blade	87.6	11.5	82	0.7	593.8
	Stem	47.2	3.7	82	3.5	150.5
<u>$CaCO_3$ g/kg/sg/yr</u>						
P. angustifolia		325.8	32.5	75	39.24	2367.0
P. australis		354.6	21.3	198	6.9	1726.6
P. sinuosa		718.1	50.4	35	167.29	1294.8
A. antarctica	Blade	718.1	50.4	35	167.29	1294.8
	Stem	164.3	13.0	35	64.35	366.4
A. griffithii	Blade	448.5	35.6	82	27.43	1306.1
	Stem	236.8	8.2	81	91.22	435.7

Table 7.5. Results of Nemenyi *post hoc* analysis of variance showing where productivity of epiphytes on particular seagrass species are significantly (sg) or not significantly (ns) different. Qcrit$_{0.05,\infty,8}$ = 4.286

A. CaCO$_3$ g m^{-2} yr^{-1}	*P. angustifolia*	*P. australis*	*P. sinuosa*	*Posidonia* sp.	Blade *A. antarctica*	Stem *A. antarctica*	Blade *A. griffithii*	Stem *A. griffithii*
P. angustifolia	-							
P. australis	sg	-						
P. sinuosa	ns	ns	-					
Posidonia sp.	ns	ns	ns	-				
Blade *A. antarctica*	sg	sg	sg	sg	-			
Stem *A. antarctica*	sg	sg	sg	sg	sg	-		
Blade *A. griffithii*	ns	sg	sg	ns	sg	sg	-	
Stem *A. griffithii*	sg	sg	sg	sg	sg	ns	sg	-

B. CaCO$_3$ g kg^{-1} sg yr^{-1}	*P. angustifolia*	*P. australis*	*P. sinuosa*	*Posidonia* sp.	Blade *A. antarctica*	Stem *A. antarctica*	Blade *A. griffithii*	Stem *A. griffithii*
P. angustifolia	-							
P. australis	sg	-						
P. sinuosa	sg	ns	-					
Posidonia sp.	sg	ns	ns	-				
Blade *A. antarctica*	sg	sg	sg	sg	-			
Stem *A. antarctica*	sg	sg	sg	sg	sg	-		
Blade *A. griffithii*	ns	sg	sg	sg	sg	sg	-	
Stem *A. griffithii*	sg	sg	sg	sg	sg	sg	sg	-

P. angustifolia is present at the site and it also has the lowest seagrass biomass of all the sites. Values at Streaky Bay and Ardrossan have high productivity in terms of both per/m^2 and per/g/kg/seagrass, ie. both seagrass density and epiphyte productivity are high. Normanville, which was prominent in standing stock values remains above the average, but is not so important in terms of epiphyte productivity as first observed.

7.4.3. The West Island Case

The productivity of epiphytic carbonate is based on the turnover values of seagrass calculated by previous studies. Table 7.6 indicates the range of turnover rates used and the range of productivity values obtained from these.

The productivity results can only be used as an approximation as the turnover rates at West Island were not measured. However, they do accentuate the importance of carbonate productivity *Amphibolis* blades (71.5 – 151.3 g/m^2, 340 – 721 g/kg of seagrass) over *Posidonia* blades (39.2-72.8 g/m^2, 180-334.9 g/kg of seagrass). It should be noted that on a regional scale *Posidonia* is the overall larger contributor because of the regional extent compared to *Amphibolis*. The productivity values also indicate that although the standing stock values of carbonate from *Amphibolis* stems is greater, the actual productivity values are higher from *Amphibolis* blades, indicating the importance of turnover rates. The only other study known where the relative contributions of *Amphibolis* stems and blades were calculated separately, agree with the trend seen here (Lord 1998a&b).

This difference is attributed to the longevity of *Amphibolis* sp. stems. *Amphibolis* stems are perennial (Walker 1985) and hence the epipyhtes have a much longer time over which to accumulate and grow. It is likely that during their life time there is a continuous loss of epiphytic carbonate as well as the build-up, therefore the productivity calculated is conservative. Walker and Woelkerling (1988) found that standing stock of $CaCO_3$ was greater on *Amphibolis* blades compared to stems – cited in Sim 1991. They suggested this was due to different surface areas and competitive interaction between non-calcareous epiphytes and coralline algae species. Results from Sim (1991), however, suggest that it is more related to environmental conditions.

7.4.4 Extrapolation to the entire South Australian coastline

The calcareous epiphytes on the seagrasses along the South Australian coastline produce 2,018,520 metric tonnes of $CaCO_3$ per year! This estimation is based on a seagrass area of

Table 7. 6. The turnover rates determined previously for West Island, and the carbonate productivity rates calculated by their use.

Genera	Turnover rates	CaCO$_3$ productivity ("calcirates")	
		g/m^2 /yr$^-$	g/kg seagrass/yr$^-$
Posidonia	2.8-5.2	39.2-72.8	180-334.9
Amphibolis stem	1 every 2 years	91	203
Amphibolis blade	2.6 –5.6	71.5 – 151.3	340 – 721
Σ *Amphibolis* sp.	162.5	242	543 – 924

9,612 km^2 (Edyvane 1999a&b) and an average productivity value of 210 g/m^2/yr. This is a significant volume of carbonate sediment. The question is "does it accumulate"?

The calcareous biota are passively released as loose particles when the plant disintegrates, either at the growth site or the deposition site of the shed blades. The epiphytes may fall off into the water column as loose particles, or fall into the sediment. These particles will then be subjected to the full range of diagenetic processes, such as transportation, dissolution, neomorphism and erosion. This will be an ongoing process, e.g. before the particles are buried and it even often starts whilst the organism is still alive and attached to the plant, particularly in the case of bioerosion. Hence, an understanding of these processes and an evaluation of their affect on preservation potential is necessary.

Thm & Clarke?

Sand movement by hydrodynamic processes is likely to alter the deposition-accumulation link. Clarke (1987) used sediment tracers offshore at Brighton and West Beach at unvegetated sites 0.6, 2.4 and 5 km offshore and at another site 2.4 km offshore but in seagrass. This study indicated that sediment movement through the seagrass was at a similar rate to that at the comparable unvegetated site. Movement was in a north-east direction. Similar speeds, "explained by the well-documented fact that seagrass causes sedimentation is only true in low water velocities. In storm conditions, when most of the sediment movement occurs, the seagrass no longer acts as a barrier and sediment is suspended equally from within the seagrass and in unvegetated areas. The study suggested that approximately 75 x10^3 m^3/yr of sediment moves inshore." Sediment size showed little difference between vegetated and unvegetated areas, suggesting that the carbonate produced epiphytically on seagrass blades (mainly by coralline algae) is winnowed from amongst the seagrass (Thomas & Clarke 1987).

7.4.4 Carbonate Sediment Accumulation Rates

The average accumulation rate over the South Australian seagrass bed area is 7.4 cm/1000 yrs (Table 7.7), assuming:-

i) $CaCO_3$ S.G. of 2.18 g/cm^2
i) zero porosity
ii) zero recycling.

These estimations are based on *Posidonia* sp. having a turnover rate of 3 crops per year, and *Amphibolis* sp. having a turnover rate of 5 blade crops per year and 0.25 "stem crops" every year. There are no estimations, however, of seagrass turnover rates in South Australia and

Should be cm/1000 yrs ??

?

Table 7.7. Sediment accumulation in seagrass beds of calcareous epiphytic particles, over a period of 1,000 years, at various field sites. See text for assumptions made to produce these figures.

	$CaCO_3$ g/m^2/ky	± st dev		$CaCO_3$ g/m^2/ky	± st dev
Streaky Bay	23.5	18.6	WI01/01	5.7	4.5
Port Lincoln	5.5	2.1	WI02/99	14.3	7.1
Tumby	16.2	12.6	WI03/00	11.5	7.4
Cape Hardy	9.2	1.9	WI03/01	5.2	2.1
Dutton	1.8	1.0	WI05/19	11.0	5.2
Cowlers	4.7	1.5	WI06/00	3.5	1.4
Whyalla	1.3	0.6	WI09/99	11.6	7.1
Chinaman Creek (1)	4.3	2.5	WI09/99	7.8	7.8
Chinaman Creek (2)	2.0	1.9	WI10/00	6.5	4.9
Chinaman Creek (3)	2.9	1.0	WI11/99	13.2	5.9
Moonta	9.3	3.4	WI03/00deep	10.5	10.3
Stansbury	3.6	1.5	WI05/99deep	3.5	2.0
Tiparra	1.8	0.7	WI06/00deep	7.0	6.7
Port Moorowie	8.6	4.3	WI11/99deep	4.4	4.9
Ardrossan	16.2	7.2			
Semaphore	2.1	0.9			
Torrens	1.8	0.6			
Marino	2.5	1.4			
Normanville	18.6	6.7			
Cape Jaffa	7.0	4.5			
Kingston	4.4	2.2			

hence these figures are largely based on those from similar/same species/conditions found in Western Australia and New South Wales.

Evaluation of the amount of this carbonate reaching the sediment was not within the scope of this project, although sediment was collected and photographed from each site (see CDs). However, even if 90% of the carbonate was lost each year, e.g. due to recycling or dissolution in the water column, this would still represent an accumulation of 0.74 mm of sediment per decade. It is important to remember that this figure is only the calcareous epiphytic contribution to the sediment accumulation rates, and does not include any non-epiphytic carbonate accumulation.

The abundance of carbonate being produced at any one site had no significant relationship with the concentration of carbonate within the sediment. The only trend observed was a decrease in the carbonate content within the sediment with an increase in the carbonate on the seagrass. This is not what would be expected, as it would be hoped that with high productivity would also come high sediment retention, but this does not seem to be the case. Maybe the utilisation of the carbonate is high enough that recycling is also high.

7.4.5. Estimation of regional biomass from epiphytic carbonate sediment

It is potentially possible to estimate the regional biomass of seagrass that was present at a site by measuring the amount of epiphytic carbonate present in the accumulated sediment. This figure could only be an estimate at best, as many carbonate grains could be attributed to environments other than a seagrass meadow, i.e. many calcareous epiphytes are equally likely to be found in other environments where they have used substrates other than seagrasses. It is the understanding of assemblages that is critical to the accuracy of the estimate.

7.5 SEAGRASSES IN THE ROCK RECORD

Evolution of seagrass, their migratory route and their possible influence on the sedimentology of an area is a topic that needs scrutiny. Could carbonate sediments contain a history of seagrass evolution? Along with seagrass evolution in the early Cretaceous around the Tethys Sea came high quantities of carbonate deposition. When did the deposition of the temperate Great Australian Bight (GAB) carbonate platform take place and did it coincide with the arrival of seagrass into Australian coastal waters?

The dominant components of temperate carbonate sediment are bryozoans, coralline algae (red algae), molluscs and foraminifers. This compares to tropical facies that are typically composed of corals, ooids, cooccoliths, calcareous green algae and foraminifers. The location of carbonate production in tropical environments is well-established, However, in temperate environments the source location is less obvious as there are no true reefs. Some species have the ability to attach directly to sediment particles, but in shallower areas there are few locations where sediment remains stable for suitable periods of time because of wave activity. Rock outcrops are limited, particularly in the GAB, hence the only consistent and large surface area of available substrate is seagrass, hence the potential importance of epiphytes as sediment producers.

Identifying seasonality in the fossil record enables more detailed understanding of the climate regimes of the deposits, including environmental factors such as latitude, water depth, local and regional oceanography and climate, water-column stratification and upwelling of the potential amount of carbonate, as well as the paleobiology of the fossil organisms (O'Dea & Okamura and refs therein 2000).

Recognition of the depositional regime and the origin of the sediment, either as friable sediment or limestone, is information that is either critical or useful to answer many geological questions. One example is the recognition of ancient beaches. Beach sands are an important target in the petroleum industry, and their recognition plays a role in the assessment of reservoir quality, which is essential for the development and recovery processes for the petroleum industry.

This study will enable more confidence in the assessment of the littoral/sub-littoral environment in the geological record through the recognition of seagrass facies.

CHAPTER 8

DISCUSSION

8.1 INTRODUCTION

The production of carbonate sediment grains by calcareous epiphytes on seagrasses is a significant geological process.

This statement has been indisputably proven by this research project.

It has also been shown that such carbonate production is entirely dependent upon the presence and state of the seagrass, i.e. the substrate for the calcareous epiphytes.

8.2 SEAGRASS

8.2.1 Seagrass in Australia

The evolutionary history of seagrass is not fully known due to the poor preservation potential of the plant. The time at which marine grasses reached the Australian continental margin is unclear, but was no earlier than the Eocene. Since the Miocene seagrasses in Australia have become relatively isolated, leading to high endemism.

The distribution pattern of modern seagrass species around Australia has been attributed to the spatial and temporal pathways of evolutionary dispersion. It is likely that the source of genetic material was from the north and that radiation occurred with time in an anticlockwise direction around the continent. Exchange of genetic material is believed to have initially occurred during the Pliocene/early Pleistocene, at which time Australia had collided with the Asian continent and sea levels were lower. Australia, during the Holocene, has become relatively isolated, dramatically reducing, if not completely cutting off, pathways for further genetic exchange. Even though Australia has a high endemic seagrass population, it appears that some forms are remnant pockets of what were once much more widely distributed species. The ecological impact of seagrasses on shallow marine environments would have been substantial. It is probable that, not only did the seagrasses evolve once they reached Australia, but that the related calcareous epiphytic fauna and flora also evolved concomitantly. Hence, evidence for the evolution of seagrass may be found in several ways, one being the evolution and/or adaptation of these epiphytic species to the 'new' seagrass ecological habitat.

