2000

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Recommended Citation

Reid, T. R. (2000). *The effect of leaf movement on algal epiphytes in seagrass meadows*.
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USE OF THESIS

THE EFFECT OF LEAF MOVEMENT ON ALGAL EPIPHYTES IN SEAGRASS MEADOWS

BY

T.R. REID

A Thesis submitted in partial fulfilment of
the requirements for the award of
Bachelor of Science (Environmental Management) Honours
at the School of Natural Sciences,
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DATE OF SUBMISSION: 28 November 2000

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ABSTRACT

Artificial seagrass units were used to determine whether seagrass leaf movement influences the biomass, species richness and composition of epiphytic macroalgae on the leaves of seagrasses, and whether the influence of leaf movement is altered by the degree of exposure to water movement and to depth. The influence of leaf movement on epiphytic biomass is important from an environmental management perspective, as there is the potential for epiphytic productivity to be underestimated if leaf movement is reducing the standing crop of epiphytes on seagrass leaves. Two forms of artificial seagrass units were used in three experiments to achieve these objectives; untethered units mimicked natural seagrass leaves, that were free to move in response to water movement, and tethered units mimicked seagrass leaves that were unable to move. The first experiment examined the effect of seagrass movement on the biomass, species richness and species composition over time. The second and third experiments examined the influence of exposure and depth on the effect of seagrass leaf movement on epiphytic biomass.

In all three experiments the epiphytic biomass, measured in terms of dry weight (DW) and ash free dry weight (AFDW), was far greater in tethered than untethered units, where the epiphytic biomass was on average eight times higher on tethered leaves. Similarly species richness was shown to be greater in tethered vs untethered units. These results provide clear evidence that the movement of seagrass leaves has a profound effect on the accumulation of epiphytic algae. In addition, ordination revealed clear differences in epiphytic species composition and species richness between the tethered and untethered units, and over time. Algae of the genus *Hypnea* were characteristic of tethered leaves, while *Griffithsia australe* and *Antithamnion* spp. were characteristic of untethered units.

Differences between tethered and untethered sets of artificial seagrass leaves, reflecting the influence of leaf movement, could be due to any combination of several processes affected by leaf movement. These include physical contacts between leaves abrading epiphytes, movement influencing grazing abundance/activity and movement influencing the settlement and growth of algal propagules.

Untethered leaves at sheltered and exposed sites showed no difference in epiphytic biomass. This suggests, that even though there were large differences in energy between the sheltered and exposed sites, both exposures may have had sufficient energy to exceed the critical amount needed to produce a maximum effect related to leaf movement. The results also showed that there was no difference in epiphytic biomass on the untethered leaves between deep and shallow sites but that tethered leaves had a significant higher biomass at shallow depths. From the tethered results it can be concluded that differences in light, nutrients or some other environmental factor may be influencing the standing crop of epiphytic biomass at different depths, but the untethered results suggest that the influence of leaf movement overshadows any of these effects related to depth differences.

The results of this study provide strong evidence that the movement of seagrass leaves strongly influences the biomass, species richness and species composition of epiphytic algae. However, it is not as clear whether the process of leaf movement is reducing the standing crop of epiphytes through abrasion, or if leaf movement is in fact inhibiting the settlement of propagules onto the seagrass leaves. If leaf movement results in an abrasional loss of epiphytic algae, previous studies may have underestimated epiphytic production in our seagrass meadows, thus the production of seagrass ecosystems and their inherent value. However, if leaf movement is instead limiting the settlement of propagules then the underestimation of epiphytic productivity is not as likely.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any institution of higher education; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Signature

Date 1/2/00

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. Paul Lavery, who even though escaping to Sweden, still managed to be a long distance supervisor. I would also like to thank Dr Glenn Hyndes and Beverley Van Elven who made excellent ad-hoc supervisors in Dr Lavery's absence.

I am also grateful for my diving and boat buddies, Lea McQuillan, Bev Van Elven and Julia Wilson for braving the Winter Ocean and all the weather could throw at us on my many field trips. I am also indebted to the Centre for Water research at UWA, particularly Bridget Alexander, who devoted considerable time to helping me prepare and use the ADV.

A special thankyou goes to my close friends Julia, Bev, Nick, Hayley, Robyn, Kelli and Lea for keeping me sane through some very trying times.

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CHAPTER 1: INTRODUCTION

1.1. SEAGRASS AND EPIPHYTIC FUNCTION

Seagrasses are vascular plants that live in marine and estuarine environments, often forming large meadows (Walker & McComb, 1992). Seagrass meadows have important effects on the physical, biological and chemical status of their environment (Kirkman, 1989). Physically, seagrass meadows provide habitats and substrates for fish and invertebrates, such as molluscs and crustaceans, and also provide fauna with physical shelter from predators (Australian Heritage Commission, 1996). Seagrass rhizomes act to stabilise the sediments, while the leaves act as baffles which aid in reducing wave and current energy (Walker & McComb, 1992). These mechanisms help prevent extreme erosion and accretion events (Kirkman, 1989). Biologically, seagrasses are important food sources for many marine animals, through the leaves themselves and their associated epiphytes (Australian Heritage Commission, 1996). They form areas of high productivity and their associated epiphytes are generally the main primary producers in their environment (Klumpp *et al.*, 1989). Chemically, seagrasses and their epiphytes are involved in the cycling of nutrients (Klumpp *et al.*, 1989), and the production of calcium carbonate ($CaCO_3$) through the growth of coralline algae, contributing to sediment production (Walker *et al.*, 1987; Walker & Woelkerling, 1988; Cockburn Cement Ltd, 1994).

Epiphytic macroalgae are among the most important organisms in seagrass ecosystems, contributing significantly to trophic and ecological functions, though their importance is often underestimated (Kendrick & Burt, 1997). They are of significance to the trophic structure of seagrass meadows, as they are not only highly productive, often exceeding the productivity of the seagrasses themselves (Kirkman, 1992), but are also an important food source within the system (Klumpp *et al.*, 1989). Grazers show a preference for epiphytic algae over seagrasses due to their low fibre content, which makes them easier to digest than seagrass leaves (Klumpp *et al.*, 1989).

Given the importance of epiphytic macroalgae, understanding the functions of seagrass ecosystems, such as productivity and nutrient cycling, requires an understanding of the associated epiphytes and their functions. Several studies have addressed the role of epiphytic macroalgae in trophic structure, productivity and nutrient cycling of seagrass ecosystems (eg. Orth & van Montrans, 1984; Borowitzka & Lethbridge, 1989), but many are likely to have underestimated their significance. Typically, estimating functions such as epiphytic productivity within a meadow requires the measurement of the standing crop (Penhale, 1977). An assumption is often made that the standing crop of epiphytic algae is equivalent to the gross epiphytic production over the lifespan of the leaf (Hegge *et al.*, 1998).

These estimates ignore the processes of leaf movement such as of physical contact between leaves reducing epiphytic biomass. When calculations on the significance of these meadows are made using estimates of net epiphytic growth, the significance of the meadows and their primary functions have the potential to be seriously underestimated. Such underestimations could have strong implications to management decisions of our coastal environment. For example, seagrass loss has been reported worldwide (Walker & McComb, 1992). More than 45 000 ha of seagrass meadow has been lost this century (Silberstein *et al.*, 1986), including Cockburn Sound, Western Australia, where at least 75% of *Posidonia* meadows have been lost since the 1960s (Kirkman, 1989). The seagrass losses in Australia have been caused through a variety of processes, mainly through anthropogenic means such as increased pollution and nutrient enrichment (Silberstein *et al.*, 1986) and mining that involves dredging of seagrass meadows

(Hegge *et al.*, 1998). All of these factors affect the gross productivity of seagrass meadows and their epiphytes. The underestimation of the productivity of seagrass ecosystems by using only net production could therefore potentially underestimate the impact of seagrass degradation of our seagrass meadows caused through the above factors.

1.2. FACTORS INFLUENCING EPIPHYTIC BIOMASS AND COMPOSITION

Several processes, which can be simultaneous or sequential, determine the epiphytic algal assemblage composition present at any given time in a seagrass meadow. These include recruitment processes such as propagule dispersal and settlement and post-recruitment processes such as biological and physical factors that influence algal growth and survival after settlement (Santelices, 1990). These physical factors can include light attenuation, salinity, nutrient availability (Kendrick *et al.*, 1997) and water motion (Kendrick & Burt, 1997). Biological factors include host interactions (Lobban & Harrison, 1994), competition and grazing (Jernakoff & Nielson, 1998). Both biological and physical factors can potentially influence algal epiphyte recruitment and post-recruitment (Lobban & Harrison, 1994).

Conceptually, there are a number of factors influencing the standing crop of epiphytic biomass. Some of the factors directly influence the biomass of epiphytes, while others are indirect through a variety of other factors. The most relevant factors in this study are seagrass leaf movement, exposure and depth (Figure 1.1).

The standing crop of epiphytes present at any given time on a leaf is not likely to be a true reflection of gross epiphytic growth over the lifespan of a seagrass leaf. Physical movement of leaves in a seagrass meadow can cause the leaves to come into contact with each other (Figure 1.1). This can potentially result in epiphytic material being "knocked off" or abraded, thus diminishing the standing epiphytic crop. (Harlin, 1980). This loss of biomass is defined for this study as the loss of accumulated epiphytic material from a seagrass leaf occurring specifically through physical contact between leaves, but also including other processes such as grazing. Alternatively, contact between leaves could be limiting the accumulation of epiphytic biomass onto the leaves. This process of leaf movement could result in the standing crop of epiphytes present at any given time on a leaf not being a true reflection of gross epiphytic growth over the lifespan of a seagrass leaf. Instead, this reflects the net epiphytic growth after processes such as physical contact and grazing have reduced the gross biomass production. Therefore, the net epiphytic growth, or standing crop, represents biomass per area of leaf, while the gross epiphytic growth represents biomass per area of leaf over time.