8.2.2 Modern seagrass in South Australia

There are 12 species from 5 genera of seagrass that cover an area of ~ 9,612 km^2 in South Australia. Seagrass is important in the shallow marine realm for a number of reasons including high productivity, habitat modification, and sediment stabilisation. Loss of seagrass causes increased sediment transport, increased onshore and/or near shore wave activity and decreased sediment production.

Research on seagrass indicates that their load of calcareous epiphytes is important at a regional scale in terms of productivity, habitat providers and sediment stability. There is little, so far, to suggest how important their role has been in the past. Do calcareous epiphytes hold the key to their story? Will the impact of anthropogenic activities significantly affect seagrass and the calcareous epiphytic assemblages? These are question that need to be addressed by coastal management agencies.

This study has greatly extended the understanding of the interdependence of seagrass, calcareous epiphytes, and carbonate sediment production in shallow water in temperate environments.

8.3 FIELD AND LABORATORY METHODS AND RATIONALE

8.3.1 Site selection

The 21 sites chosen along the South Australian coastline covered the complete spectrum of environments in which seagrass is found. These settings vary from the those at the head of reverse estuaries (Gulf St. Vincent and Spencer Gulf) to those exposed to the Southern Ocean, from water depths of 0.4 to 15.5 m, across a salinity range of 32.2 to 43.7‰, and with surface water temperatures varying from 14.1 to 25.8°C.

- the sites represented a number of different environments, thus allowing estimates of carbonate production across the region.
- some sites had parameters in common, thereby permitting comparisons and contrasts on different aspects of calcareous epiphyte carbonate production.
- the sampling method gave representative samples of each area, yet at the same time retained information at various spatial scales.

8.3.2 Laboratory methods

8.3.2.1 Separation of calcareous epiphytes from seagrasses

All the standard methods were tested, but no technique retained all of the seagrass, all the calcareous epiphytes and any loosely attached sediment grains, and so they were all rejected.

A new labour-intensive method (approximately 10 hours laboratory time and 1.5 weeks "waiting time" to complete one transect) was devised and this allowed:-

- retention of all of the calcareous epiphytic material for later examination, i.e. it remained relatively whole for identification and the skeletal chemistry was not altered in any way
- quantitative analysis of the carbonate epiphytes;
- quantitative determination of the biomass of the epiphyte host, i.e. of the seagrass.

8.3.2.2 Sediment analysis

Descriptions of the composition and quantitative analysis of the carbonate/non-carbonate ratio determined for every site provided not only valuable information on the modern environment, but also showed what might be expected, by extrapolation, in the rock record.

8.4 BIOMASS

8.4.1 Seagrass biomass

Greater than 74% of the quadrats sampled had seagrass biomass values between 50 and 500 g/m^2. The few sites which had higher biomass values indicate that the more favourable conditions for plant growth are relatively atypical, i.e. low current velocity and relatively high salinity, as found at Chinaman Creek.

The significantly higher biomass of communities dominated by *Amphibolis* sp., compared with those dominated by *Posidonia* sp., is attributed to higher shoot density of *Amphibolis* per unit area. *Posidonia* sp. has a greater surface area for a typical shoot at West Island and hence it is assumed that the biomass of a single shoot of *Posidonia* is also greater than an individual shoot of *Amphibolis*. Seagrass biomass has a peak value at 2-4 m water depth and this acme is attributed to the level at which photosynthetic inhibition and desiccation are reduced. Seagrass biomass decreases below 4 m mwd, probably in response to progressive light attenuation with water depth. Variance at each depth level is high, indicating that there are other as yet undetermined controlling factors for seagrass biomass.

8.4.2 Calcareous epiphytes biomass

Standing stock values of epiphytic carbonate have average values of 79 g/m^2 or 162 g/kg of seagrass. The predominant control on the abundance of calcareous epiphytes is seagrass biomass, i.e. the more seagrass, the more surface area for recruitment, the greater the abundance of calcareous epiphytes. Greater abundance of calcareous epiphytes was recorded on *Amphibolis* rather than on *Posidonia* due to the accumulation of calcareous epiphytes over time on the relatively long-lived *Amphibolis* stems. There is no apparent correlation between calcareous epiphyte abundance and salinity and nutrient concentration within the range of normal open marine environments. Temperature data indicates the optimal temperature for calcareous epiphyte production is 16-18°C.

The decline in $CaCO_3$ production during autumn/winter is attributed to the simultaneous decrease in seagrass biomass, hence reducing substrate space. Independent measure of $CaCO_3$ g/kg of seagrass, however, showed a greater substrate abundance of calcareous epiphytes in autumn/winter than in spring/summer. This is also attributed to the availability of substrate space, in that an increase in seagrass productivity in spring also increases the amount of substrate available for recruitment, effectively diluting the abundance of epiphytes on each unit of surface area. This relationship implies that the epiphyte propagule availability and settlement rate does not vary significantly throughout the year.

West Island
The detailed study at West Island showed that 80% of the epiphytic $CaCO_3$ is associated with *Amphibolis* stems and that *Amphibolis* blades have significantly greater abundances of calcareous epiphytes associated with them than do *Posidonia* blades. It appears that *Amphibolis* is more susceptible to calcareous epiphyte recruitment than *Posidonia*. This may explain why *Amphibolis* plants are one of the first species to recede when, due to anthropogenic nutrient input, non-calcareous algal epiphytes increase, thereby outcompeting calcareous epiphytes for settlement space.

8.5 CALCAREOUS EPIPHYTES

8.5.1 Biodiversity and relative abundance

Coralline algae, the dominant calcareous epiphyte in terms of both frequency and abundance (53.6%), was not significantly species rich (8 genera) in comparison to foraminifers and bryozoans (30 species and 61 species respectively). The latter, combined, produced a significant quantity of the $CaCO_3$ 17.4% and 16.4% respectively). The remainder percentage of carbonate producing epiphytes was made up from spirobids (8%, 11 morphological types recognised), bivalves (0.3%, 5 species), serpulids (2 morphological types recognised) and ostracods (<0.1%, 14 species) and other insignificant biota. e.g. bivalves et al.

Estimations of the amount of carbonate derived from each species within each taxon can be calculated using the abundance ratio of each species and the standing stock values of calcareous epiphyte abundance from each site on each seagrass species present.

8.5.2 Dominant calcareous epiphyte biota

8.5.2.1 Coralline Algae (8 genera / 5 morphological groups)

The high ratio of coralline algae compared to other epiphyte taxa found in this study is comparable to other world-wide studies. Corallines were dominant on all seagrass species and components, although they were significantly lower on A. *antarctica* blades.

The abundance of non-geniculate corallines may be a function of slower growth rate and longer life span. Alternatively, it maybe that non-geniculates have fast recruitment and metamorphosis, hence survive better, or that they are preferentially adapted to colonise on seagrass blades. If the latter were true, then this would be apparent on the different seagrass components, i.e. r vs K strategists.

Comparison of coralline algae types (encrusting/erect) on *Amphibolis* blades and *Amphibolis* stems indicates a preference for encrusting types on blades and for erect types on stems. This difference, however, does not allow for the number of algal colonies, nor on stems does it allow for the loss by breakage, which is more likely to occur with erect colonies.

8.5.2.2 Bryozoans

Sixty-one species of bryozoans were found to use seagrass as a substrate in South Australia. An additional 44 species were found in close association, e.g. using epiphytic calcareous algae as substrate.

8.5.2.3 Foraminifers

Thirty species from 18 genera occur on seagrass in South Australia. An additional 23 species were found in close association, i.e. loosely adhering to the seagrass.

The findings from this study indicate that although the coralline algae flora on seagrass has a low species richness, in terms of productivity, it is the most important. Bryozoans had the highest species richness, but were not so important in terms of carbonate production. In terms of paleoenvironmental tools, bryozoans would be more important than corallines due to the likelihood of the break down of some corallines to unrecognisable fine mud particles.

8.6 CARBONATE SEDIMENTS FROM CALCAREOUS EPIPHYTES

The abundance of epiphytic carbonate produced at any one site showed no significant relationship with the concentration of carbonate within the underlying sediment. In fact, the trend observed was a decrease in the carbonate content within the sediment when there was an increase in calcareous epiphytes on the seagrass. It may be that the utilisation of the carbonate is high enough that recycling is also high.

Evaluation of this epiphytic carbonate (average of 210 g/m^2 sg/yr) and its transfer to the underlying sediment was outside the scope of this project. However, even if 90% of the carbonate was lost each year due to recycling and dissolution in the water column, the remainder would still represent a significant contribution to the seafloor sediment budget.

8.7 CALCAREOUS EPIPHYTES IN THE ROCK RECORD

The evolution and geographic dispersion of seagrass occurred at a critical period in geological time. -There is evidence to indicate that seagrasses evolved around the Tethyan shoreline during the early Cretaceous. This was a time of high sealevel, and warm waters. Carbonate platforms were then at their largest and most widespread in the geological column at this and were also largely distributed around the Tethys sedimentary margins.

The examination of assemblages of calcareous epiphytes on seagrasses in today's environment can provide a comparison tool to use to recognise similar environments in the rock record.

Species richness in seagrass beds is greater compared to that of surrounding sandy sea-floor environments. It is possible, therefore, to differentiate seagrass bed areas from non-seagrass areas. Identification of seagrass areas from other environmental habitats such as rock beds can also be achieved by species assemblage differences. However, it is more complex to try and identify seagrass areas from other ecologically-rich niches in similar conditions which also leave no or very little trace of their original substrate, e.g. algal beds, sponge beds, etc.

The significance of species richness is several fold. The presence of seagrass increases species richness. Consequently, examples within the rock record of high species richness of assemblages comparable with Modern seagrass assemblages may indicate the presence of something else other than bare sand, i.e. the environment may have been an area of seagrass.

The dominant components of temperate carbonate sediment are bryozoans, coralline algae (red algae), molluscs and foraminifers. This overall composition is similar to the components found as calcareous epiphytes on seagrasses in the same environment. The recognisable difference is in the ranking of the components, with coralline algae being the dominant calcareous epiphyte.

CHAPTER 9

CONCLUSIONS

1. The production of carbonate sediment grains by calcareous epiphytes on seagrasses is a geologically significant phenomenon.

2. The evolution and geographic dispersion of seagrass occurred during the Cretaceous, and since that time Australian seagrasses have become progressively more endemic

3. The predominant control on the abundance of calcareous epiphytes is seagrass biomass

4. Over 74% of the quadrats sampled during this study had seagrass biomass values between 50 and 500 g/m^2.

5. Seagrass biomass has a peak value at 2-4 meters water depth.

6. Epiphytic carbonate abundance changes significantly with water depth, increasing from 0 to 10m mwd and then decreasing as depth increases.

7. Each of the 21 sites examined had different abundances of calcareous epiphytes indicating that estimates of regional abundance may be difficult without a detailed understanding of the controlling factors.

8. Greater abundance of calcareous epiphytes is associated with *Amphibolis* compared to *Posidonia*. This is because the accumulation of calcareous epiphytes over time on the relatively long-lived *Amphibolis* stems.

9. *Amphibolis* is more susceptible to calcareous epiphyte encrustation than *Posidonia.*

10. The decline in $CaCO_3$ production during autumn/winter is attributed to the simultaneous decrease in seagrass biomass, hence reducing recruitment space.

11. Species richness in seagrass beds is comparably higher than that in surrounding open sandy sea-floor environments.

12. Abundances of coralline algae >> bryozoans = foraminifers >> all other calcareous epiphytes.

13. The non-geniculate type corallines are more common on seagrasses than geniculate types.

14. Accumulation rates of calcareous epiphytic sediment grains are of the order of 7.4 cm/1000 yrs in Modern shallow water environments in South Australia.

15. Modern calcareous epiphyte assemblages can be extrapolated to recognise seagrass environments in the rock record.

16. South Australian Modern calcareous epiphyte assemblages and their abundances can be extrapolated to determine factors regarding paleoclimates, e.g. cool water vs warm water.

REFERENCES

Abal EW & Dennison WC. 1996. Seagrass depth range and water quality in Southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* 47: 763-771.

Abelson A. 1997. Settlement in flow: upstream exploration of substrata by weakly swimming larvae. *Ecology* 78: 160-166.

Alcoverro T, Manzanera M, Romero J. 2000. Nutrient mass balance of the seagrass *Posidonia oceanica*: The importance of nutrient retranslocation. *Marine Ecology Progress Series* 194: 13-21.

Arber A. 1920. *Water plants.* Cambridge: Cambridge University Press.

Aridis J, Rosenbaum H, Jupp I & McDonald M. 1993. *The status of seagrass ecosystems in Australia.* Melbourne: Australian Conservation Foundation.

Armstrong ME. 1989. Modern carbonate sediment production and its relation to bottom variability, Graham's Harbor, San Salvador, Bahamas. MSc thesis. University of Cincinnati, Ohio, USA. 100 pp.

Ascherson P. 1867. Vorarbeiten zu einer Uebersicht der phanerogamen Meergewächse. *Linnaea* 35: 152-208.

Backman TW & Barilotti DC. 1976. Irradiance reduction: effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. *Marine Biology (Berl.)* 34: 33-40.

Baluk W & Radwanski A. 1977. Organic communities and facies development of the Koryntnica basin (middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geolica Polonica* 27: 85-123.

Barkman JJ. 1958. Phytosociology & ecology of cryptogamic epiphytes. Chapter II. *Ecology.* Assen: Van Gor cum. 628 pp.