A number of factors also have the potential to affect the movement of seagrass leaves in a meadow. These can include water velocity and turbulence (Koehl & Alberte, 1988), wind, swell (Hurd, 2000) and the shoot density of the meadow (Mann & Lazier, 1996). The standing crop of seagrass epiphytes in more exposed areas that are characterised by increased water velocity, waves and swell, are more likely to be affected by physical contact between leaves (Figure 1.1).

The process of leaf movement could potentially limit the settlement of epiphytes onto seagrass leaves, thus limiting the standing crop of epiphytes. The recruitment of epiphytes onto seagrass leaves also has the potential to be affected by leaf movement and by the other processes outlined in the conceptual diagram (Figure 1.1). These are all likely to be varieties of recruitment factors that could potentially influence or be influenced by leaf movement, thereby reducing the standing crop of epiphytes. The factor most likely to be encountered in this study is the settlement of algal epiphytic propagules onto the artificial seagrass leaf substrate (Lobban & Harrison, 1994).

The degree of exposure can also potentially influence the standing crop of epiphytes on seagrass leaves (Phillips *et al.*, 1997) (Figure 1.1). The velocity and the direction of water movement in a seagrass meadow can not only physically remove whole or parts of plants by hydrodynamical forces (Gaylord *et al.*, 1994; Denny *et al.*, 1998), but also significantly alter the morphologies of the epiphytes and host seagrass leaves. The morphology of the seagrass leaf or algal epiphyte can affect the ability of the epiphytes to settle onto the seagrass leaf, or to remain attached to the leaf under varying energy conditions (Denny *et al.*, 1985; Denny *et al.*, 1998). In addition, the intensity and quality of submarine illumination will often directly affect the rates of photosynthesis and productivity of epiphytes (Dawes, 1998). Therefore, the reduction of available light, through influences such as shading or an increase in depth, can decrease the gross epiphytic biomass found on a seagrass leaf (Gordon *et al.*, 1994) (Figure 1.1).

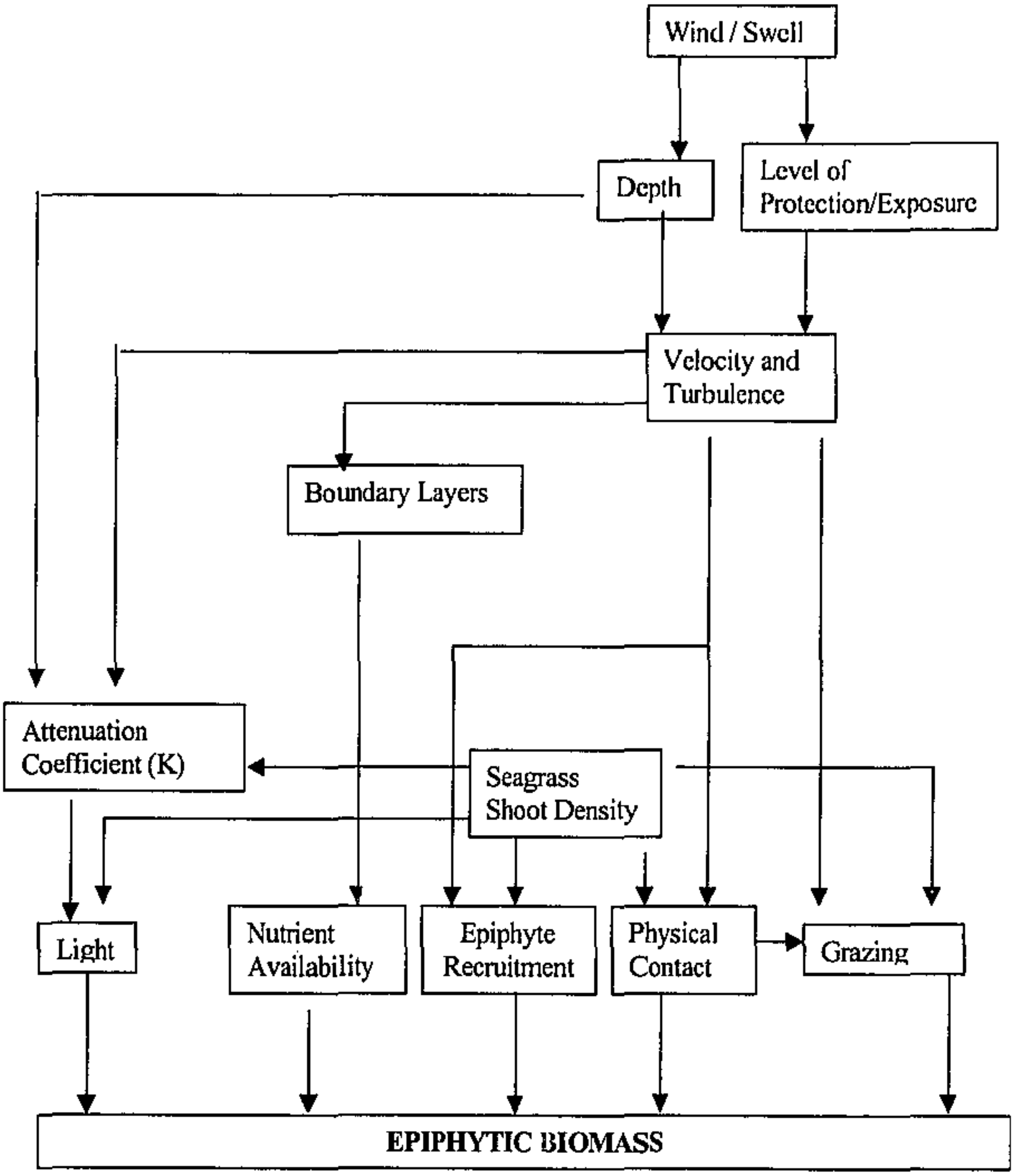


Figure 1.1. **Conceptual model of factors influencing the accumulation of epiphytic biomass**

1.3. THE ROLE OF LEAF MOVEMENT ON EPIPHYTES IN SEAGRASS MEADOWS

All of the factors discussed in the conceptual diagram (Figure 1.1) show that when physical movement between leaves is prevented, a higher biomass can accumulate. In an earlier study by Reid (Unpublished data), these differences in epiphytic accumulation between leaves that were free to move, and leaves that could not move, were found to be significant. This study, at a single site, determined that the epiphytic biomass accumulated on artificial seagrass leaves over 28 days, was up to 12 times higher in the absence of leaf movement. This was similar to the findings of Department of Environmental Protection (unpublished data) who estimated that leaf movement induced a difference of two orders of magnitude greater than the standing crop of epiphytes on leaves that could not move. This challenged the validity of the assumption that the difference between the gross epiphytic accumulation and the standing crop is not significant.

The scope of Reid's earlier study however, was limited and only confirmed a significant difference at one site. This difference was proposed to be caused through physical movement between leaves. It failed to determine whether the differences observed at one site were applicable to a range of sites and conditions, and whether this process may influence the composition of epiphytes growing on the leaves. This study was designed to address some of the questions raised in Reid's earlier study.

1.4. SIGNIFICANCE

An understanding of the factors influencing the loss of epiphytes on seagrass through leaf movement is relevant to environmental management because if epiphytic biomass (standing crop) continues to be used as a measure for determining seagrass meadow functions, such as productivity, then those measurements should be as accurate as possible. If epiphytic production is underestimated because managers have not taken into account this potential difference between standing crop and gross accumulation, then the functions of the meadows are likely to be underestimated, and thus the significance of seagrass meadows and their components in our coastal ecosystems undervalued. However, if leaf movement is primarily influencing the settlement of epiphytes, not reducing the standing crop through abrasion, then epiphytic production is not likely being underestimated.

For instance, epiphytic contribution of calcium carbonate ($CaCO_3$) has been determined to assist in the production of mineral sands (Hegge *et al.*, 1998). Previous estimates of the contribution of epiphytes to $CaCO_3$ sediment production (calcirates) in Cockburn Sound on Success Bank (Fremantle, Western Australia) have shown that epiphytes can potentially only contribute approximately fifteen percent of total sediment production (Kendrick *et al.*, 1988; Hegge *et al.*, 1998). These calcirates, however, were calculated under the assumption that epiphytes stay on the seagrass leaves for the entire lifespan of the leaves, and did not take into account any processes that could remove biomass or limit its accumulation (Cockburn Cement Ltd, 1994; Hegge *et al.*, 1998). Therefore these calcirates could be potentially underestimated, when influences such as leaf movement are taken into consideration.

The original calculated sediment production from epiphytes led Cockburn Cement Ltd to conclude that epiphytes were insignificant as sediment producers and that it was more likely the erosion of landmass that was forming the sediments on Success Bank (Cockburn Cement Ltd, 1994; Hegge *et al.*, 1998). However, if processes such as leaf movement influencing epiphytic accumulation are taken into consideration, then the role of epiphytes in producing sediment on Success Bank could be far greater.

As productivity in our seagrass meadows is usually measured through the biomass of the epiphytic standing crop (Penhale, 1977), productivity estimates of our seagrass meadows could also be potentially underestimated if seagrass leaf movement is reducing the standing crop of epiphytic biomass through leaf movement processes such as abrasion. Since large areas of seagrasses can be lost through any significant underestimates in nutrient enrichment and pollution (Walker & McComb, 1992), any significant underestimates in productivity of seagrass epiphytes is likely to undervalue the loss of this form of production in our coastal ecosystems.

1.5. AIMS

The primary aim of this study was to determine whether seagrass leaf movement influences the standing crop and composition of macroalgal epiphytes on seagrass leaves.

Further aims of this study were to determine whether the influence of the movement of seagrass leaves on epiphytic standing crop is affected by exposure and depth.

1.6. STRUCTURE OF THESIS

This chapter (Chapter 1) introduced the study and its various components, provided a general background on seagrasses and epiphytes in the marine environment, and the roles of energy and physical movement in seagrass ecosystems. It also explained the relevance of this study to environmental management. Chapter 2 will cover the experimental design, the methods used for each experiment and the analyses used within each component. Chapter 3 presents the results of all three experiments, and Chapter 4 discusses the results and relates these findings to physical and ecological processes in the marine environment, and the implications of these results relating to environmental management issues.

CHAPTER 2: METHODS AND MATERIALS

2.1. STUDY AREA

The study was conducted at sites on the eastern shoreline of Garden Island and in the Marmion Marine Park near Perth (Figure 2.1 & Table 2.1).

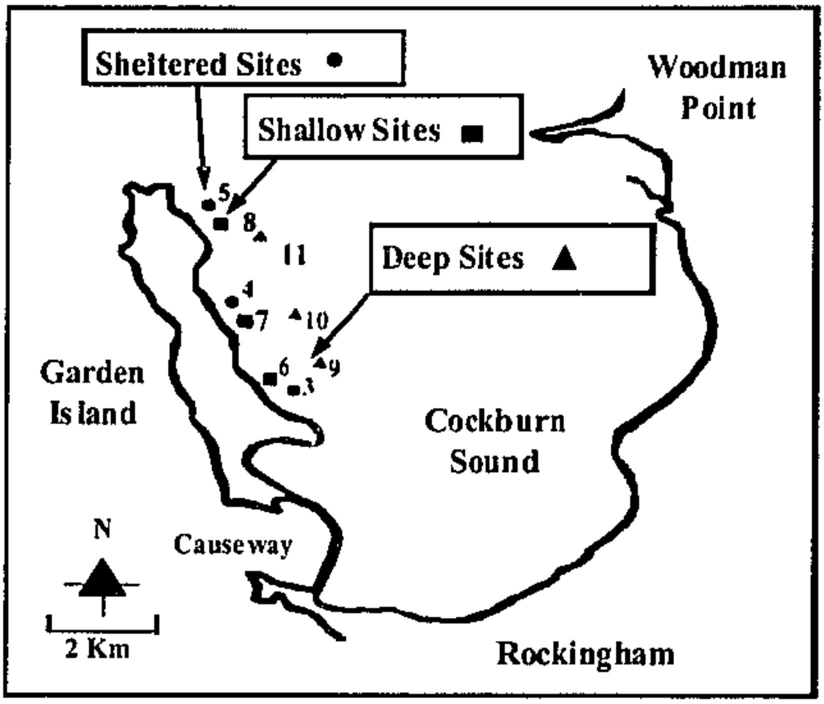
Garden Island (32° 15′ S, 115° 45′ E) is part of a limestone reef and island chain that runs approximately parallel to the coastline. Waters between this island and the mainland represent sheltered regions as they are protected from prevailing southwesterly and westerly winds and seas (Environmental Protection Authority, 1998). The island is surrounded by extensive benthic habitats with rich seagrass communities that support a high biomass of epiphytic algae (Department of Conservation and Land Management, 1994). The seagrasses commonly found in this region consist of *Posidonia sinuosa, Posidonia australis, Amphibolis antarctica and Halophila ovalis* (Department of Conservation and Land Management, 1990).

Marmion Marine Park is an 'A' class reserve encompassing an area of approximately 9 500 ha from Trigg Island north to Burns Rocks and out to sea for 5.5km (Department of Conservation and Land Management, 1992). These waters represent considerably more exposed sites than the Garden Island region due to large swells and lack of protection from prevailing southwesterly winds (Department of Conservation and Land Management, 1990). The study was conducted in winter when the passage of low-pressure systems can bring north-westerly and stronger southwesterly winds and gales (Department of Conservation and Land Management, 1990). The Marine Park area is also subject to a prevailing, long period southwesterly and westerly swell that is continuously generated by storms and the 'Roaring Forties' in the Indian Ocean (Department of Conservation and Land Management, 1990).

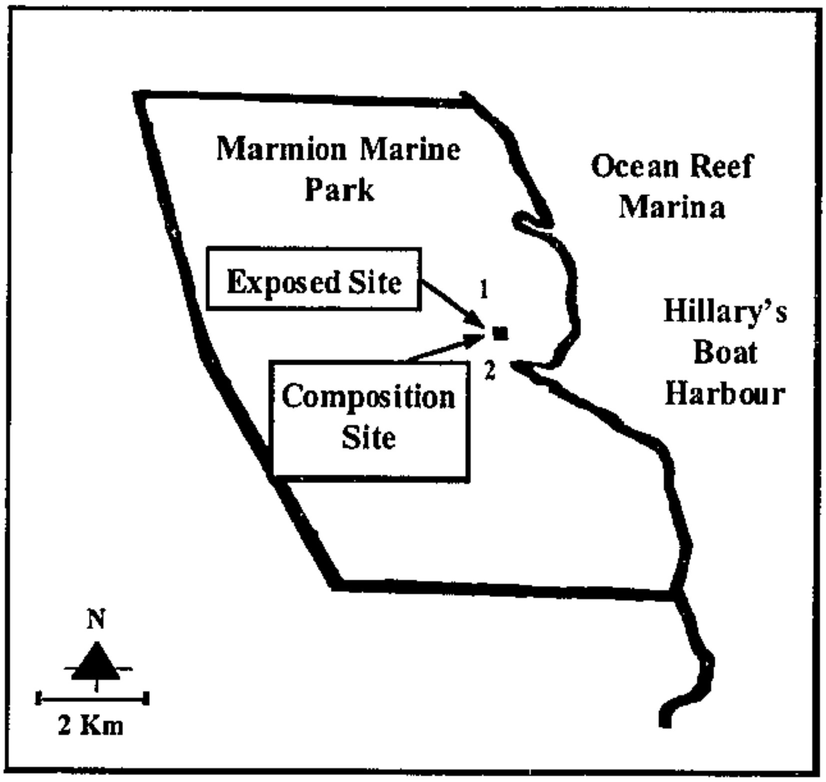
The park has high habitat diversity due to the high variation in geomorphology, water depth and exposure to wave energy and light (Department of Conservation and Land Management, 1990). The subtidal benthic communities include sandy sea floor, limestone reefs and seagrass meadows (Department of Conservation and Land Management, 1992). The common seagrasses found in the Marine Park are *Posidonia sinuosa, Amphibolis antarctica and Halophila ovalis* (Department of Conservation and Land Management, 1990).

Table 2.1. Australian Map Grid Coordinates and depth (m) of sites.

Site No	Depth (m)	Seagrass Species	Location / Description	Coordinates	
1	4	*Posidonia sinuosa,* *P. australis*	Marmion Marine Park Exposed site	0379512	6479199
2	4	*P. sinuosa* *P. australis*	Marmion Marine Park Assemblage Site	0379512	6479199
3	3	*P. sinuosa*	Garden Island (Cockburn Sound) Sheltered site 1	0376981	6434623
4	3	*P. sinuosa, P. australis*	Garden Island (Cockburn Sound) Sheltered site 2	0375255	6437655
5	3	*P. sinuosa P. australis*	Garden Island (Cockburn Sound) Sheltered site 3	0375189	6440073
6	3	*P. sinuosa*	Garden Island (Cockburn Sound) Shallow site 1	0376981	6434623
7	3	*P. sinuosa, P. australis*	Garden Island (Cockburn Sound) Shallow site 2	0375255	6437655
8	3	*P. sinuosa P. australis*	Garden Island (Cockburn Sound) Shallow site 3	0375189	6440073
9	8	*P. sinuosa*	Garden Island (Cockburn Sound) Deep site 1	0376592	6444621
10	8	*P. sinuosa*	Garden Island (Cockburn Sound) Deep site 2	0377551	6443112
11	8	*P. sinuosa, P. australis*	Garden Island (Cockburn Sound) Deep site 3	0377189	6444671



A) CS



B) MMP

Figure 2.1 Location of study sites. MMP = Marmion Marine Park, CS = Cockburn Sound. 1& 2 = Exposed and Composition site, 3-5 = Sheltered sites, 6-8 = Shallow sites, 9-11 = Deep sites. A) = Garden Island/Cockburn Sound, B) = Marmion Marine Park

2.2. MEASURING THE INFLUENCE OF LEAF MOVEMENT ON THE STANDING CROP OF EPIPHYTES ON SEAGRASS LEAVES.

All three experiments in this study required a means of measuring the effect of leaf movement on the standing crop. This was achieved by using artificial seagrass units designed specifically to determine the standing crop of epiphytes, that would accumulate in the presence or absence of leaf movement. These units are described in the following section.