Barnabas AD. 1982. Fine structure of the leaf epidermis of *Thalassodendron ciliatum* (Forsk.) den Hartog. *Aquatic Botany* 12: 41-55.

Bathurst RGC. 1975. *Carbonate sediments and their diagenesis.* Second edition. Amsterdam, Developments in Sedimentology 42: 805-824.

Bell JD & Pollard DA. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. pp. 565-609 in *Seagrasses: A treatise on the Biology of Seagrasses with special reference to the Australasian region.* Ed. AWD Larkum, AJ McComb, SA Shepherd. Amsterdam: Elsevier.

Best MA & Thorpe JP. 1994. Particle size, clearance rate and feeding efficiency in marine bryozoa. In *Biology and palaeobiology of bryozoa.* Proceedings of 9th International Bryozoology Conference. Swansea. Ed. PJ Hayward, SJ Ryland, PD Taylor. Fredenborg: Olsen & Olsen.

Bittaker HF & Iverson R.L. 1976. *Thalassia testudinum* productivity: A field comparison of measurement methods. *Marine Biology* 37: 39-46.

Blanc-Vernet L. 1984. *Les Foramineres de l'herbier a* Posidonia oceanica *en Mediterranée: Analyses des assemblages, aspects regionaux application aux microfaunes fossiles.* Presented at International Workshop *Posidonia oceanica* beds, Port-Croz: GIS Posidonie Publication.

Bock P. 1982. Bryozoans (Phylum Bryozoa). In *Marine Invertebrates of southern Australia, part 1.* Ed. SA Shepherd, IM Thomas. Adelaide: D.J. Woolman, Government Printer.

Bock P. 2001. Recent and Fossil Bryozoa. www.civgeo.rmit.edu.au/bryozoa.

Bologna PAX & Heck KL. 1999. Differential prediation and growth rates of bay scallops within a seagrass habitat. *Journal of Experimental Marine Biology & Ecology* 239: 299-314.

Bone Y & James NP. 1993. Bryozoans as carbonate sediment producers on the cool-water Lacepede Shelf, southern Australia. *Sedimentary Geology* 86: 247-271.

Borowitzka MA & Lethbridge RC. 1989. Seagrass epiphytes. pp. 458-499 in *Biology of seagrasses: A treatise on the biology of seagrasses with special reference to the Australasian region.* Ed. RC Phillips & CP McRoy. Amsterdam: Elsevier.

Borowitzka MA, Lethbridge RC & Carlton L. 1990. Species richness, spatial distribution and colonizatioin pattern of algal and invertebrate epiphytes on the seagrass *Amphibolis griffithii. Marine Ecology Progress Series* 64: 281-291.

Bosence D. 1989. Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science* 44: 419-433.

Boudouresque CF, Crouzet A & Pergent G. 1983. Un nouvel outil au service de l'étude des herviers à *Posidonia oceanica*: la Lépidochronologie. *Rapport commission internationale Mer Méditerranée* 28: 111-112.

Bramwell MD & Woelkerling WJ. 1984. Studies on the distribution of Pneophyllum - Fosliella plants (Coralinaceae, Rhodophyta) on the leaves of the seagrass *Amphibolis antarctica* (Cymodoceacae). *Australian Journal of Botany* 32:31-37.

Brasier MD. 1975. An outline history of seagrass communities. *Palaeontology* 18: 681-702.

Brasier MD. 1996. Seagrass biology: Rottnest Island. *International Workshop on Seagrass*, Ed. J Kuo, DI Walker & H Kirkman. Faculty of Sciences, University of Western Australia.

Bressan G & Tomini I. 1982. Quelques observations sur la croissance des algues rouges calcaires du genre *Fosliella* (Rhodophycophyta, Corallinaceae). *Vie et Milieu* 31: 283-291.

Bretsky PW. 1978. Gradual species replacement in the Mahantango shales (Middle Devonian, central Pennsylvania). *Abstracts with Programs, Geological Society of America* 10: 371.

Bridges KW & Phillips RC. 1995. Seagrass. www.botany.hawaii.edu/seagrass.

Brouns JJWM & Heijs FML. 1986. Production and biomass of the seagrass *Enhalus acoroides* (L.f.) Royle and its epiphytes. *Aquatic Botany* 25: 21-45.

Brown KM, Bone Y, Cheshire A & James NP. 2000a. Seasonal variation of calcareous epiphytes on artificial seagrass: Preliminary studies, West Island, South Australia. Presented at 15th Australian Geological Convention, Sydney.

Brown KM, Cheshire A, Bone Y & James NP. 2000b. Calcareous epiphytes on *Posidonia* sp. and *Amphibolis* sp. along the South Australian coastline; their distribution, abundance and importance. Presented at Australian Marine Sciences Asssociation Inc., Sydney.

Bulthuis DA. 1987. Effects of temperature on photsynthesis and growth of seagrasses. *Aquatic Botany* 27: 27-40.

Bulthuis DA & Woelkerling WJ. 1981. Effects of *in situ* nitrogen and phosphorous enrichment of the sediments on the seagrass *Heterozostera tasmanica* (Martens ex Ashcer) den Hartog in Western Port, Victoria, Australia. *Journal of Experimental Marine Biology & Ecology* 53: 193-207.

Bulthuis DA & Woelkerling W.J. 1983a. Seasonal variation in standing crop density and leaf growth rate of the seagrass *Heterozostera tasmanica* in Westernport and Port Phillip Bay, Victoria, Australia. *Aquatic Botany* 16: 111-136.

Bulthuis DA & Woelkerling W.J. 1983b. Biomass accumulation and shading effects of epiphytes on leaves of *Heterozostera tasmanica*, in Victoria, Australia. *Aquatic Botany* 16: 137-148.

Burkholder JM & Doheny TE. 1968. *The biology of eelgrass.* Hempstead, Long Island, NY: Department of Conservation and Waterways Contribution 3. 120 pp.

Butler A & Jernakoff P. 1999. *Seagrass in Australia: Strategic review and development of an R & D plan.* Collingwood: CSIRO Publishing. 210 pp.

Cambridge ML, Chiffings AW, Brittan C, Moore L & McComb AJ. 1986. The loss of seagrass in Cockburn Sound, Western Australia. II, Possible causes of seagrass decline. *Aquatic Botany* 24: 269-285.

Cambridge ML & Hocking PJ. 1997. Annual primary production and nutrient dynamics of the seagrasses *Posidonia sinuosa* and *Posidonia australis* in south-western Australia. *Aquatic Botany* 59: 277-295.

Cambridge ML & Kuo J. 1979. Two new species of seagrasses from Australia, *Posidonia sinuosa* and *P. angustilfolia* (Posidoniacaeae). *Aquatic Botany* 6: 307-328.

Carruthers T. 1994. Leaf production, canopy structure and light climate of a density manipulated *Amphibolis griffithii* meadow. MSc. Thesis, University of Western Australia, Perth.

Carruthers TJB. 1999. Within canopy growth strategies of the two seagrass species *Amphibolis griffithii* (J. Black) den Hartog and *Amphibolis antarctica* (Labillardiere) Sonder & Ascherson ex Ascherson. pp 41-50 in *The Seagrass Flora and Fauna of Rottnest Island, Western Australia.* Ed. DI Walker & FE Wells. Perth: Western Australian Museum.

Challinor J. 1986. *Challinor's Dictionary of Geology*. Cardiff, University of Wales Press.

Chalmer PN. 1982. Settlment patterns of species in a marine fouling community and some mechanisms of succession. *Journal of Experimental Marine Biology & Ecology* 58: 73-85.

Cheshire AC, Westphalen G, Wenden A, Scriven LJ & Rowland BC. 1996. Photosynthesis and respiration of phaeophycean-dominated macroalgal communities in summer and winter. *Aquatic Botany* 55: 159-170.

Chester R. 1990. *Marine geochemistry*. London: Chapman & Hall. 698 pp.

Clarkson ENK. 1993. Bryozoans. In *Inveterbrate Palaeontology and Evolution.* Ed. ENK Clarkson. London: Chapman and Hall.

Clarkson ENK. 1998. Bryozoans. In *Inveterbrate Palaeontology and Evolution.* Ed. ENK Clarkson. London: Blackwell Science.

Coles RG, Lee Long WJ, Watson RA & Derbyshire KJ. 1993. Distribution of seagrasses and their fish and penaeid prawn communities in Cairns Harbour, a tropical estuary, Northern Queensland, Australia. *Journal of Marine and Freshwater Research* 44: 193-210.

Colmenero LR & Lizaso JLS. 1999. Effects of *Calpensia nobilis* (Esper 1796) (Bryozoa: Cheilostomida) on the seagrass *Posidonia oceanica* (L.) Delile. *Aquatic Botany* 62: 217-223.

Connolly RM, Melville AJ & Keesing JK. 2002. Abundance, movement and individual identification of leafy seagdragons, *Phycodurus eques* (Pisces: Syngnathidae). *Marine and Freshwater Research* 53: 777-780.

Copertino M. 2002. Production ecology and ecophysiology of turf algal communities on a temperate reef, West Island, South Australia. PhD thesis. Adelaide, University of Adelaide.

Cottrell JF. 1974. Traces of marine grasses from fossil molluscan shells. *Geological Society of America Abstracts with Program* 6: 697.

Coupland G. 1997. Rhizome and shoot structure, growth and response to sediment burial in *Amphibolis griffithii* (Black) den Hartog. Unpublished Honours thesis, Department of Botany, University of Western Australia, Perth.

Davies GR. 1970. Carbonate bank sedimentation, eastern Shark Bay, Western Australia. pp. 85-168 In *Carbonate sedimentation and environments, Shark Bay, Western Australia.* Ed. BW Logan, GR Davies, JF Read & DE Cebulski. Tulsa, OK: American Association of Petroleum Geologists Memoir.

Dawes CJ. 1998. *Marine Botany*. New York: John Wiley & Sons. 480 pp.

Delgado O, Ruiz J, Pérez M, Romero J & Ballesteros E. 1999. Effects of fish farming on seagrass (*Posidonia oceanica*) in a Mediterranean bay: seagrass decline after organic loading cessation. *Oceanologica Acta* 22: 109-117.

den Hartog C. 1970. *The Seagrasses of the World.* Amsterdam: North Holland Publishing Co. 275 pp.

den Hartog C. 1989. Distribution of the seagrass *Halophila decipens* Ostenfeld in the Indian Ocean. *Acta Botanica Neerlandica* 38: 81-83.

Dennison WC. 1990. Leaf production. In *Seagrass Research Methods*, Ed. RC Phillips & CP McRoy. Paris: UNESCO.

Dennison WC & Alberte RS. 1986. Photoadaptation and growth of *Zostera marina* L. (eelgrass) transplants along a depth gradient. *Journal of Experimental Marine Biology & Ecology* 98: 265-282.

Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW & Batiuk RA. 1993. Assessing water quality with submersed aquatic vegetation: habitat requirements as barometers of Chesapeake Bay health. *BioScience* 42: 86-94.

Dirnberger JM. 1993. Dispersal larvae with a short planktonic phase in the polychaete *Spirobis spirillum* (Linnaeus). *Bulletin Marine Science* 52: 898-910.

Dixon J, Schroeter SC & Kastendick J. 1981. Effects of the encrusting bryozoan *Membranipora membranacea* on the loss of blades and fronds by the giant kelp *Macrocystis pyrifera* (Laminaraiales). *Journal of Phycology* 17: 341-345.

Domning DP. 1977.An ecological model for Late Tertiary Sirenian evolution in the North Pacific Ocean. *Systematic Zoology* 25: 352-362.

Domning DP. 1991. Dugongs threatened by Kuwait oil spill. Sirenews 15:11-13.

Domning DP. 1999. Fossils explained: Sirenians (seacows). *Geology Today* 15: 75-79.

Drexel JF, Preiss WV & Parker AJ. 1993. The Geology of South Australia. Volume 1. The Precambrian. *Geological Survey of South Australia Bulletin* 54.

Duarte CM. 1991. Seagrass depth limits. *Aquatic Botany* 40: 363-377.

Ducker SC. 1979. The genus *Metagoniolithon* Weber - van Bosse (Corallinaceae, Rhodophyta). *Australia Systematic Botany* 27: 67-101.

Ducker SC, Foord NJ & Knox RB. 1977. Biology of Australian seagrasses, the genus *Amphibolis* C. Agardh (Cymodoceaceae). *Australian Journal of Botany* 25: 67-95.

Ducker SC & Knox R.B. 1978. Alleloparasitism between a seagrass and algae. *Naturwissenschaften* 65: 391-392.

Ducker SC & Knox RB. 1984. Epiphytism at the cellular level with special reference to algal epiphytes. In *Encyclopedia of plant physiology*. pp. 113-33 in Ed. H-F Linskens, J Heslop-Harrison. Berlin: Springer.

Eacott G. 2000. Geochemical interactions between calcareous epibionts and their substrates: potential significance for palaeoenvironmental analysis. Honours thesis. Adelaide: Adelaide University. 101 pp.

Eckman JE. 1983. Hydrodynamic processes affecting benthic recruitment. *Limonology and Oceanography* 28: 241-257.

Edgar GJ. 1997. *Australian Marine Life: the plants and animals of temperate waters*. Kew: Reed Books.

Edyvane K. 1999a. *Conserving Marine Biodiversity in South Australia, Part 1. Background, Status and Review of Approach to Marine Biodiversity.* Conservation in South Australia. Report 38. Adelaide: PIRSA, SARDI.

Edyvane K. 1999b. *Conserving Marine Biodiversity in South Australia, Part 2. Identification of Areas of High Conservation Value in South Australia.* Conservation in South Australia, Report 39. Adelaide: PIRSA, SARDI.