2.2.1. Artificial Seagrass Units

This study used artificial seagrass leaves, resembling the strap-like leaves of *Posidonia* (Figure 2.2). Artificial seagrasses are considered to be especially useful in performing colonisation studies and are easily replicated (Lethbridge *et al.*, 1988). Importantly for this study, they remove the effect of any potential interactions between the host media and epiphytes, while also providing identical habitats, a known surface area and known age enabling comparisons between replicates (Lethbridge *et al.*, 1988). Many functions of seagrass and epiphytes have been determined through the use of artificial seagrasses (Brouns & Heijs, 1986), as these studies have shown that artificial seagrass units yield similar epiphytic communities and accumulation of biomass to those growing on natural seagrasses (Horner, 1987). Therefore, processes related to leaf movement, which influence accumulation of epiphytic biomass, can also be determined through the use of artificial seagrass leaves.

Artificial seagrass leaves were constructed of clear plastic polyethylene strips, 1mm thick, 20mm wide and 250 mm long, that are not known to inhibit epiphytic algal recruitment (Horner, 1987). Thirty of these plastic leaves were stapled to plastic coated wire grids measuring $0.25m^2$ at an even density of 35 leaves $0.25m^2$. Two forms of artificial seagrass units were constructed, tethered (T) and untethered (UT). The tethered units (Figure 2.2a) consisted of the grids mounted into cubic ($0.25m^3$) marine grade stainless steel frames. The plastic leaves were threaded into the grids and stapled at both top and bottom. The untethered units (Figure 2.2b) consisted simply of leaves stapled into the grids. The untethered units mimic natural seagrass leaves, being free to move in response to local hydrodynamics. The tethered units also simulate a natural seagrass leaf but with the potential of movement removed. Each unit was weighted with large iron weights weighing approximately 10 kg each, securing them to the substratum.

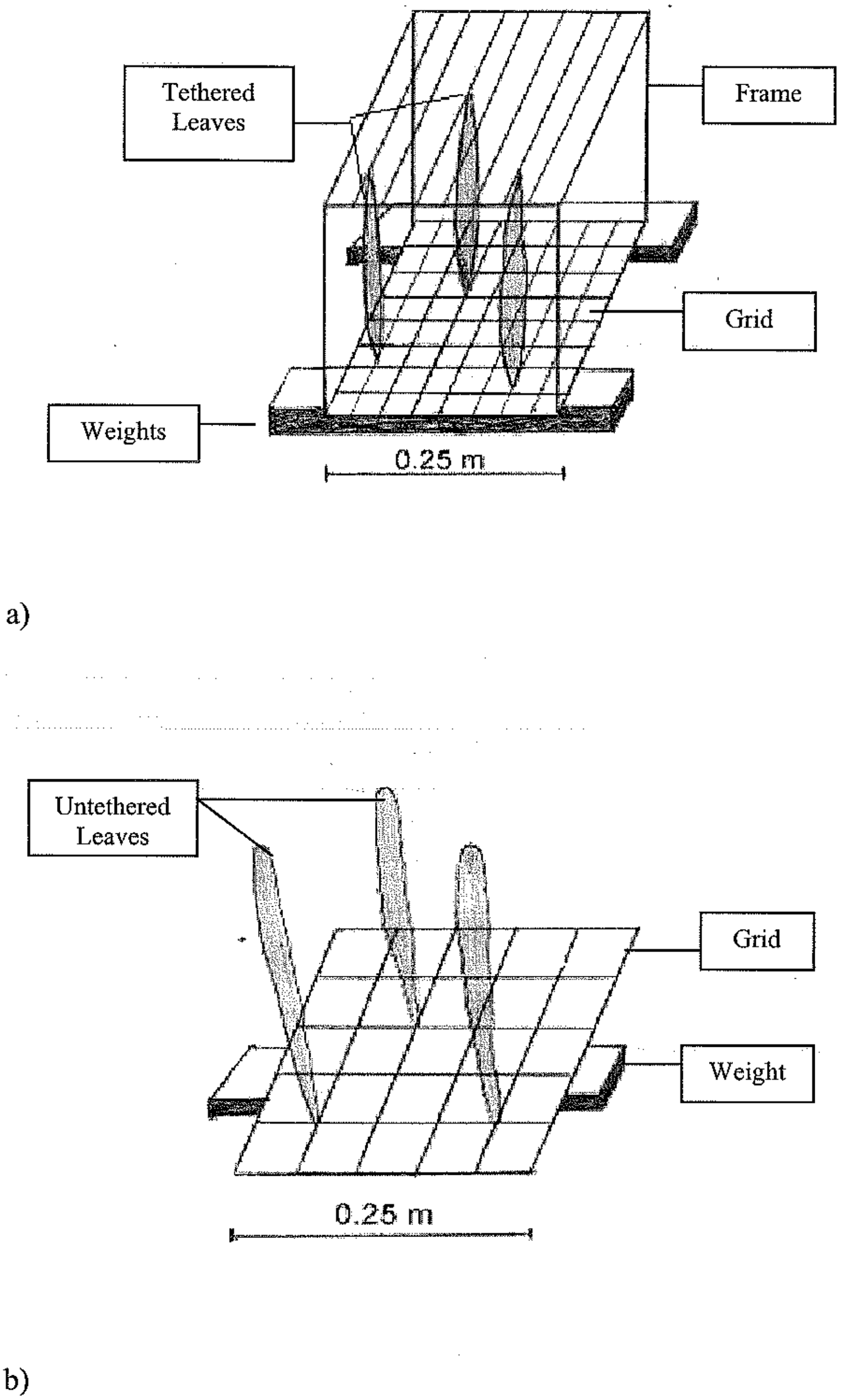
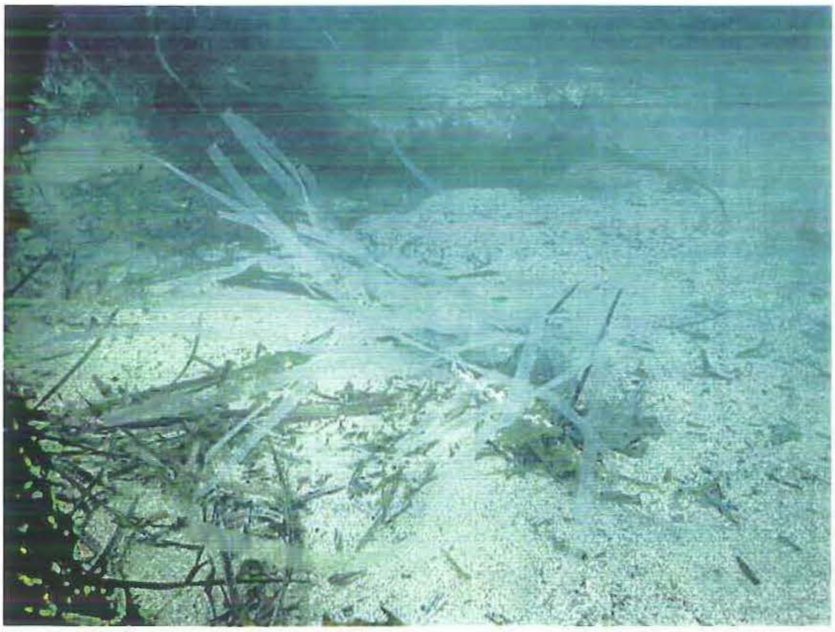


Figure 2.2. Artificial seagrass units used to measure effect of leaf movement on macroalgal epiphytic biomass. a) = Tethered unit, b) = Untethered unit.

a)



b)

Plate 2.1. Example of artificial seagrass units in situ. a) = Tethered artificial seagrass unit after four weeks showing accumulation of macroalgal biomass on artificial leaves. b) Untethered artificial seagrass unit outside of meadow showing accumulation of biomass under influence of leaf movement.

2.2.2. Deployment and Retrieval of Artificial Seagrass Units

The artificial seagrass units were deployed for different periods corresponding to each separate experiment. The tethered artificial seagrass units were placed randomly along a bare sand patch surrounded by a seagrass meadow, using a random numbers table that corresponded to the number of fin kicks from a haphazardly chosen starting point. The untethered units were then placed in close proximity to the tethered units to limit any confounding differences in variability due to placement.

The units were retrieved using a surface operated winch and SCUBA operated lifting bag to bring a number of units to the surface simultaneously. Units were placed in bags underwater to ensure minimal loss of epiphytic material during handling. On board, grids were then separated from the weights and frames and immediately labelled and placed into individual plastic bags containing seawater. Samples were kept in a cool, dark container for transport to the laboratory where they were processed within 12 hours.

2.2.3. Selection of Samples

The samples were processed in large trays containing filtered seawater to prevent desiccation of the algal epiphytes. Each artificial leaf was cut from the grid at its point of attachment using a flat-edged razor blade. The leaves to be processed for subsequent analysis were selected randomly using a random numbers table. After removal, the sampled leaves were stored frozen until biomass analysis.

In the diversity experiment, a further five artificial leaves were then sampled for analysis of species composition (section 2.2.5). These samples were preserved immediately in a solution of 5% formalin in filtered seawater.

2.2.4. Determination of Sample Size

The optimum number of artificial seagrass leaves required to accurately assess epiphytic biomass was a compromise between several considerations: the limited amount of time available in the study (*ie.* effort required to scrape epiphytes from leaves), the limited number of shoots available for sampling and the small biomass found on untethered units. These considerations had to be met while still collecting a sufficient sample size to reduce variability. From a pilot study, 10 shoots were determined as the optimum for sampling of epiphytic biomass. A species area analysis undertaken as part of the pilot study indicated that five artificial seagrass leaves were required to provide an accurate representation of species richness in an artificial seagrass unit (Appendix A).