Eggleston D. 1972. Patterns of reproduction in the marine Ectoprocta of the Isle of Man. *Journal of Natural History* 6: 31-38.

Encyclopaedia Britannica Inc. 1998. www.britannicaq.com.

Encyclopaedia Britannica Inc. 2000.www.britannica.com.

English S, Wilkinson C & Baker V. 1997. *Survey Manual for Tropical Marine Resources*. Townsville: Australian Institute of Marine Science. 390 pp.

EPA. 1998. *Changes in seagrass coverage and links to water quality off the Adelaide metropolitan coastline*. Adelaide: Environment Protection Agency.

Fairhead A. 2001. Ecophysiological and production ecology of the kelp *Ecklonia radiata* (C Agardh) at West Island, South Australia. PhD thesis. Adelaide: University of Adelaide.

Figueiredo MA, Norton TA & Kain JM. 1997. Settlement and survival of epiphytes on two intertidal crustose coralline algae. *Journal of Experimental Marine Biology and Ecology* 213: 247-260.

Fitzpatrick J & Kirkham H. 1995. Effects of prolonged shading stress on growth and survival of seagrass *Posidonia australis* in Jervis Bay, New South Wales, Australia. *Marine Ecology Progress Series* 127: 279-289.

Fonseca MS, Fisher JR & Zieman JC. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine, Coastal and Shelf Science* 15: 351-364.

Fonseca MS & Kenworthy WJ. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* 27: 59-78.

Frankovich TA & Zieman JC. 1994. Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science* 54: 679-695.

Frankovich TA & Zieman JC. 1995. A comparison of methods for the accurate measurement of Epiphytic carbonate. *Estuaries* 18: 279-284.

Frenkel H. 1974. Observations on some shallow benthonic foraminifera in the Gulf of Elat, Israel. *Journal of Earth Sciences* 23: 63-67.

Friday A & Ingram D. 1985. *The Cambridge Encyclopedia of Life Sciences*. Cambridge: Cambridge University Press.

Gaffey SJ & Bronnimann C.E. 1993. Effects of bleaching on organic and mineral phases in biogenic carbonates. *Journal Sedimentary Petrology* 63: 752-754.

Gerard VA. 1982. *In situ* water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. *Marine Biology* 69: 51-54.

Gordon DM, Grey KA, Chase SC & Simpson CJ. 1994. Changes to the structure and productivity of a *Posidonia sinuosa* meadow, during and after imposed shading. *Aquatic Botany* 47: 265-275.

Greig TJ. 2000. Investigating the effects of substrate texture on the recruitment of sessile marine organisms: an experimental approach. Honours thesis. University of Adelaide, Adelaide. 42 pp.

Hageman SJ, Bone Y, McGowran B & James NP. 1996a. Bryozoan species distributions on the cool-water Lacepede Shelf, southern Australia. In *Bryozoans in space and time: Proceedings of the 10th International Bryozoology conference*, ed. DP Gordon, AM Smith & JA Grant-Mackie, pp. 109-17. Wellington, New Zealand: NIWA.

Hallock P, Cottey TL, Forward LB, Halas J. 1986. Population biology and sediment production of *Archaias angulatis* Foraminiferida in Largo Sound, Florida, USA. *Journal of Foraminiferal Research* 16: 1-8.

Hamamoto K & Mukai H. 1999. Effects of larval settlement and post-settlement mortality on the distribution pattern and abundance of the spirobid Tube Worm *Neodexiospira brasiliensis* (Grube) (Polychaetaa) living on seagrass. Marine Ecology 20: 251-272.

Harbison P & Wiltshire D. 1992. *BHP Marine Environment Studies Report WRO45*, Adelaide: PH Environment.

Harlin MM. 1980. Seagrass epiphytes. pp. 117-51 in RC Phillips & CP McRoy Eds, *Handbook of* *seagrass biology: an ecosystem perspective.* New York: Garland STPM Press.

Hart D. 1997. *Near-shore seagrass change between 1949 and 1996*, Adelaide: Environment Protection Authority, Department of Environment and Natural Eesources, South Australia, and S.A. Water.

Harvey M & Bourget E. 1997. Recruitment of marine invertebrates onto arborescent epibenthic structures: active and passive processes acting at different spatial scales. *Marine Ecology Progress Series* 153: 203-215.

Hayward PJ. 1974. Observations on the bryozoan epiphytes of *Posidonia oceanica* from the island of Chios (Aegean Sea). pp 347-356 In Pouyet S, Ed. *Bryozoa 1974.* Lyon: Université Claude Bernard.

Hegge B. 1998. *Estimates of in situ calcium carbonate production on Success Bank, Owen Anchorage (Western Australia). Report 95/008/3.* Perth: DA Lord & Associates Pty Ltd.

Heijs FML. 1984. Annual biomass and production of epiphytes in 3 monospecific seagrass communities of *Thalassia hemprichii* (Ehrenb. Ashchers.). *Aquatic Botany* 20: 195-218.

Heijs FML. 1985. The seasonal distribution and community structure of epiphytic algae on *Thalassia hemprichii* (Ehrenb. Ashcers) from Papua New Guinea. *Aquatic Botany:* 21: 295-324.

Hillman K, McComb AJ, & Walker DI. 1995. The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the Swan Canning estuary, Western Australia. *Aquatic Botany* 51: 1-54.

Hillman K, Morrison PF, Jernakoff P & Nielsen J. 1994. *Perth coastal water study: Determination of time series changes in marine communities. Report Project E2*, Perth: Water Authority of Western Australia.

Hillman K, Walker DI, McComb AJ & Larkum AWD. 1989. Productivity and nutrient limitation. In *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Ed. AWD Larkum, AJ McComb & SA Shepherd. Amsterdam: Elsevier 841 pp.

Hillman K, Lukatelich RJ, Bastyan G & McComb AJ. 1990. *Distribution and biomass of seagrasses and algae, and nutrient pools in water, sediments and plants in Princess Royal Harbour and Oyster Harbour.* Perth: Environmental Protection Authority Technical Series 40.

Hoffman A. 1977. Synecology of macrobenthic assemblages of the Koryntnica clays (Middle Miocene: Holy Cross Mountains, Poland). *Acta Geologica Polonica* 27: 227-280.

Holmes NJ, Harriott VJ & Banks SA. 1997. Latitudinal variation in patterns of colonisation of cryptic calcareous marine organisms. *Marine Ecology Progress Series* 155: 103-113.

Hooker JD. 1858. The botany of the Anyarctic voyage of HM Discovery ships *Erebus* and *Terror* in the years 1839-1843. III Flora Tasmaniae. London: Reeve.

Horner SMJ. 1987. Similarity of epiphyte biomass distribution on *Posidonia* and artificial seagrass leaves. *Aquatic Botany* 27: 159-163.

Howard RK, Edgar GJ & Hutchings PA. 1989. Faunal assemblages of seagrass beds. pp 536-564 In *Seagrasses: a treatise on the biology of seagrasses with special reference to the Australasian region.* Ed. AWD Larkum, AJ McComb & SA Shepherd. Amsterdam: Elsevier.

Humm HJ. 1964. Epiphytes of the sea grass *Thalassia testudinum. Bulletin Marine Science* 14: 306-341.

Hunt HL & Scheibling RE. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* 155: 269-301.

Hutchings PA, Wells FE, Walker DI & Kendrick GA. 1991. *Seagrass, sediment and infauna - A comparison of* Posidonia sinuosa *and* Amphibolis antarctica, *Princess Royal Harbour, South Western Australia. II Distribution, composition and abundance of macrofauna.* Presented at Proceedings of the Third International Marine Biological Workshop: the Flora and Fauna of Albany, Perth: Western Australia.

Ichiki S, Mizuta H & Yamamoto H. 2000. Effects of irradiance, water temperature and nutrients on the growth of sporelings of the crustose coralline alga *Lithophyllum yessoense* Foslie (Corallinalies, Rhodophyceae). *Phycological Research* 48: 115-120.

Issacs A, Daintith J & Martin E. 1996. *Concise Science Dictionary*. Oxford: Oxford University Press.

James NP, Bone Y, von der Borch CC & Gostin VA. 1992. Modern carbonate and terrrigenous clastic sediments on a cool water, high energy, mid-latitude shelf, Lacepede Shelf, southern Australia. *Sedimentology* 39: 877-903.

James NP, Bone Y, Collins LB & Kyser TK. 2001. Surficial sediments of the Great Australian Bight: facies dynamics and oceanography on a vast cool-water carbonate shelf. *Journal of Sedimentary Research* 71: 549-567.

James NP & Bone Y. 2000. Eocene cool-water carbonate and biosiliceous sedimentation dynamics, St. Vincent Basin, South Australia. *Sedimentology* 47: 761-786.

Jernakoff P, Brearley A & Nielsen J. 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. pp 109-162 In *Oceanography and Marine Biology: An annual review*. Ed. AD Ansell, RN Gibson & MB Barnes. 43: 109-62. London: Allen & Unwin.

Jernakoff P & Nielsen J. 1997. The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. *Aquatic Botany* 56: 183-202.

Jernakoff P & Nielsen J. 1998. Plant-animal associations in two species of segrasses in Western Australia. *Aquatic Botany* 60: 359-376.

Johansen HW. 1981. *Coralline algae, a first synthesis*. Boca Raton, Florida: CRC Press.

Johhnstone IM. 1982. Ecology and distribution of the seagrasses. *Monographiae Biologicae* 42: 497-552.

Jones PL & Woekerling WJ. 1983. Some effects of light and temperature on growth and conceptacle production in *Fosliella cruciata* Bressan (Corallinaceae, Rhodophyta). *Phycologia* 22: 449-452.

Kendrick G, Campey M, Lavery P, Westera M & Wheeler K. 1998a. *Shells and dredging environmental management programme. Project S1: Ecological significance of seagrass. Primary Production Report, Project S1, Task 7*. Perth: The University of Western Australia and Edith Cowan University.

Kendrick GA, Langtry S. Fitzpatrick J, Griffiths R & Jacoby CA. 1998b. Benthic microalgae and nutrient dynamics in wave-disturbed environments in Marmion Lagoon, Western Australia, compared with less disturbed mesocosms. *Journal of Experimental Marine Biology and Ecology* 228: 83-105.

Keough MJ. 1983. Patterns of recruitment of sessile invertebrates in two subtidal habitats. *Journal of Experimental Marine Biology & Ecology* 66: 213-245.

Keough MJ & Jenkins GP. 2000. Seagrass meadows and their inhabitants. pp. 221-239 in AJ Underwood & MG Chapman eds. *Coastal marine ecology of temperate Australia*. Sydney: University of New South Wales Press.

Keough MJ & Raimondi PT. 1995. Responses of settling invertebrate larvae to bioorganic films: effects of different types of films. *Journal of Experimental and Marine Biology and Ecology* 207: 59-78.

Kikuchi T. 1980. Faunal relationships in temperate seagrass. pp. 153-172 In *Handbook of seagrass biology: an ecosystem perspective*. Ed. RCM Phillips & CP McRoy. New York: Garland STPM Press.

King RJ, Hutchings PA, Larkum AWD & West RJ. 1991. Southeastern Australia. pp. 429-459 In *Intertidal and Littoral Ecosytems*. Ed. AC Mathieson & PH Nienhuis.

Kirkman H. 1997. *Seagrasses of Australia*. Australia, State of the Environment Technical Paper Series (Estuaries & Seas). Canberra: Department of the Environment. 12 pp.

Kirkman H, Griffiths FB & Parker RR. 1979. The release of reactive phosphate by a *Posidonia* *australis* seagrass community. *Aquatic Botany* 6: 329-337.

Kirkman H & Kuo J. 1990. Pattern and process in southern Western Australian seagrasses. *Aquatic Botany* 37: 367-382.

Kirkman H & Reid DD. 1979. A study of the role of seagrass *Posidonia australis* in the carbon budget of an estuary. *Aquatic Botany* 7:173-183.

Kirkwood LF. 1967. *Inorganic phosphate, organic phosphorous and nitrate in Australian waters.* CSIRO Australian Division of Fisheries & Oceanography Technical Paper 25.

Klumpp DW, Salita Espinosa JS & Fortes MD. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquatic Botany* 43: 327-349.

Knight-Jones P & Knight-Jones EW 1973. Spirobinae (Serpulidae: Polychaeta) from south-eastern Australia. A new genus, four new subgenera and seven new species. *The Bulletin of the British Museum (Natural History)* 24: 230-257.

Lalli CM & Parsons TR. 1997. *Biological oceanography: an introduction.* Oxford: Reed Elsevier. 314 pp.

Land LS. 1970. Carbonate mud: production by epibiont growth on *Thalassia testudinum. Journal of Sedimentary Petrology* 40: 1361-1363.

Langer MR. 1993. Epiphytic foraminifera. *Marine Micropaleontology* 20: 235-265.

Langer MR, Silk MT & Lipps JH. 1997. Global carbonate and carbon dioxide production: the role of reef foraminifera. *Journal of Foraminiferal Research* 27: 271-277.

Lapointe BE, Tomasko, DA & Metzie WR. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* 54: 696-717.

Larkum AWD, McComb AJ & Shepherd SA. 1989. *The biology of seagrasses.* Amsterdam: Elsevier. 841 pp.

Larkum AWD & den Hartog C. 1989. Evolution and biogeography of seagrasses. In *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Ed. AWD Larkum, AJ McComb & SA Shepherd. 841 pp. Amsterdam: Elsevier.

Lavery P & Vanderklift MA 2000. Comparison of spatial patterns in seagrass epiphyte assemblages using species and functional group-level data. *Biologia Marina Meditarranea* 7: 251-254.

Lavery P, Vanderklift M, Brearley A, Hyndes G & Wells F. 1998. Cockburn Cement Shells and Dredging Environmental Management Programme. The Ecological Significance of Seagrasses on Success Bank; Flora and Fauna Diversity. Final report of project S-1 Task 6 to Cockburn Cement Pty. Ltd. Dec 1998.

Lavery P, Westera M, Kendrick G, Brearley A, Campey M, Hegge B & Hillman DK. 2000. *Shells and dredging environmental management programme.* Perth: The University of Western Australia and Edith Cowan University.

Lawrence E. 1989. *Henderson's dictionary of biological terms.* London: Longman Scientific and Technical.

Lethbridge RC, Borowitzka MA, Benjamin KJ. 1988. The development of an artificial *Amphibolis*-like seagrass of complex morphology and preliminary data on its colonization by epiphytes. *Aquatic Botany* 31: 153-168.

Leukart P. 1994. Field and laboratory studies on depth dependence, seasonality and light requirements of growth in three species of crustose coralline algae (Corallinales, Rhodophyta). *Phycologia* 33: 281-290.

Lewis R, Aust T, Clarke S, Edyvane K, Fisher R, Fotheringham D, McLennan B, McShane P, Newland N, Noye J, Neverauskas V, Steffensen D, White M., Zacharin W & Zeidler W. 1997. *Description, use and management of South Australia's Marine and estuarine environment.* Adelaide: The South Australian Marine and Esturaine Strategy Comittee.

Lisitzin AP. 1996. *Oceanic sedimentation: lithology and geochemistry.* Washington, AGU.

Lobban CS & Harrison PG. 1994. *Seaweed Ecology and Physiology.* Cambridge: Cambridge University Press.

Lord D Associates. 1998a. *Estimate of* in situ *calcium carbonate production on Success Bank, Owen Anchorage (Western Australia)*, DA Lord & Associates Pty Ltd. Prepared for Cockburn Cement Limited, Perth.

Lord D Associates. 1998b. *Association between seagrass meadows and sediments on Success Bank, Owen Anchorage (Western Australia). Report 95/008/3*, Prepared for Cockburn Cement Limited, Perth.

Mann KH. 1982. Seagrass, Marsh grass and Mangrove systems. In *Studies in ecology. ecology of coastal waters: a systems approach.* Melbourne: Blackwell Scientific.

Marbà N & Walker DI. 1999. Growth, flowering, and population dynamics of temperate Western Australian seagrasses. *Marine Ecology Progress Series* 184: 105-118.

Masini RJ. 1990. The ecological significance of benthic macroalgae in Western Australian aquatic ecosystems. PhD thesis. University of Western Australia, Perth. 191 pp.

Masini RJ, Cary JL, Simpson CJ & McComb AJ. 1990. *Effects of light and temperature on the photosynthesis of seagrasses, epiphytes and macroalgae and implications for management of the Albany harbours.* Perth: Environmental Protection Authority Technical Series 32.

Masini RJ & Manning CR. 1997. The photosynthetic responses to irradiance and temperature of four meadow-forming seagrasses. *Aquatic Botany* 58: 21-36.

May V, Collins AJ & Collett LC. 1978. A comparitive study of epiphytic algal communities on two common genera of seagrasses in eastern Australia. *Australian Journal of Ecology* 3: 91-104.

Mazzella L & Alberte RS. 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. *Journal of Experimental Marine Biology & Ecology* 100: 165-180.

McKerrow WS. 1986. Oceans, island-arcs and olistostromes: the use of fossils in distinguishing sututes, terranes and environments around the Iapetus Ocean. Journal of the Geological Society of London 143: 185-191.

McKinney FK & Jackson JBC. 1989. *Bryozoan evolution.* Boston: Unwin Hyman. 238 pp.

McRoy CP & Helfferich C. 1980. Applied aspects of seagrasses. In *Handbook of seagrass biology: an ecosystem perspective*, ed. RC Phillips & McRoy CP. New York: Garland STPM Press.

Menon NR. 1972. Heat tolerance, growth and regeneration in three North Sea bryozoans exposed to different constant temperatures. *Marine Biology* 15: 1-11.

Milliman JD & Droxler A. 1996. Neritic and pelagic carbonate sedimentation in the marine environment: ignorance is not bliss. *Geology Rundschau* 85: 496-504.

Milliman JD, Troy PJ, Balch WM, Adams AK, Li Y-H & Mackenzie FT. 1999. Biologically mediated dissolution of calcium carbonate above the chemcial lysocline? *Deep Sea Research* 46: 1653-1669.

Moore KA, Neckles HA & Orth RJ. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Series* 142: 247-259.

Morgan D & Kitting CL. 1984. Productivity and utilisation of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnology & Oceanography* 29: 1066-1076.

Nels~~o~~en JE & Ginsburg RN. 1986. Calcium carbonate production by epibionts on *Thalassia* in Florida Bay. *Journal of Sedimentary Petrology* 56: 622-628.

Nelson JE, Keane SL & Head PS. 1988. Non-tropical carbonate deposits on the modern New Zealand shelf. In Nelson CS (ed.) Non-tropical shelf carbonates - modern and ancient. *Sedimentary*

Geology 60: 71-94..

Neu TR. 1994. Biofilms and microbial mats. In *Biostabilization of sediments*. pp. 9-15 In Ed. WE Krumbein, DM Paterson & LJ Stal. Oldenburg, Germany: Bibliotheks und Informationssytem - Verlag.

Neverauskas V. 1987. *Port Adelaide Sewage Treatment Works Sludge Outfall. Effect of Discharge on the Adjacent Marine Environment.* Adelaide: Engineering and Water Supply Department, South Australia.

Neverauskas V. 1988a. Accumulation of periphyton on artificial substrata near sewage sludge outfalls at Glenelg and Port Adelaide, South Australia. *Transactions of the Royal Society of South Australia* 112: 175-177.

Neverauskas V. 1988b. Response of a *Posidonia* community to prolonged reduction in light. *Aquatic Botany* 31: 361-366.

O'Dea A & Okamura B. 1999. The influence of seasonal variation in temperature, salinity and food availability on module size and colony growth in the estuarine bryozoan, *Conopeum seurati*. *Marine Biology* 135: 581-588.

O'Dea A & Okamura B. 2000. Life history and environmental inferences through retrospective morphometric analysis of bryozoans: a preliminary study. *Journal of the Marine Biology Association*: 3596-3599.

Ólafsson EB, Peterson CH & Ambrose WGJ. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Annual Review Oceanography & Marine Biology* 32: 65-109.

Paton JB & Paton DC. 1977. Seabird Islands No. 51 West Island. *South Australia Corella* 1: 68-69.

Patriquin DG. 1972. Carbonate mud production by epibionts on Thalassia: an estimate based on leaf growth rate data. *Journal of Sedimentary Petrology* 42: 687-689.

Pawlik JR. 1992. Chemical ecology of the settlment of benthic marine invertebrates. *Oceanography and Marine Biology: an annual review* 30: 273-335.

Penhale PA. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *Journal of Experimental Marine Biology & Ecology* 26: 211-224.

Penrose D & Chamberlain YM. 1993. *Hydrolithon farinsoum* (Lamouroux) comb. nov: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 32: 295-303.

Pergent G & Pergent-Martini C. 1999. A study of Morph-chronological variations in four species of marine phanerograms of the genus *Posidonia*. In *The Seagrass Flora and Fauna of Rottnest Island, Western Australia*. pp. 25-40 In Ed. DI Walker, & FE Wells. Perth: Western Australian Museum.

Peterson CH, Summerson HC & Duncan PB. 1984. The influence of seagrass cover on population structure and individual growth of a suspension feeding bivalve, *Mercenaria mercenaria*. *Journal of Marine Research* 42: 123-138.

Petta TJ & Gerhard LC. 1977. Marine grass banks - a possible explanation for carbonate lenses, Tepee zone, Pierre Shale (Cretaceous), Colarado. *Journal of Sedimentary Petrology* 47: 1018-1026.

Poag CW. 1982. Environmental implications of test-to-substrate attachment among some modern sublittoral foraminifera. *Geological Society of America Bulletin* 93: 252-268.

Pollard DA. 1984. A review of ecological studies on seagrass - fish communities, with particular reference to recent studies in Australia. *Aquatic Botany* 18: 3-42.

Ralph PJ & Gademann R. 1999. Photosynthesis of the seagrass *Posidonia australia* Hook. f and associated epiphytes, measured by *in situ* fluorescence analysis. In *The Seagrass Flora and Fauna of Rottnest Island, Western Australia*. pp. 63-71 In Ed. DIW Walker & FE Wells. Perth:

Western Australian Museum.

Reyes J & Sanson M. 2001. Biomass and production of the epiphytes on the leaves of *Cymodocea nodosa* in the Canary Islands. *Botanica Marina* 44: 307-313.

Ribes T, Salvadó H, Romero J & Gracia M. 2000. Foraminiferal colonization on artificial seagrass leaves. *Journal of Foraminiferal Research* 30: 192-201.

Robertson AI. 1980. The structure and organisation of an eelgrass fish fauna. *Oecologia* 47: 76-82.

Robertson EL. 1984. Seagrasses. In *The Marine Benthic Flora of Southern Australia, Part 1.* pp.57-122 In Ed. HBS Womersley. Adelaide: South Australia, Goverment Printer.

Robertson EL. 1986. Family Posidoniaceae. In *Flora of Australia Part IV.* pp. 1724-1729 In Ed. JP Jessop & HB Toelken. Adelaide: South Australia, Government Printer.

Robinson T, Canty P, Mooney T & Ruddock P. 1996. *South Australia's Offshore Islands.* Canberra: Australian Heritage Commission.

Rochford DJ. 1984. Effect of the Leeuwin Current upon sea surface temperatures off southwestern Australia. *Australian Journal of Marine and Freshwater Research* 35: 487-489.

Rochford DJ. 1986. Seasonal changes in the distribution of Leeuwin Current waters off Southern Australia. *Australian Journal of Marine and Freshwater Research* 37: 1-10.

Rodríguez A, Ojeda FP & Inestrosa NC. 1993. Settlment of benthic marine larvae. *Marine Ecology Progress Series* 97: 193-207.

Ronov AB & Yaroshevskiy AA. 1969. Chemical composition of the Earth's crust. *The Earth's crust and upper mantle.* American Geophysical Union, Washington 13: 37-57.

Roughgarden J, Gaines S & Possingham H. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460-1466.

Russel DJ. 1990. Epiphytes: biomass and abundance. pp. 113-114 In Eds. RC Phillips & CP McRoy *Seagrass Research Methods.* Paris: UNESCO.

Ryland JS. 1970. *Bryozoans.* London: Hutchinson University Library.

Ryland JS. 1976. Physiology and ecology of marine bryozoans. *Advances in Marine Biology* 14: 285-443.

Sanderson GW & Thorpe JP. 1996. Effects of temperature on the feeding activity of some temperate intertidal Bryozoa. In *Bryozoans in space and time: Proceedings of the 10th International Bryozoology conference.* pp. 271-281 In Ed. DP Gordon, AM Smith & JA Grant-Mackie. Wellington, New Zealand: NIWA.

Saunders R & Connell SD. 2001. Interactive effects of shade and surface orientation on the recruitment of spirobid polycheates. *Austral Ecology* 26: 109-215.

Scheer BT. 1945. The development of marine fouling communities. *Biological Bulletin* 89: 103-121.

Scholz J & Krumbein WE. 1996. Microbial mats and biofilms associated with bryozoans. pp. 283-298 In *Bryozoans in space and time: Proceedings of the 10th International Bryozoology conference.* Ed. DP Gordon, AM Smith & JA Grant-Mackie. Wellington, New Zealand: NIWA.

Scoffin TP. 1971. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology* 40: 249-273.

Sculthorpe CD. 1967. *The biology of Aquatic Vascular plants.* London: Edward Arnold.

Searle DJ. 1984. *Sediment Transport System, Perth Sector Rottnest Shelf, Western Australia.* Perth: University of Western Australia.

Seddon S. 2000. Causes and ecological consequences of the Spencer Gulf seagrass dieback. PhD thesis, University of Adelaide. 171 pp.

Seddon S, Connolly RM & Edyvane KS. 2000. Large-scale seagrass dieback in northern Spencer

Gulf, South Australia. *Aquatic Botany* 66: 297-310.

Semeniuk TA. 2001. Epiphytic foraminifera along a climatic gradient, Western Australia. *Journal of Foraminiferal Research* 31: 191-200.

Shepherd SA. 1970. *Prelimary report upon degradation of seagrass beds at North Glenelg. Report 33.* Adelaide: Department of Fisheries.

Shepherd SA. 1973. Studies on southern Australian abalone genus *Haliotis*, I Ecology of five sympatric species. *Journal of Marine and Freshwater Research* 24: 217-257.

Shepherd SA, McComb AJ, Bulthius DA, Neverauskas V, Steffensen DA & West R 1989. Decline of seagrasses. In *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Ed. AWD Larkum, McComb AJ & Shepherd SA. 841 pp. Amsterdam: Elsevier.

Shepherd SA & Robertson EL. 1989. Regional studies - seagrasses of South Australia, western Victoria and Bass Strait. In *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Ed. AWD Larkum, AJ McComb & SA Shepherd. 841 pp. Amsterdam: Elsevier.

Shepherd SA & Thomas IM. 1982. *Marine invertebrates of southern Australia, part 1.* Adelaide: DJ Woolman, Goverment Printer. 491 pp.