2.2.5. Measuring Biomass

For each experiment, ten randomly sampled artificial leaves were used to determine dry weight (DW) and ash free dry weight (AFDW). A 5-cm section was removed from the bottom of each leaf to exclude staples and ensure the surface area of each leaf was identical. The epiphytes, which were then removed from both sides of each leaf by scraping a flat edged razor blade along the length of the leaves. Epiphytes were then placed into pre-weighed crucibles.

The samples were dried at 70 ^{0}C for 48 hours, cooled to room temperature in a desiccator, and weighed to obtain dry weights, then combusted at 550 ^{0}C for 2 hours in a muffle furnace and reweighed when cooled to room temperature to determine the AFDW. The dry weight includes both organic and inorganic mass of the epiphytes, such as $CaCO_3$ in calcifying species plus any sediment, whereas the AFDW represents the organic component of the epiphytic material.

Three standards of glycerin were used to correct for uneven or incomplete combustion in the determination of AFDW. Standards in pre-weighed crucibles were placed into the front, rear and middle of each furnace for each separate firing. These standards were weighed after cooling in the desiccator. When the standards were not completely combusted, corrections were made to the weights of samples (situated in the corresponding third of the furnace) where appropriate.

In all experiments, the difference in epiphytic accumulation between tethered and untethered units was measured by comparison of the biomass of epiphytes accumulated on the two different forms of artificial seagrass units over set periods of time. The difference in the biomass accumulated on tethered and untethered units is therefore a quantification of the effect of leaf movement on epiphyte accumulation through a range of factors potentially influenced by leaf movement, such as physical contact between leaves, altered recruitment, or grazing, and can be expressed as a percentage difference:

$$\%\ \text{Difference} = \frac{\text{Mean biomass of Untethered units}}{\text{Tethered units}} \times 100$$

2.2.6. Identification of Epiphytes

For the samples collected for the epiphytic composition experiment (see section 2.3), epiphytes were identified to the lowest taxonomic level possible, using a dissecting microscope, with the aid of the identification keys of Womersley, (1984, 1987, 1994, 1996) and Huisman & Walker, (1990). The presence of epiphytic algal species were recorded on the preserved leaves, to determine whether differences in epiphytic assemblages between the leaves occurred through only the presence of a species. The percentage cover of epiphyte species was recorded by calculating the percentage cover of each species present on each leaf, and was used to determine whether differences occurred through the abundance of the species present. Since the measurement of epiphytic abundance is problematic due to the small size of some epiphytic algae and the difficulty in determining discrete units, these methods were considered to be the most appropriate.

2.3. EXPERIMENT: EFFECT OF LEAF MOVEMENT ON ACCUMULATION OF BIOMASS, SPECIES RICHNESS AND COMPOSITION OF EPIPHYTIC MACROALGAL ASSEMBLAGES

2.3.1. Experimental Design

This experiment examined the influence of leaf movement on the accumulation of algal epiphytic biomass, species richness and the composition of epiphytic assemblages using tethered and untethered artificial seagrass units. The experiment was conducted at Marmion Marine Park (Figure 2.1a) over a proposed period of four time intervals.

The original design involved deploying sixteen replicate sets of artificial seagrass units. Four randomly selected replicates of each type of artificial seagrass unit were to be removed after four, eight, 12 and 16 weeks. Epiphytic biomass and composition of tethered and untethered units were recorded at each time interval, as described in section 2.2. However, after the eight week interval, storms completely destroyed or buried the remaining artificial seagrass units. Consequently, the analyses were performed for only two time intervals (week four and week eight). Epiphyte biomass was compared between the artificial seagrass units and between the time intervals (Table 2.2). The epiphytic assemblages on the units were also compared between the units and between the time intervals.

Table 2.2. Two-factor orthogonal ANOVA testing the influence of time on the accumulation of epiphytic biomass and epiphytic assemblage using artificial seagrass units.

TIME INTERVAL	**4 WEEKS**		**8 WEEKS**	
TREATMENT	T	UT	T	UT
REPLICATION	4 of each ASU		4 of each ASU	

(T = Tethered units, UT = Untethered units outside meadow)

2.3.2. Statistical Analysis

2.3.2.1. Univariate Analysis

Differences in mean biomass and mean species richness between time intervals and between tethered and untethered artificial seagrass units for this experiment were tested by two-factor orthogonal Analysis of Variances (ANOVA) using SPSS^{TM} (SPSS Inc.) software. Biomass and species richness were first tested for homogeneity of variances using Levene's Test ($p > 0.05$). Since both biomass and species richness data showed homogeneity of variances, it was therefore considered appropriate to continue with the parametric analyses without transforming the data.

A statistically significant difference detected by ANOVA using a cut-off of $p < 0.05$, between the tethered and untethered artificial seagrass units was interpreted as indicative of physical movement of leaves influencing the accumulation of epiphytic biomass as species richness.

2.3.2.2. Multivariate Analysis

The species composition of epiphytes on leaves of tethered and untethered artificial seagrass units was compared by multivariate analyses using PRIMER software (Plymouth Routine in Multivariate Ecological Research) (Clarke & Warwick, 1994), to explore whether patterns in the epiphytic assemblages were linked to the influence of leaf movement.

The species percentage cover data (n = 40 for tethered artificial seagrass shoots, n = 40 for untethered artificial seagrass shoots), which were not transformed were used to construct the similarity matrix. The Bray Curtis similarity measure was used, as it is the most commonly used measure of association in ecological studies and is also robust to non-linear species responses, which are typical of ecological data (Faith *et al.*, 1987).

Ordinations using non-metric multi-dimensional scaling (MDS) were performed on the similarity matrix to visually reveal patterns of similarity among epiphyte assemblages from different types of artificial seagrass units and different time intervals (Faith *et al.*, 1987). In all cases, stress values were not high (< 0.2), indicating that the ordination plot was a good representation of the underlying similarity matrix (Clarke & Warwick, 1994). Multivariate Dispersion (MVDISP) was used to calculate the dispersion of sample groups by ranking dissimilarity among replicates (Clarke & Warwick, 1994).

Analysis of Similarities (ANOSIM), was used to determine whether the species composition in *a priori* defined groups (tethered week 4, untethered week 4, tethered week 8, untethered week 8) differed significantly (Clarke & Warwick, 1994). A two-way crossed ANOSIM was used to test for differences between time intervals and between types of artificial seagrass unit.

Where differences were significant, pair-wise comparisons were performed to determine which habitats were different, using the procedure available within the ANOSIM module. Similarity of Percentages (SIMPER) was used to determine the species that were responsible for the observed patterns in the similarity/dissimilarity between groups. This procedure examines the contribution of individual species by computing the average dissimilarity between all pairs of group samples, then breaking the average down into the separate contributions of each species to the average dissimilarity (Clarke & Warwick, 1994).

2.4. EXPERIMENT: INFLUENCE OF EXPOSURE ON THE EFFECT OF LEAF MOVEMENT ON EPIPHYTIC ALGAL STANDING CROP.

2.4.1. Experimental Design

This experiment examined the influence of exposure on epiphytic accumulation between tethered and untethered units. The epiphytic accumulation was originally planned to be determined at six sites (Table 2.1). Three replicate 'sheltered' sites were located in Cockburn Sound, along the eastern side of Garden Island and three 'exposed' sites were located in Marmion Marine Park (Figure 2.1).

At each site three replicate sets of artificial seagrass units were deployed to determine differences in epiphytic standing crop due to leaf movement and exposure as described in section 2.2. This design corresponded to a two-factor nested ANOVA with the two fixed factors treatment and exposure and the factor Site nested within exposure level (Table 2.3).

Table 2.3. Two-factor nested ANOVA testing the influence of exposure on the accumulation of epiphytic biomass using artificial seagrass units.

EXPOSURE	Exposed									Sheltered								
SITE Nested in Exposure	1			2			3			1			2			3		
TREATMENT	T	U1	U2	T	U1	U2	T	U1	U2	T	U1	U2	T	U1	U2	T	U1	U2
REPLICATION	3 of each ASU			3 of each ASU			3 of each ASU			3 of each ASU			3 of each ASU			3 of each ASU		

(T= Tethered units, U1= Untethered units outside meadow, U2= Untethered units inside meadow, ASU = Artificial Seagrass Unit)

The units were intended to be left *in situ* for eight weeks. Statistically significant differences in epiphytic biomass, and thus the effect of leaf movement on standing crop between exposure levels, would support the hypothesis that the level of exposure influences the effect of leaf movement in the accumulation of epiphytic standing crop. Significant differences between sites nested within exposure would indicate spatial variability among sites, which was not related to exposure. In addition, and irrespective of any significant differences, the results quantified the effect of leaf movement on the accumulation of the standing crop over a wide spatial range.

Due to factors beyond human control, the above design could not be fully implemented. Storm events in the three exposed sites (Marmion Marine Park) either completely destroyed the artificial seagrass units, or buried them under almost 2m of sand in some instances. Fortunately, the epiphytic assemblage experiment (section 2.3) was conducted in a very similar location in the Marine Park, and so data from that experiment could be compared to the data from the sheltered sites at Garden Island. However, as this yielded only one exposed site and three sheltered sites it was necessary to analyse the results as an orthogonal ANOVA as outlined in Table 2.4.

Table 2.4. Two-factor orthogonal ANOVA testing the influence of exposure on the accumulation of epiphytic biomass on artificial seagrass units.