Short FT. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquatic Botany* 27: 41-57.

Silberstein K. 1985. *The effects of epiphytes on seagrasses in Cockburn Sound, Western Australia. Report 63.* Perth: Department of Conservation and Environment,

Silberstein K, Chiffings AW & McComb AJ. 1986. The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook. F. *Aquatic Botany* 24: 355-371.

Sim CB.1991. Analysis of calcium carbonate from coralline epiphytes (Corallinaceae Rhodophyta) of the seagrass *Amphibolis antarctica* (Labill.) Sonder et Aschers. Honours thesis, Deaprtmetn of Botany, University of Western Australia, Perth.

Sim CB. 1999. Recruitment ecology of crustose coralline algae (Corallinales, Rhodophyta) at Rottnest Island, Western Australia. Unpublished PhD thesis, Botany Department, University of Western Australia, Perth.

Sladeckova A. 1962. Limnological investigation methods for the periphyton community. *Botany Review* 28: 286-350.

SMCWS. 1996. *Southern Metropolitan Coastal Waters Study (1991-1994). Final Report, Report 17.* Perth, Western Australia: Department of Environmental Protection.

Smith SV. 1972. Production of calcium carbonate on the mainland shelf of Southern California. *Limnology & Oceanography* 17: 28-41.

Smith SV & Atkinson MJ. 1983. Mass balance of carbon and phosphorus in Shark Bay, Western Australia. *Limnology & Oceanography* 28: 625-639.

Soule JD & Soule DF. 1977. Fouling and bioadhesion: life strategies of bryozoa. pp. 437-457 In *Biology of bryozoans.* Ed. RM Woollacott & RL Zimmer. London: Academic Press.

Spindler M. 1980. The pelagic gulfweed *Sargassum natans* as a habitat for the benthic Foraminifera *Planorbulina acervalis* and *Rosalina globularis. Fossilvergesellschaftungen* 111.

Steinker PJ & Steinker DC. 1976. Shallow-water foraminifera, Jewish Cay, Bahamas. *Marine Sedimentology Special Publication* 1: 171-180.

Steneck RS. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative strategies. *Annual Review of Ecology and Systematics* 17: 273-303.

Stevenson J & Melville AJ. 1999. Settlement and recruitment of the abalone *Haliotis cyclobates*

Péron, 1816. *Marine and Freshwater Research* 50: 229-234.

Ström R. 1977. Brooding patterns of bryozoa. In *Biology of bryozoans.* pp. 23-55 In Ed. RM Woollacott & RL Zimmer. London: Academic Press.

Taylor PD. 1990. Encrusters. pp. 346-351 In *Paleobiology; a synthesis.* Ed. DEG Briggs & Crowther PR. Melbourne: Blackwell Scientific Publications.

Terrados J & Duarte CM. 2000. Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. *Journal of Experimental Marine Biology and Ecology* 243: 45-53.

Thomas DP. 1978. The ecology of diatom epiphytes of *Zostera* sp. in the Onkaparinga Estuary, South Australia (1974-1977). PhD thesis University of Adelaide. 162 pp.

Thomas RI & Clarke SM. 1987. Sedimentology and morphology of clastic seagrass beds in Holdfast Bay, South Australia. *Estuarine, Coastal and Shelf Science* 57.

Thomas RI & Clarke SM. 2002. Sedimentolgy and morphology of clastic seagrass beds in Holdfast Bay, South Australia. *Seagrass Restoration Workshop for Gulf St Vincent, 15-16 May 2001.*

Todd CD & Turner SJ. 1986. Ecology of intertidal and sublittoral cryptic epifaunal assemblages, I. Experimental rationale and the analysis of larval settlement. *Journal of Experimental Marine Biology & Ecology* 99: 199-231.

Trautman DA & Borowitzka MA. 1999. Distributon of the epiphytic organisms on *Posidonia australia* and *P. sinuosa*, two seagrasses with differeing leaf morphology. *Marine Ecology Progress Series* 179: 215-229.

Tucker ME & Wright PV. 1990. *Carbonate sedimentology.* Oxford: Blackwell. 482 pp.

Turner JV. 1982. Kinetic fractionation of carbon-13 during calcium carbonate precipitation. *Geochemica et Cosmochimica Acta* 46: 1183-1191.

Turner SJ & Todd CD. 1993. The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rock shore in St. Andrews Bay, N.E. Scotland. *Journal of Experimental Marine Biology & Ecology* 166: 252-272.

Turner SJ & Todd CD. 1994. Competition for space in encrusting bryozoan assemblages: the influence of encounter angle, site and year. *Journal of the Marine Biological Association of the United Kingdom* 74: 603-622.

Udy JW & Dennison WC. 1997a. Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. *Journal of Experimental Marine Biology and Ecology* 217: 253-277.

Udy JW & Dennison WC. 1997b. Physiological responses of seagrasses used to identify anthropogenic nutrient inputs. *Marine and Freshwater Research* 48: 605-614.

Udy JW & Dennison WC. 1999. Seagrass and sediment nutrients: Species comparison and fertilisation responses at Rottnest Island. pp. 73-87 In *The Seagrass Flora and Fauna of Rottnest Island, Western Australia.* Ed. DI Walker & FE Wells. Perth: Western Australian Museum.

Underwood AJ. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Annual Review of Oceanography and Marine Biology* 19: 513-605.

van Keulen M. 1995. *What are seagrasses*? Perth: Murdoch University.

Walker CJ & Cambridge ML. 1995. An experimental assessment of the temperature responses of two sympatric seagrasses, *Amphibolis antarctica* and *Amphibolis griffithii*, in relation to their biogeography. *Hydrobiologia* 302: 63-70.

Walker DI. 1985. Correlations between salinity and growth of the seagrass *Amphibolis antarctica* in Shark Bay, Western Australia, using a new method of measuring production rate. *Aquatic Botany* 23: 13-26.

Walker DI. 1991. The effect of sea temperature on seagrasses and algae on the Western Australian coastline. *Journal of the Royal Society of Western Australia* 74: 71-77.

Walker DI, Dennison WC & Edgar G. 1999. Status of Australian seagrass research and knowledge. pp. 1-24 In *Seagrass in Australia: Strategic review and development of an R&D plan.* Ed. AP

Butler P Jernakoff. Collingwood: CSIRO Publishing.

Walker DI, Hutchings PA & Wells FE. 1991. *Seagrass sediment and infauna - A comparison of* Posidonia sinuosa *and* Amphibolis antarctica, *Princess Royal Harbour, south Western Australia: I. Seagrass biomass productivity and contribution to sediments.* Presented at Proceedings of the Third International Marine Biological Workshop: the Flora and Fauna of Albany, Perth, Western Australia.

Walker DI & McComb AJ. 1990. Salinity response of the seagrass *Amphibolis antarctica* (Labill.) Sonder et Aschers. *Aquatic Botany* 36: 359-366.

Walker DI & McComb AJ. 1988. Seasonal variation in the production, biomass and nutrient status of *Amphibolis antarcica* (Labill.) Sonder et Aschers, and *Posidonea australis* Hook.f. in Shark Bay, Western Australia. *Aquatic Botany* 31: 259-275.

Walker DI & Woelkerling WJ. 1988. Quantitative study of sediment contribution by epiphytic coralline red algae in seagrass meadows in Shark Bay, Western Australia. *Marine Ecology - Progress Series* 43: 71-77.

Wanless HR. 1981. Fining-upward sedimentary sequences generated in seagrass beds. *Journal of Sedimentary Petrology* 51: 445-454.

Waycott M & Les DH. 1996. An Integrated Approach to the Evolutionary Study of Seagrasses. In *Seagrass Biology*. Ed. J Kuo, DI Walker, RC Phillips & H Kirkman. Perth: Faculty of Science, The University of Western Australia.

Webster TJM & Parnankape MA. 1977. Sedimentation of organic matter in St. Margerete Bay, Nova Scotia. *Journal of the Canadian Fisheries Research Board* 32: 1399-1407.

West RJ & Larkum AWD. 1982. Seagrass primary production - a review. *Proceedingsof the Linnaean Society of New South Wales* 106: 213-223.

West RJ & Larkum AWD. 1979. Leaf productivity of the seagrass, *Posidonia australis*, in eastern Australian waters. *Aquatic Botany* 7: 57-65.

Wetzel RL & Penhale PA. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Marine Technical Society Journal* 17: 22-31.

Wheeler WN. 1980. Effect of boundary layer transport on fixation of carbon by the giant kelp *Macrosystis pyrifera. Marine Biology* 56: 103-110.

- 2000

Whitten DGA & Brooks JRV. 1972. *Dictionary of geology*. London: Penguin books.

Womersley HBS. 1984. *The marine benthic flora of Southern Australia: Part 1, Introduction.* Adelaide: South Australian Biological Printing Division. 484 pp.

Womersley HBS. 1987. *The marine benthic flora of Southern Australia: Part II.* Adelaide: South Australian Biological Printing Division. 484 pp.

Womersley HBS. 1994a. *The marine benthic flora of Southern Australia: Part IIIA.* Adelaide: South Australian Biological Printing Division. 484 pp.

Womersley HBS. 1994b. *The marine benthic flora of southern Australia; Rhodophyta.* Canberra: Australian Biological Resources study

Womersley HBS. 1996. *The marine benthic flora of southern Australia.* Canberra: Australian Biological Resources Study. 392 pp.

Wright CA & Murray JW. 1972. Comparisons of modern and Palaeogene foraminiferal distributions and their environmental implications. *Memoires du Bureau de Recherches Geologiques et Minieres* 79: 87-96.

Yallop ML & Paterson DM. 1994. Seasonal field studies: survey of Severn Estuary. pp. 279-338 In *Biostabilization of sediments*. Ed. WE Krumbein, DM Paterson & LJ Stal. Oldenburg, Germany: Bibliotheks und Informationssytem - Verlag.

Yassini I & Jones BG. 1995. *Recent foraminifera and ostracoda from estuarine and shelf environments on the southeastern coast of Australia.* Wollongong, NSW: University of Wollongong Press. 484 pp.

Yates K & Halley R. 1999. Geochemical measurements of carbonate sediment production and organic productivity in Florida Bay: a potential measure of restoration progress. p.109 in Proceedings, 1999 Florida Bay and adjacent marine systems Science Conference, Key Largo, Florida, November 1-5, 1999.

Young PC. 1987. Moreton Bay, Queensland: a nursery area for juvenile penaeid prawns. *Australian Journal of Marine and Freshwater Research* 38: 745-773.

Zann LP. 2000. The Eastern Australian Region: a dynamic tropical/temperate biotone. *Marine Pollution Bulletin* 41: 188-203.

Zar JH. 1996. *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall. 662 pp.

Zieman JC. 1968. *A study of the growth and decomposition of the sea-grass,* Thalassia testudinum. MSc thesis, University of Miami, Miami. 50 pp.

Zieman JC. 1974. Methods for the study of the growth and production of turtle grass *Thalassia testudinum* Koni. *Aquaculture* 4: 139-143.

Zieman JC & Wetzel RG. 1980. Productivity in seagrass: methods and rates. In *Handbook of seagrass biology: an ecosystem perspective.* Ed. RC Phillips & McComb CP. 97 pp. New York: Garland STPM Press.

09PH
B8772
c.2

Kirsty Brown

Calcareous epiphytes on modern seagrasses as carbonate sediment producers in shallow cool-water marine environments, South Australia

Other Comments (to accompany thesis report)

The presentation of the thesis is of a good standard. The writing is clear and lucid and generally free from errors. Where these do occur the text has been corrected in pencil and these corrections are listed in the sheets to be inserted at the back of the thesis. The CD in the back pocket is a very useful addition to the thesis; in particular as a compilation of the raw data on, for example, coralline and bryozoan occurrence and abundance but also to illustrate the different carbonate producers. It will be a useful resource for future workers.

In the introductory chapter the thesis sets out to address five main aims: Do calcareous epiphytes contribute to carbonate sediment of the southern Australian shelf? Do these epiphytes contribute to temperate carbonate sediment production? Do the epiphytic communities produce assemblages that can be used in palaeoenvironmental analysis? Are substrate stabilisation and sediment production by sea grass a significant process in shoreline stability? How do calcareous epiphytes contribute to the global carbonate cycle? All bar the last two are addressed in detail and the research has discovered many new facts, and has formulated and tested new hypotheses on the way that calcareous epiphytes on seagrass produce the calcium carbonate-rich sediments of the southern Australian shelf.

The thesis is very rich in data and the field and labwork involved has clearly taken a very large amount of time. The results however are scientifically sound and chapters 4, 4, 5, 6 and 7 will hopefully lead to posthumous publications. They all represent a significant contribution to science.

Where the thesis is weakest is in the concluding discussion chapter, which I assume the candidate had not completed before her tragic death. The new findings from this careful and thorough research from southern Australia need to be compared with other similar studies from around the world. For example we found no calcareous epiphytes on seagrass in our early studies of temperate carbonate productions off the west of Ireland and how do these results compare with the extensive *Posidonia* beds of the warm temperate area of the Mediterranean? Finally the impact of these new production rates need to be assessed in terms of the entire carbonate system in south Australia. Is it the source of the large amount of preserved temperate carbonate material on the shelf? Does it explain the huge difference between the thickness of carbonate preserved on the south Australian shelf compared with that in the Northeast Atlantic Temperate Carbonate Province where such epiphytes are absent?

Overall, I am happy to recommend the award of PhD for this piece of original scientific work.