SITE **EXPOSURE**	**1** **Exposed**		**2** **Sheltered**		**3** **Sheltered**		**4** **Sheltered**	
TREATMENT	T	UT	T	UT	T	UT	T	UT
REPLICATION	3 of each ASU		3 of each ASU		3 of each ASU		3 of each ASU	

(T = Tethered units, UT = Untethered units outside meadow, ASU= Artificial Seagrass Unit)

2.4.2. Statistical Analysis

2.4.2.1. Univariate Analysis

Differences in mean biomass between sites and between artificial seagrass units for this experiment was tested by two-factor orthogonal ANOVA using SPSS^{TM} (SPSS Inc.) software. Data were first tested for homogeneity of variance using Levene's Test, which demonstrated that these data were homogeneous ($p > 0.05$). It was then considered appropriate to continue with parametric analysis of the untransformed data. Tukey's Post Hoc testing was used to reveal whether the exposed site was significantly different from the other three sheltered sites.

Using this revised design, statistically significant differences ($p < 0.05$) between site one (exposed) and the remaining sites (sheltered) was interpreted as supporting the hypothesis that the level of exposure influences the accumulation of epiphytic algae. Differences detected between the types of artificial seagrass units were interpreted as indicative of physical movement of leaves influencing the accumulation of epiphytic biomass.

2.4.3. Measurement of Energy Regimes

To measure the energy regimes and exposure of Garden Island and Marmion Marine Park, the velocity and frequency of the back and forth movement of water, which reflects orbital wave velocities, was measured at the height of the seagrass canopy for fifteen minutes. This was performed using an Acoustic Doppler Velocimeter (ADV) Profiler (Nikora & Goring, 1998). Higher velocities and greater variation in water movement was interpreted as higher levels of exposure.

2.5. EXPERIMENT: INFLUENCE OF DEPTH ON THE EFFECT OF LEAF MOVEMENT ON EPIPHYTIC ALGAL STANDING CROP.

2.5.1. Experimental Design

This experiment examined the influence of depth on epiphytic accumulation on tethered and untethered artificial seagrass units. Three replicate 'deep' (8m) and three replicate 'shallow' (3m) sites were located in Cockburn Sound along the eastern side of Garden Island. At each site, three replicate sets of artificial seagrass units were deployed to determine the differences in epiphytic standing crop due to water depth (Table 2.5). The units were left *in situ* for eight weeks after which time they were retrieved and biomass determinations made as per section 2.2.

Table 2.5. Two-factor nested ANOVA testing the influence of depth on the accumulation of epiphytic biomass using artificial seagrass units.

DEPTH	**Deep**									**Shallow**								
SITE Nested in Depth	**1**			**2**			**3**			**1**			**2**			**3**		
TREATMENT	T	U1	U2	T	U1	U2	T	U1	U2	T	U1	U2	T	U1	U2	T	U1	U2
REPLICATION	3 of each ASU			3 of each ASU			3 of each ASU			3 of each ASU			3 of each ASU			3 of each ASU		

(T= Tethered units, U1= Untethered units outside meadow, U2= Untethered units inside meadow, ASU= Artificial Seagrass Unit)

2.5.2. Statistical Analysis

2.5.2.1. Univariate Analysis

The design of this experiment corresponds to a two-factor nested ANOVA with fixed factors of treatment and depth, and the factor site nested within depth (Table 2.5). ANOVA was performed using SPSS™ (SPSS Inc.) software. Data were first tested for homogeneity using Levene's Test that demonstrated that the variances were heterogeneous. Square-root transformation of these data resulted in a homogeneous dataset ($P > 0.05$). It was then considered appropriate to continue with parametric analysis using transformed data. When statistically significant differences between the factors were detected, multiple pair-wise comparisons of means were then performed to determine which pairs of means were different using Tukey's testing procedure (SPSS™ SPSS Inc.)

Statistically significant differences ($p < 0.05$) in epiphytic biomass between the two depths were interpreted as supporting the hypothesis that depth influences the effect of leaf movement on the accumulation of epiphytic biomass. Significant differences detected only between the sites were interpreted as indicative of spatial variability of the sites, which was not related to depth. If both factors were found to be significant then it was interpreted that the maximum potential biomass accumulation is not only related to depth, but to spatial variability within each site. Significant differences detected between the types of artificial seagrass units were interpreted as indicative of physical movement of leaves influencing the accumulation of epiphytic biomass.

CHAPTER 3: RESULTS

3.1. EFFECT OF ARTIFICIAL SEAGRASS UNIT ON THE BIOMASS AND COMPOSITION OF EPIPHYTIC ALGAL ASSEMBLAGES

3.1.1. Differences in Epiphytic Biomass

ANOVA showed that epiphytic biomass on artificial seagrass leaves, in terms of both dry weight (DW) and ash free dry weight (AFDW), differed significantly between tethered and untethered artificial seagrass units and between times (Table 3.1). Both the DW and AFDW were greater on tethered than on untethered units for both week four and for week eight (Figures 3.1 and 3.2). The large increase in epiphytic biomass in terms of DW and AFDW on tethered units and lack of an increase of epiphytic biomass in DW and AFDW on untethered units produced a significant interaction in the statistical analysis (Table 3.1).

Table 3.1. Results of two factor ANOVA testing differences in biomass of seagrass epiphytes between time intervals (four weeks and eight weeks) and between artificial seagrass units (Tethered and Untethered) over July-August 2000, in Marmion Marine Park, WA. All data were square root transformed.

FACTOR	ANOVA RESULTS				
	Effect of Time				
	d.f.	Mean square	F-value	P-value	
Dry Weight	1	103.063	38.103	0.000	*
Ash Free Dry Weight	1	112.063	67.716	0.000	*
	Effect of Type of Artificial seagrass unit				
	d.f.	Mean square	F-value	P-value	
Dry Weight	1	306.808	113.430	0.000	*
Ash Free Dry Weight	1	37.294	22.535	0.000	*
	*Time * Artificial seagrass unit*				
	d.f.	Mean Square	F-value	P-value	
Dry Weight	1	103.063	38.103	0.000	*
Ash Free Dry Weight	1	37.294	22.535	0.000	*

* Statistically significant ($p < 0.01$)

After four weeks the DW of epiphytes on tethered units was 4.8 ± 1.2 SE g/10 leaves, but only 1.2 ± 0.01 SE g/10 leaves on untethered units. After eight weeks the mean DW of epiphytes on tethered units increased to 14.4 ± 0.5 SE g/10 leaves, while the biomass for untethered units remained low at 1.15 ± 0.03 SE g/10 leaves (Figure 3.1). The mean DW of the untethered units did not vary considerably over the study period, and ranged from 1.1 to 1.2 g/10 leaves. The mean DW on tethered units, however, increased from 4.8 to 14.4 g/10 leaves over the study period.

These trends were also apparent for AFDW (Figure 3.2). The tethered units had a mean AFDW of epiphytes of 2.7 ± 0.5 SE g/10 leaves after four weeks, but for untethered units it was only 0.2 ± 0.01 SE g/10 leaves. The AFDW of epiphytes on the untethered units again did not vary considerably over time, and ranged from 0.2 to 0.5 g/10 leaves. The epiphytic biomass of the tethered units, however, again increased from a mean AFDW of 2.7 ± 0.3 SE g/10 leaves after four weeks, to 8.5 ± o.5 SE g/10 leaves after eight weeks.

This difference in the biomass of epiphytes between tethered and untethered artificial seagrass units was also significant at different exposures and different depths (Sections 3.2 and 3.3). The mean DW and AFDW on untethered units was only 12% of the epiphytic biomass on tethered units in both sheltered and exposed sites (Table 3.2). The differences in epiphytic biomass were also significant between different depths (Table 3.2). The epiphytic biomass on untethered units was only 20% of the epiphytic biomass in shallow sites and up to 35% of the epiphytic biomass on the tethered units in deep sites.

Table 3.2. Percentage contribution of epiphytic biomass of untethered artificial seagrass units (inside = inside seagrass meadow, outside = outside seagrass meadow) deployed within different exposures (sheltered, exposed), different depths (3m, 8m) and over time (4 weeks, 8 weeks) during July-August 2000 in Marmion Marine Park, Western Australia.

FACTOR		Percentage Contribution
EXPOSURE	Exposed	11.52 %
	Sheltered	12 %
DEPTH	Deep (8 m)	Inside = 22 %, Outside = 35 %
	Shallow (3 m)	Inside = 13 %, Outside = 20 %
TIME	4 Weeks	24 %
	8 Weeks	8 %

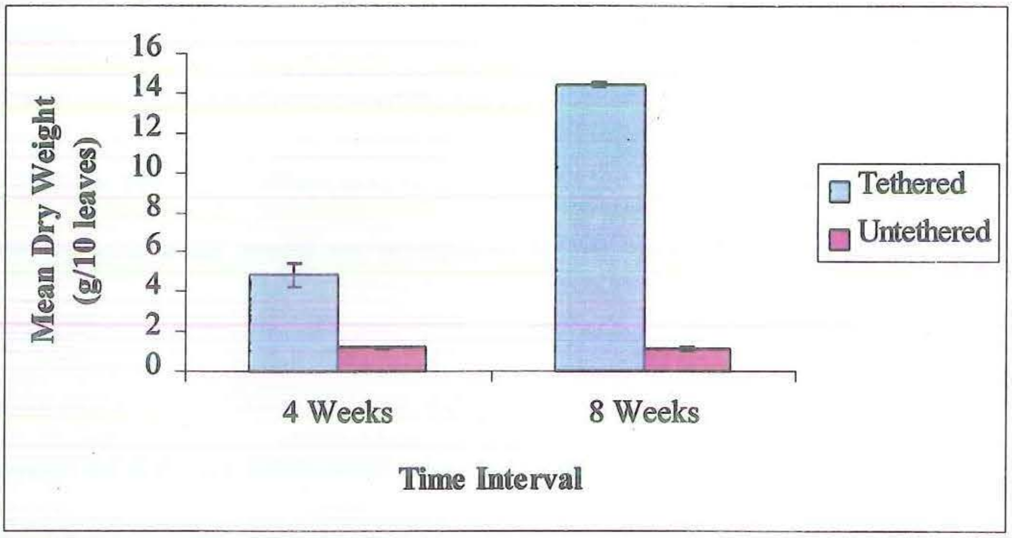


Figure 3.1. Mean dry weight of epiphytic algae (± SE, n = 4) recorded from 10 leaves each on two types of artificial seagrass unit (Tethered and Untethered) within two time intervals (four weeks and eight weeks) during July-August 2000 in Marmion Marine Park, Western Australia.

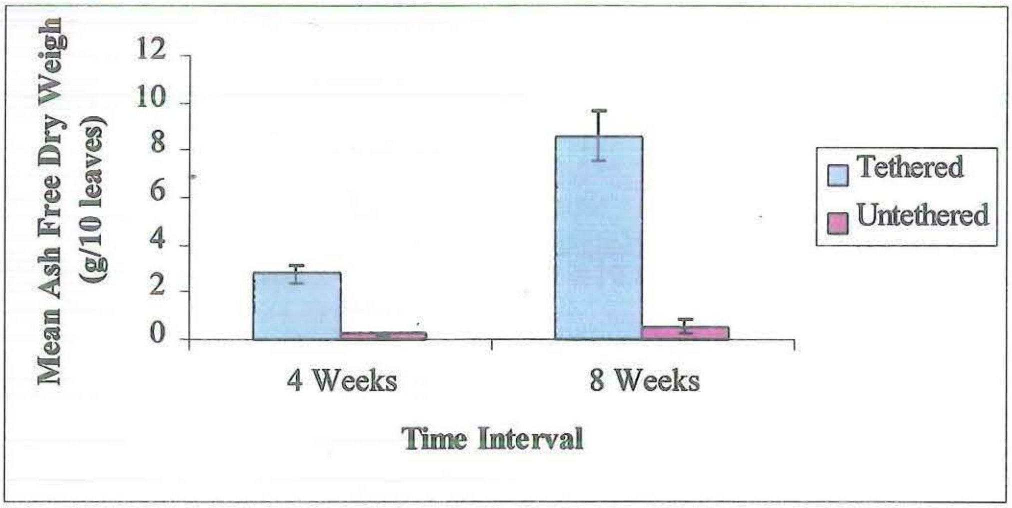


Figure 3.2. Mean ash free dry weight of epiphytic algae (± SE, n=4) recorded from 10 leaves each on two types of artificial seagrass unit (Tethered and Untethered) within two time intervals (four weeks and eight weeks) during July-August 2000 in Marmion Marine Park, Western Australia.

3.1.2. Epiphytic Assemblages on Artificial Seagrass Units

3.1.2.1. Species Richness of Epiphytes

A total of 56 species of epiphytes were found on the artificial seagrass units (Appendix B). 20 species were found on untethered leaves, while 43 species were found on tethered leaves. ANOVA showed that differences in species richness of epiphytes between types of artificial seagrass unit were significant with greater species richness occurring on tethered units (Table 3.3). The trend for a decrease in species richness between times in tethered units and compared to an increase in species richness between times for untethered units (Figure 3.3) resulted in a significant interaction.

Table 3.3. Results of two factor ANOVA testing for differences in species richness of epiphytes between time intervals (four weeks and eight weeks) and between two types of artificial seagrass units (Tethered and Untethered) during July-August 2000 in Marmion Marine Park, Western Australia. Data untransformed because Levene's Test for homogeneity of variance result of P = 0.051 indicated variances were homogeneous.

FACTOR	ANOVA RESULTS				
	Effect of Time				
	d.f.	Mean Square	F-value	P-value	
Epiphyte Species Richness	1	12.8	1.45	0.227	NS
	Effect of Type of Artificial Seagrass Units				
	d.f.	Mean Square	F-value	P-value	
Epiphyte Species Richness	1	36.2	39.015	0.00	*
	*Time * Artificial Seagrass Units*				
Epiphyte Species Richness	d.f.	Mean Square	F-value	P-value	
	1	120.05	13.932	0.00	*

NS = Not statistically significant ($p > 0.01$)

* = Statistically significant ($p < 0.01$)

Species richness was highly variable, with the mean species richness on the tethered units showing higher variability than the species richness on the untethered units (Figure 3.3). Mean species richness on tethered artificial seagrass units generally decreased over time, compared to the mean species richness on untethered artificial seagrass units, which increased slightly over the study period.

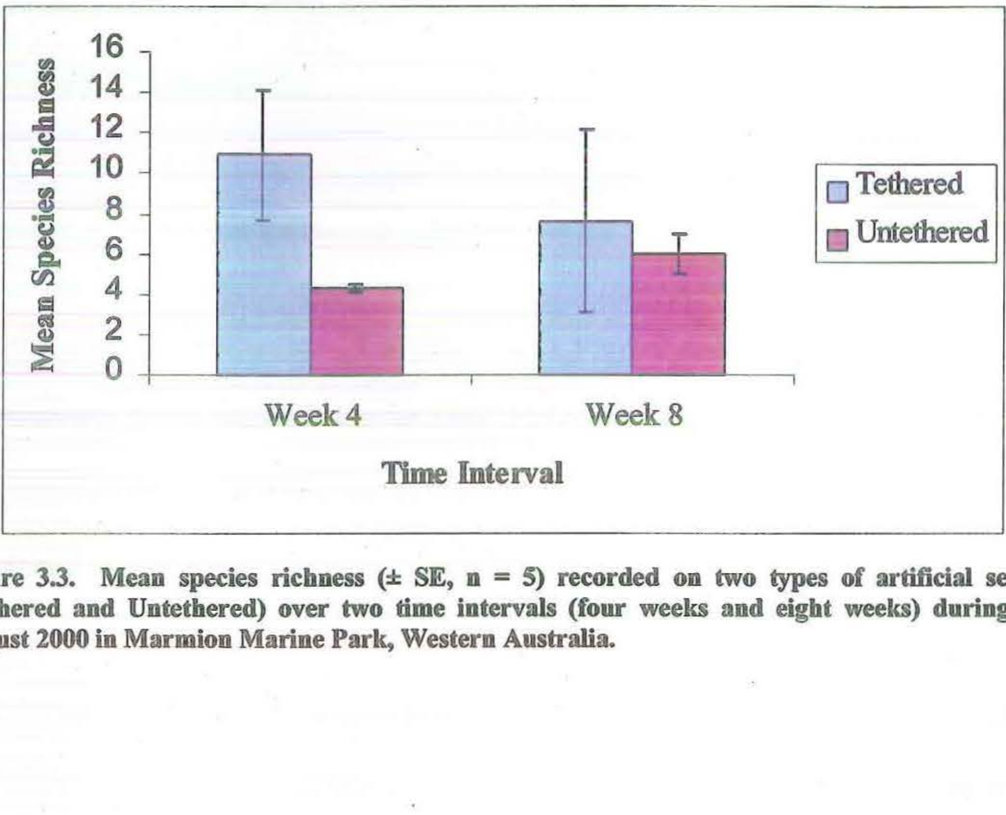


Figure 3.3. Mean species richness (± SE, n = 5) recorded on two types of artificial seagrass (Tethered and Untethered) over two time intervals (four weeks and eight weeks) during July-August 2000 in Marmion Marine Park, Western Australia.

3.1.2.2. Ordination and Analysis of Similarities

Patterns in the assemblages of algal epiphytes between types of artificial seagrass unit and over time, based on percentage cover of epiphyte species are shown in the ordination plot (Figure 3.4). This plot had a low stress value (stress = 0.1), indicating that the plot was representative of the underlying similarity/dissimilarity matrix. Within each time period, epiphytic composition on tethered leaves separated clearly from species composition on untethered leaves, with the untethered leaves clustering more tightly than the tethered leaves. This tight clustering was supported by dispersion values using multivariate dispersion (Table 3.4.)

Table 3.4. Global comparison indicating relative dispersion of groups from MDS ordination using Bray-Curtis similarity matrix. Untethered leaves are less dispersed than tethered leaves.

Time Interval and Artificial Seagrass	Relative Dispersion by Global Comparison
Week Four Untethered	0.29
Week Eight Untethered	0.84
Week Eight Tethered	1.39
Week Four Tethered	1.48

Samples from untethered leaves at four weeks showed the tightest clustering, closely followed by the untethered leaves after eight weeks. After four weeks, epiphytic compositions on the tethered leaves were more dispersed than the compositions from untethered leaves.

The plot indicated that the composition of epiphytes was different between the tethered and untethered artificial seagrass units and between sampling times. Epiphyte species on artificial seagrass units after four weeks clustered toward the upper left hand quarter of the ordination, while those after eight weeks clustered to the lower and right side (Figure 3.4). A separate ordination using presence/absence data only (Figure 3.5) showed a less defined clustering of samples and a higher stress level (0.17).