Dan Bosence, London (16/07/2005)

K. Brown
Calcareous epiphytes on modern seagrasses as carbonate sediment producers in shallow cool-water marine environments, South Australia

Comments on individual chapters and corrections to text and figures

Chapter 1. Introduction.
Good overview of seagrasses and their epiphytes, but does not assess the known role of calcareous epiphytes in carbonate sediment budgets in present day environments or where this has been interpreted from the fossil record.

Chapter 2. Methods.
Clear and concisely written however confusion may arise over use of term "reef " here and for s number of locality names. As I understand it in this temperate area there are no carbonate dominated organic build-ups such as coral reefs occurring and that the term is being used here in its navigational context as an area of sublittoral rock outcrop. This is not made clear in the text, but has been my assumption in reading the thesis.

Chapter 3. Seagrass biomass and distribution
Careful and thorough documentation of seagrass biomass for various taxa and how this relates to different environmental parameters. Establishes that *Amphibolis* dominated beds have significantly higher biomass than *Posidonia* dominated beds within the study area, but that biomass is highly variable. Biomass peaks at 2-4m and decreases with depth. There is a huge amount of work backing up this rather concise account. 34 transects were diver sampled in 413 quadrats. The lab work took 10 hours plus 1.5 weeks (standing time) so if it is assumed that the diving took 1-2 days per transect then that's 2 weeks per transect equalling 68 weeks work in total for the data for this chapter.

Chapter 4. Calcareous epiphyte production
Important new correlation found between epiphyte abundance and seagrass biomass; which may then be applicable to other areas. Also an unexpected result of 6the exponential increase in epiphytes with increase in biomass. i.e. high epiphyte coverage does not appear to affect the seagrass in any way. Well presented and discussed chapter with new scientific contributions coming from this careful analysis. Discussion of possible controls is well thought out and presented; data are not over-interpreted.

Chapter 5. Seasonal effects on calcareous epiphytes; West Island
This detailed study of two sites shows that calcareous epiphyte biomass varies significantly between different seagrass genera and in *Amphibolis* summer biomass may be 2 to 3 times winter biomass. In detail, carbonate per m2 decreases through autumn to winter but carbonate per kg of seagrass shows a slight increase for this time period, possibly controlled by slower turnover rates of the grass blades in winter. This is new information and throws doubt on production rates in previous studies, albeit from the tropics, that have not considered production from different seagrass taxa or seasonal effects.

Chapter 6. Calcareous epiphytes

Contrary to view in first line of this chapter there are, or is, a study assessing ratios of calcareous epiphytes on seagrass (Bosence 1989 reference in thesis!).

It is unfortunate that the coralline algal taxa (the most abundant epiphytes found) were not identified to similar levels as the bryozoa and foraminifera, however it is accepted that coralline id to species level is specialist and time consuming. Or, were they identified? Page 203 mentions 8 genera occurring but these are not mentioned in the coralline algal section. Similarly 8 genera are mentioned on p. 206 where it also states that the identification in this study was only morphological. So the reader is left with no clear conclusion as to whether identification to generic level was actually carried out. The 8 genera referred to are not listed. This affects the summary section for this chapter where it is stated that the corallines have low species richness. This does not appear to have been ascertained.

High diversity of bryozoans with 65 species and different morphotypes occurring on seagrass and producing an extraordinarily high amount of carbonate (mx. 20g/kg of seagrass. Major difference with respect to subtropical Florida Bay.

I could not find the illustrations of the "other epiphytes" on the CD mentioned in 6.3.7. and from the description given I have no idea either of what these may be.

I would disagree with some of the points made in the discussion section to this chapter on pages 208-9. Whilst the monostromatic Melobesia-Fosliella group that are known to be abundant on grass blades are lightly calcified, and indeed are difficult to preserve within sediments as recognizable particles the thicker, more robust encrusters (her type 1) are preserved and have a good geological record. In Florida Bay the grass encrusting corallines are seen (geochemically and mineralogically) as a major contributor to the Mgcalcite portion of the muds (which are of mixed mineralogy rather than being "mostly aragonite" p. 209). (Refs Bosence 1989, in thesis and Bosence, 1995). These detailed comments do not alter the main findings of this chapter.

(BOSENCE, D.W.J. (1995) Anatomy of a Recent biodetrital mud-mound from Florida Bay, USA. In: Monty, C., Bosence, D.W.J., Bridges, P. and Pratt, B. *Carbonate Mud-Mounds: Their Origin and Evolution.* Special Publication International Association of Sedimentologists)

Chapter 7 Calcareous epiphytic productivity

The seasonal variation in carbonate standing crop, that took a huge investment of time, effort and ingenuity to establish, has been disregarded for annual production rate calculations. This seems a pity as it gives a first order variation that has not been recognised by other workers; winter biomasses are shown to be 2-3 times lower than summer biomasses. Conversely she has taken pains to calculate productivity of different seagrass taxa and blades versus stems in *Amphibolis*.

Table 7.7 is not consistent with table heading or with the text. It seems that the units should be cm/1000 yrs not $CaCO_3$ g/m2/ky? The accumulation rates could usefully have been doubled to allow for porosity in the accumulating sediment.

I hope that others will follow up the "observations" on page 224 that the carbonate composition of the sediment does not increase with increased carbonate productivity by seagrass epiphytes (note the data on this are plotted up in sediment % file in CD and that she comments that this negative relationship is not very strong, or words to that effect!). Similarly it is hoped that the carbonate components of the sediment samples will also be studied in the future as these may well provide the clue as to the fate of the large amount of biogenic carbonate sediment that has been shown in this thesis to be produced by seagrass epiphytes. It is not clear why some 90% of this biogenic carbonate is thought to be recycled or dissolved, there is no evidence to support such a high figure. The discrepancy between production and accumulation might just as well be caused by transport, in which case it might be all accumulating; but somewhere else. My preference is to stick with the figures in Table 7.7 (however it would be very useful for subsequent readers to have the units checked for this table by the supervisors).

Chapter 8 Discussion

This chapter is more conclusions of each chapter and section than a discussion of implication of these conclusions.

Some minor corrections

Refs to Nelson pp 15-16 should read Nelsen,?? And reference amended.
Table 1.2 "Temperate: Western Australia" should this read subtropical to temperate?? It includes Shark Bay. Cf. pp. 30-1 and tropical – subtropical distribution of seagrass.
Page 70. Figure 3.1 is correct here and it contains seven species.
Fig.3.4. > 10 not < 10 mwd
Fig.3.5. individual
Fig. 4.6. Not clear what "transect position" is on these graphs re transects in fig. 2.2.
Fig. 4.8. Spelling of exponential.
Fig. 5.3 B and C. Are these sea floor maps? If so some scale should be added. Text says that sites A and B were sampled by the standard transect method and not a plan area.
p. 158. "Its" rather than "the" seems to make more sense here.
p. 159. Delete "s" in propogule.
p. 161. Environment.
p. 165 delete "are"
p. 169 and fig. 6.1; foramanifera.
p. 169 "were" rather than "was".
p. 169. The coralline algae are said to show a decrease in abundance northward into the Spencer Gulf but some of the highest relative abundances are in locations in the north of the Gulf. Examination of Table 6.1 indicates that the weight of corallines does indeed decrease but that its percentage value is variable with some of its higher values in the north. Suggest amendment to lines 8-9 up from bottom of page to insert "percentage" before "carbonate abundances" and refer to Figs 6.1 and 6.2 rather than 6.3 in this sentence.
p. 202. "preliminarily" is the adverb.
p.205. Spelling of "ecosystems"
p.207. Use of word "colony" here seems to be incorrect as it is referring to a coralline alga. Correct term is thalli, plural of thallus; the name for the entire macroalgal structure. Similarly on p. 208 "branches" would be better term than "blades".
p.210. No reference given for "recent survey" and no entry for Wood and Lavery in reference list.

09PH
B8772
C.2

CALCAREOUS EPIPHYTES ON MODERN SEAGRASSES AS CARBONATE SEDIMENT PRODUCERS IN SHALLOW COOL-WATER MARINE ENVIRONMENTS, SOUTH AUSTRALIA

Ph. D. Thesis by K.M. Brown

Comments by Dr. Brian Jones

General Comments

1. This thesis tackles an important problem for carbonate sedimentology, namely that of providing detailed information on how the calcareous epiphytes that live on marine sea grasses contribute to the carbonate sediment load. To my knowledge, this is the most comprehensive study of sea grass epiphytes that has ever been undertaken.

2. It is readily apparent that this thesis is based on a enormous amount of fieldwork and laboratory work. It is also readily apparent that considerable care was taken in assembling the data that form the backbone of the thesis.

3. This is a data-rich thesis.

4. In general, the thesis is well written and, for the most part, easy to read. Some sections that deal with the specifics of the data and/or the statistical information derived from those data are more difficult to understand and comprehend.

5. I would have liked to see more discussion on the non-calcareous epiphytes and how they relate to the calcareous epiphytes. For example, are diatoms found on the sea grass and, if so, how do they relate to the calcareous epiphytes?

6. This study does not distinguish between the upper and lower surfaces of the sea grass leaves. I would have liked to see some data and discussion on the epiphytes that occur on the different surfaces.

7. The different types of epiphytes are identified and described in some detail. What is the spatial arrangement of the different epiphytes on the sea grass leaves – are they randomly intermixed or is there order to their distribution? Do some epiphytes prefer the basal part of a leaf whereas others prefer the leaf tip? Is there any indication of layering that might indicate a community succession scheme?

8. I would have liked to see a discussion that compared the cool-water sea grasses and their epiphytes with their tropical water counterparts. In the Caribbean, with which I am most familiar, *Thalassia* is the dominant sea grass. As in Australia, the blades of this seagrass are covered with epiphytes – commonly to the point where the blade appears white. The same groups of epiphytes are involved (different taxa). Some of the studies that have examined the epiphytes were cited in the thesis, but no attempt was made to compare the epiphytic assemblages from the two areas.

9. The issue of patchiness of the sea grasses is raised numerous times throughout the thesis. In some cases, for example, it is used to explain the spatial variance in the seagrass biomass. There is, however, no discussion of this issue in any detail. Are air photographs available for any of the study areas? If so, do those air photographs show the distribution of the sea grasses in the shallow waters? If so, various GIS methods could be used to measure the patchiness of the sea grasses. This would have allowed this parameter to be integrated into the overall model and discussion of the sea grasses and their epiphytes.

10. The issue of plant density is also alluded to in various parts of the thesis. Again, I would have liked to see some real data on the density of these plants. Although the sea grass biomass partly reflects plant density it is not a direct measure of plant density. This parameter also feeds back into the issue of patchiness (see point #9). Analysis of air photographs might help to resolve this issue.

11. This thesis contains original data and original ideas. The overall quality of the thesis is very high. In general, it is well-written and clearly presented. This thesis represents a significant contribution to carbonate sedimentology, especially in the context of cool water carbonates. This will become a well-cited document over the next 10 years or so as the rest of the carbonate community struggles to understand the dynamics of carbonate sedimentation in cool-water settings and how that compares with carbonate sedimentation in tropical settings.

Specific Comments (keyed to page and line numbers)

Chapter 1.

Page 1. I am not sure that I totally agree with the statement that it is only recently recognized that calcareous epibionts on sea grasses contribute significantly to the sediment load. There have been a number of studies in the Caribbean and Florida Kleys that have addressed this issue.

Fig. 1.3 This is not a very good figure, the greenish color really distracts from the information it is trying to show.

Page 11. I understand why the study was limited to the epiphytes that had a calcareous skeleton and could therefore contribute to the sediment on the seafloor. Nevertheless, it would have been interesting to know if other organisms do, in fact, live on the sea grasses. For example, do diatoms live on the sea grasses? If so, what happens to their siliceous skeletons.

Page 19. List of organisms known to have calcareous epiphytic species – where did this list come from?

Page 23. I am not sure that I agree with placing so much information on a CD – might be better placed in a series of appendices in the thesis.

Page 19-27. For each organism there is a list of the features that are used to identify them to generic/species level (with reference to the CD in each case). I would have liked to see a little more information on how the organisms were actually identified, especially given that many of these organisms are difficult to identify. Was identification achieved by comparisons with various publications (if so, they should be specified), or were they identified with the help of experts in the field (if so, they should be named).

Page 39. Loss of 2000 km^2 sea grass – is this worldwide, all of Australia, or part of Australia? The specifics of this measurement need to be spelt out clearly. Also, how much is this in terms of percentage of the original sea grass coverage?

Page 40 – line 1: line should not be indented.

Chapter 2.

Page 53, line 9: This describes how two transects were used to sample the sea grass – was this scheme used at every locality or only at selected localities? The usage of this two-transect method should be more clearly expressed.

Page 53, line 18: How much sediment was collected in each sample? Similarly, how much water was collected in each sample?

Page 55, line 5: OK, what exactly is a TPS WP84 – is this a meter or what?

Page 55, line15: List of parameters observed and noted. How were these parameters noted – what sorts of scales were used?

Page 55, line 26: Could the relationship between the sampled area and the area in general be assessed from air photographs?

Page 57, bottom of page: Why was the biological method adopted for this project? I would have liked to see some debate and reasons why this method was chosen over the geological and chemical methods.

Page 64, line 10: Biomass refers to standing stock of the seagrass – does this refer solely to the sea leaves? What about the root system – surely that is part of the biomass.

Page 64, line 12/13: Why was the dry weight of the biomass multiplied by 4? Although reference is made back to section 2.4.1 I could not find any explanation of why a factor of 4 is used. This needs to be explained.

Page 64/65: Why was this particular method of cluster analysis used? Also, why was the Bray-Curtis association measure used for the similarity matrix? There are many different similarity indices that can be used and many different ways of producing a dendrogram from that matrix. There should be some discussion why these particular methods were chosen.

Page 65, points vi and vii: How were these estimates made – visually or how?

Chapter 3.

Figure 3.1. This is a nice figure and one that is very important in terms of the seagrass distribution. It would help if the boxes in the key were bigger – at the moment some of them are so small that it is difficult to distinguish colors from one to the other. Also there is no indication of where this map is located – neither in the caption nor by the way of labels on the map itself.

Page 77, line 5: I am assuming that the heading "Biomass" refers to the biomass of the seagrass as opposed to the epiphytes. It might be worth changing this heading to Seagrass Biomass so that this is 100% clear.

Figure 3.3: Same comment as for Figure 3.1 re size of boxes in key.

Page 79, lines 12-13: States that "significant variation is in the form of a negative correlation" – OK, so does this mean that the biomass decreases with depth? It might be worth making this clear here.

Page 79, line 17: Site average results include 8 different seagrasses – which 8? This is a little confusing given that on page 70, it is stated that only 6 seagrass species were sampled. This apparent contradiction needs to be clarified.

Figure 3.4. Same comment as above re size of boxes in legend.

Page 83, line 5: The issue of plant density versus biomass of individual plants raises an interesting question – namely that of plant density in the areas that were sampled. This sentence suggests that plant density varied form place to place – yet this parameter does not appear to have been measured.

Page 83, paragraph 3, line 2: Is it valid to calculate the surface area using both sides of a blade – do the epiphytes live on both sides or do some taxa show preference for the upper surface (or vice versa)?

Figure 3.7. Same comment as above re size of boxes in legend. Also, what is meant by "sg biom2" and "tot biom2" in the legend. These abbreviations need to be explained.

Page 93, paragraph 1: Comparisons in seagrass biomass between this study and other studies – are these based on similar methods, or is there a danger that different methods may have induced differences?

Page 93, last paragraph: Can the patchiness be assessed from air photographs? There are various GIS methods that can be used to provided a measure of the degree of patchiness.

Page 94, lines 4-5: The issue of plant density versus surface area of the leaves on different plants is once again an issue here. These issues should probably have been separated because the causes of low/high plant density are probably very different from factors that control the volume of the plants.

Chapter 4.

Page 98, line 1 of Results: "The data was" should be "The data were"

Figures 4.2. 4.3: Same comment as previously regarding size of boxes used in legend.

Page 106, paragraph 2: At what level is a correlation coefficient deemed high ("good") or low "poor"). Most of the correlation coefficients cited in this paragraph seem low (< 0.5) and should be treated with caution.

Page 119, second paragraph: Discussion here that relates amount of $CaCO_3$ and biomass attributes it to the surface area provided by the seagrass biomass. Is this based on both sides of leaves or only one side? This might be an important issue if certain epiphytes prefer one side of a leaf over the other.

Pages 118-126 (Discussion): Although I have read this section a number of times, I still find it difficult to fully understand and even more difficult to decipher the key issues that are being discussed. If this section becomes part of a paper in the future, then it will need to be rewritten so that its main points are more clearly expressed.

Chapter 5.

Page 128: The introduction to this chapter is weak because it consists of statements regarding what was done in previous chapters and then statements of what will be done in this chapter. In most cases these are statements of action and, as such, provide little or no precise information that is pertinent to Chapter 5.

Figure 5.2: Symbols on graphs are small and a little difficult to distinguish from one another. The yellow triangles are particular difficult to see.

Page 133, paragraph 1 of Results: The issue of patchiness is once again raised but not dealt with in any detail. Perhaps this issue should have been tackled in more detail.

Page 134, lines 3/4: Any idea of why the values were higher than those measured by Cheshire et al. (1996).

Page 135, lines 4/5: What is meant by "a considerable fraction".

Page 137 (and p. 133, bottom), 2nd paragraph: In both cases, it is noted that 5 sea grasses were sampled at White Island. It would help the reader if these 5 taxa were listed with some idea as to the abundance of each one.

Figure 5.4. Boxes in legend need to be bigger.

Page 152, line 2 of section 5.4.1.2: words "speciesmore" need a space between them.

Page 152, line 2 of section 5.4.1.2: Notion here is that some species of sea grass are more sensitive to light than other species. It would help the reader, if this was explained in more detail and emphasis being placed on how it affects this study.

Page 152, last line: Again the issue of patchiness is raised with no real measure of the patchiness.

Page 159, 2nd paragraph: Was any attempt made to determine if there was a ecological succession to the order in which the epiphytes colonized the sea grass leaves? Was this a random process or one that involved a definite community succession?

Page 165, line 6: "spirorbids are reproduce all year around" – should be "spirorbids reproduce all year around"

Page 165, lines 9, 10: If spirorbids are negatively phototactic, is there any indication that they prefer the underside of the leaves as opposed to their upper surface.

Chapter 6.

Page 168, list of individual blades: Does the variation in the number of blades and stems examined from each type of grass reflect the abundance of that grass. It is not clear from the text why different numbers of stems and blades were examined from different species – why not a constant number from each type of sea grass.

Page 168, bottom of page: How were these precise percentages (for each epiphytic type) established? What are the error margins associated with these numbers?

Page 169, line 8: % symbol – in this context, should be spelt out as percent (an elsewhere in chapter)

Page 169, second paragraph: Extrapolation of % ratio data to the actual abundances of carbonate from each taxa – how was this achieved? More explanation is needed as to how these numbers were calculated.

Figure 6.1: The boxes in the legend are too small and it is almost impossible to separate the colors and thereby understand the distribution of the different epiphytes. Also, the map needs some names on it so that the reader knows which area it represents.

Figures 6.2, 6.3, 6.4: Same issue of box size in the legend.

Figure 6.4B: What does the curved line represent?

Page 179, line 7 from bottom: remove space before comma.

Page 198, line 4 from bottom: The assumption that the ostracods picked from the sediment were detached from the sea grass may be a false one. I find it curious that only 14 ostracod species were found on the sea grasses whereas an additional 38 species were found in the sediment around the sea grass – it seems strange that so many species in the sediment were not actually found on the sea grass. Could it be that the ostracods did not live on the sea grass but lived in the sediment or were brought into the area by storms etc. The assumption that proximity indicates the origin on the grass is a dangerous one. Also, were the 14 species found on the sea grass also found in the sediment?

Page 203, second paragraph from bottom: The difference in species diversity between the sea grass beds and the surrounding sediment assumes that there has been no mixing by storm activity. This also makes the assumption that all of these microfossils could actually be identified in an ancient rock.

Page 207: Could the type of surface of the sea grass affect recruitment patterns? Are certain types of surface more attractive than others for these micro-organisms?

Chapter 7.

Page 215, third paragraph: First sentence of this paragraph is difficult to follow and understand. I am not sure that I fully understand how the final figure of 3.5/yr was achieved.

Page 220, 2nd paragraph, lines 1, 2: turnover values of seagrass calculated form previous studies – yet none of these studies are cited?

Page 220, last line: This number clearly indicates the vast amount of sediment being produced by the epiphytes. Do you have any estimates of how much carbonate sediment is produced each year, from all sources? In other words, although this is a huge amount of sediment, there is no measure of this as a percentage contribution to the total sediment load.

Page 224, 2nd paragraph: Was any comparison done between the epiphytes found in the sediment between the sea grass roots and the epiphytes that lived on the plants? It would be interesting to know what percentage of the epiphytes identified from the sea grasses themselves are also found in the sediment around the plants.

Chapter 8

Line 1 – the statement that has been indisputably proven by this research – where did that statement come from? Is this a statement made by the author or one taken from another paper?

Overall, this chapter seems to be more of a summary rather than a discussion. Each section in this chapter seems to reiterate the main points derived from each section of the thesis. I am not convinced that this is really needed.

09PH
B8772
c.2

CD (Part 1): DATA et al.

Contents	Topic	CD file name
Bryozoa	Glossary	Bryo.glossary.xls
	Taxonomy	BryoTax.xls
	Bryo SEM images list	KB_BRYO.xls
	Abundance of species at sample sites	
Calcareous Epiphytes	Defining use of term “epi” in marine environment	definingEPI.doc
	Bivalves	bivalve sp list.xls
	Abundances at sample sites	Phyllum abundance.xls
Carbonate Production	Carbonate weight vs seagrass biomass	$CaCO_3$vs biomass
	Compilation of all data	$CaCO_3$All.data
	Compilation of density in various scenarios	$CaCO_3$ vs biomass
	Sediment % at all sites	carb site sed%.xls
	Carbonate per seagrass species	carb species.xls
	Monthly records of production	month,depth,gen.xls
	Comprehensive per seagrass species	CarbSeagrass.xls
	Seagrass Productivity 1	productivity.xls
	“ “ 2	productivity2.xls
	Site/species/carbonate production	species.xls
Coralline Algae	specific examples of production	coralline algae.xls
	Abundance at sample sites	coralline freq.xls
Foraminifers	Foraminfers taxonomy	foram taxonomy.xls
	Foraminifer frequency	for freq.xls
General	Preliminary evaluation of quadrat results	Prelim.EvalofData.doc
	Biomass - multiple files and data	biomass.xls
	Productivity et al. 1	transect.xls
	“ “ 2	transect2.xls
	“ ‘ 3	transects.xls
	Acronyms/Abbreviations	abreviations.doc
Methods	Diving protocol	diving.doc
Oceanographic Parameters	Light	Light.doc
	Provinces in South Australia	Oceans.doc
	Nutrients	Nutrients.doc
	Meteorology	Meteorology.xls
	Climatology	climate averages.xls
	Various parameters	Ocean. parameters.xls
	Adelaide seawater composition	metro outfall comp.xls
	Seawater analyses	water samples.xls
Ostracods	Ostracod frequency	ost freq.xls
Sample Sites	Co-ordinates of sample sites	sites.lats.longs.doc
	Field Notes	field notes.doc
	Field data	field data.xls
Seagrass	*Posidonia* biomass at all sample sites	*Posidonia*.biomass.xls
	All seagrasses biomass at samples sites	Seagrass.biomass.xls
	Biomass along transects at samples sites	SGpBioTransects.xls

	Taxonomy	seagrass.taxo.doc
	Species present at all sites - week 1	pres.abs.wk1sg.xls
	Biomass at sample sites	biomass2.xls
	Patchiness of seagrass on seafloor	Patchiness.xls
	Productivity as quad averages	quad averages.xls
	Comprehensive data set	quadrat.xls
	Comprehensive productivity set	quadsite.xls
	“ “ “ 2	quadspec.xls
	Measurements	sg measurements.xls
Sediments	Sediment on seafloor within seagrass	sed.seagrass.biomass.xls
	Example of description of sediment	sed.descrip.doc
	Sediment quantities assoc. with various seagrasses at sample sites	sed.biomass2.xls
	Grainsize analyses	sediment grain size%.xls
	Sediment analysis	sediment analyses.xls
Spirorbids	Spirorbid frequency	spirorbid freq.xls
West Island	Comprehensive data	West Island.xls
	Field data	WIfield data.xls
	Calcareous epiphyte assemblages	West Island folder
	Seasonal changes	Cluster folder
	Seagrass parameters	Seasonality folder
	Carbonate production vs season	WestCarbonate/season/depth xls

CD (Part 2): SEM Images and Photographs

Contents

Biota	Mix of various biota - no catalogue
Bivalves	no catalogue
Bryozoa	SEM images (catalogue is in Part 1)
Coralline Algae	Field photographs - no catalogue
Foraminifers	SEM images (catalogue is in Part 1)
Ostracods	SEM images (catalogue is in Part 1)
Seagrass	SEM images of seagrass as a substrate
Spirorbids	SEM images - no catalogue
Sediments	Field photographs
Serpulids	SEM images - no catalogue
Spirorbids	SEM images

O9PH
B8772
c.2

ABSTRACT

CALCAREOUS EPIPHYTES ON MODERN SEAGRASSES AS CARBONATE SEDIMENT PRODUCERS IN SHALLOW COOL-WATER MARINE ENVIRONMENTS, SOUTH AUSTRALIA.

The main aims of this research was:-

i) to assess whether the quantity of carbonate sediment produced by calcareous epiphytes contributes significantly to temperate carbonate sediments,

ii) to determine the controlling factors of the productivity of calcareous epiphytes,

iii) to assess wether calcareous epiphyte assemblages can indicate the health of modern seagrass environments, and

iv) to assess whether calcareous epiphyte assemblages can indicate palaeo-environments in the rock record.

The study was carried out along the coastline of South Australia. This area is important because it not only hosts the largest E-W trending temperate water carbonate platform in the world, but also because virtually no assessment of calcareous epiphyte productivity has been done in this region, although it hosts nearly 15,000 km^2 of seagrass.

The number of sites sampled and estimations of productivity over time, have limited previous estimations of calcareous epiphyte productivity. This study obtained samples from 20 locations, ranging from the north-west coast of Eyre Peninsula through to the region south of the Coorong, an area covering approximately 1300 km of coastline. A total of 429 quadrats (50x50 cm) were observed and sampled. The data thus obtained was used to address the aims.

A two-year data series from one site (West Island, near Victor Harbor) was used to determine the effect of seasonality. The other sites were selected to test the effect of other physical, chemical and biological parameters. Carbonate values were estimated using a separation process developed for this project, which allows the retainment of the carbonate particles. Faunal and floral assemblages information was determined by visually estimating their abundance and identity on 1600 individual blades and stems from the sites.

Positive answers were obtained for all the aims.