ANOSIM indicated that there were significant differences in the species composition of epiphytes between artificial seagrass units (Global R = 0.593, $p < 0.01$) and between time intervals (Global R = 709, $p < 0.01$) (Table 3.5). It showed that all groups were significantly different from each other. The R-values were high for both artificial seagrass units and time, indicating that the differences were strong in both cases.

Table 3.5. Results of two-factor crossed ANOSIM pair-wise comparisons testing for differences using Bray-Curtis similarity matrix in two types of artificial seagrass units (Tethered and Untethered) over two time intervals (four weeks and eight weeks) during July-August in Marmion Marine Park, Western Australia. All groups were significantly different from each other. 4T = 4 weeks Tethered, 4UT = 4 weeks Untethered, 8T = 8 weeks Tethered, 8UT = 8 weeks Untethered.

Groups Used	Statistical R-Value	Permutations: Possible (Used)	Significant Statistics	P	
4T, 4UT	0.910	20000 (5000)	0	0.000	*
4T, 8T	0.624	20000 (5000)	0	0.000	*
4T, 8UT	0.981	20000 (5000)	0	0.000	*
4UT, 8T	0.563	20000 (5000)	0	0.000	*
4 UT, 8UT	0.561	20000 (5000)	0	0.000	*
8T, 8UT	0.508	20000 (5000)	0	0.000	*

* Statistically significant ($p < 0.01$)

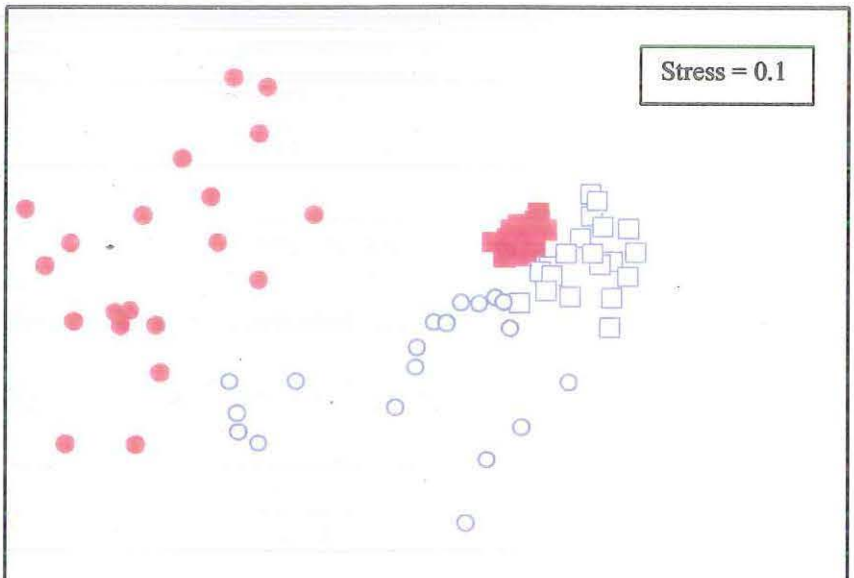


Figure 3.4. Two dimensional ordination of epiphyte assemblages (n=80), using percentage cover data on non-metric MDS, over two time intervals (four weeks and eight weeks) for two types of artificial seagrass unit (Tethered and Untethered) during July-August 2000 in Marmion Marine Park, Western Australia.

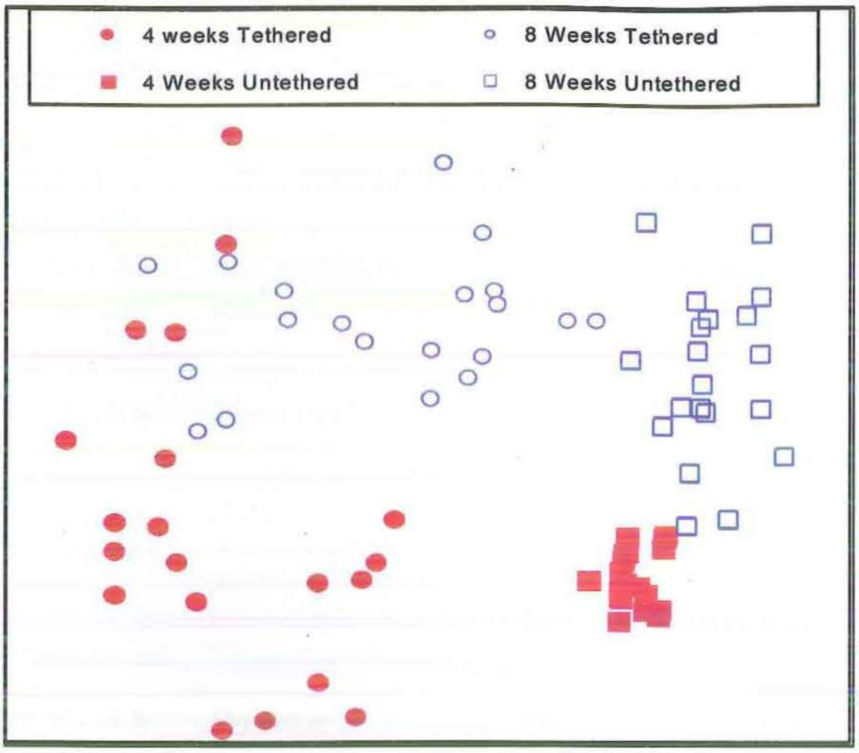


Figure 3.5. Two dimensional ordination of epiphyte assemblages (n=80), using presence/absence data on non-metric MDS, over two time intervals (four weeks and eight weeks) for two artificial seagrass units (Tethered and Untethered) during July-August 2000 in Marmion Marine Park, Western Australia.

A variety of species characterised the ordination groups (Table 3.6). Plants of the species *Hypnea* sp 2, a red corticated terete algae, were only present on tethered artificial seagrass leaves. However, higher abundances of plants of the species *Griffithsia australe* and *Antithamnion* sp 2, both filamentous red algae, were characteristic of untethered units. Plants of the species *Antithamnion* sp 2 were also present only on untethered shots at four weeks, but were present on both forms of leaves at eight weeks. Plants of the species *Heterosiphonia* sp 1, another red corticated terete algae, were only found on untethered leaves at four weeks but were found on both forms of leaves at eight weeks (Table 3.6).

Table 3.6. Results of SIMPER showing species contribution to assemblage structure of epiphytes collected from two types of artificial seagrass units (Tethered and Untethered) over two time intervals (4 weeks and 8 weeks) during July-August 2000 in Marmion Marine Park, Western Australia.

PAIR-WISE COMPARISON		EPIPHYTE SPECIES PRESENT			
Group A	**Group B**	**Group A**	**Ratio**	**Group B**	**Ratio**
Week 4 Tethered	Week 4 Untethered	*Hypnea* sp 2	2.04	*Antithamnion* sp 2	6.95
				Griffithsia australe	3.2
Week 8 Tethered	Week 8 Untethered	*Hypnea* sp 2	1.08	*Antithamnion* sp 2	1.37
				Griffithsia australe	2.2
Week 4 Tethered	Week 8 Tethered	*Green* sp 1	1.48	*Antithamnion* sp 2	1.32
		Hypnea sp 2	1.48		
		Antithamnion sp 1	1.45		
Week 4 Untethered	Week 8 Untethered	*Heterosiphonia* sp 1	4.68	*Antithamnion* sp 2	1.43
				Griffithsia australe	1.55
Week 4 Tethered	Week 8 Untethered	*Hypnea* sp 2	2.04	*Antithamnion* sp 2	5.49
				Griffithsia australe	2.2
Week 4 Untethered	Week 8 Tethered	*Antithamnion* sp 2	1.45	*Hypnea* sp 2	1.08
		Heterosiphonia sp 1	4.68		
		Griffithsia australe	3.21		

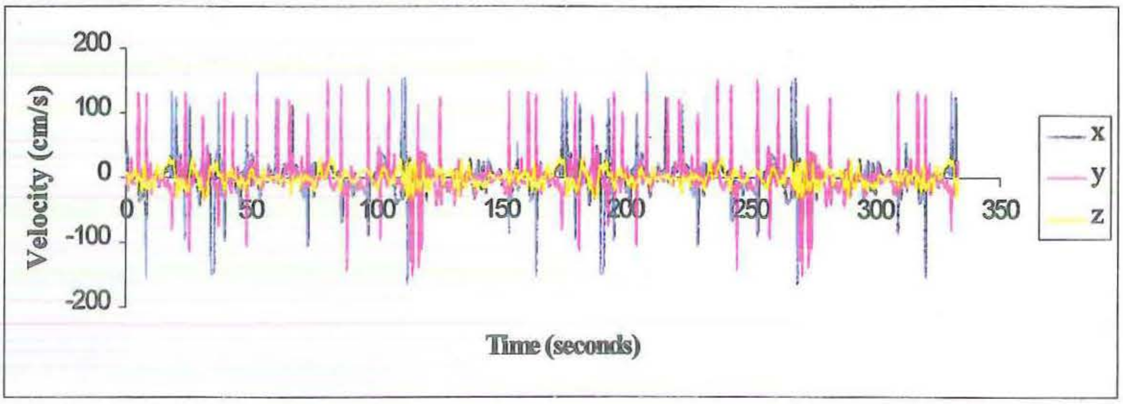
3.2. INFLUENCE OF EXPOSURE ON THE BIOMASS OF ALGAL EPIPHYTES

3.2.1. Water Velocity at the Study Sites

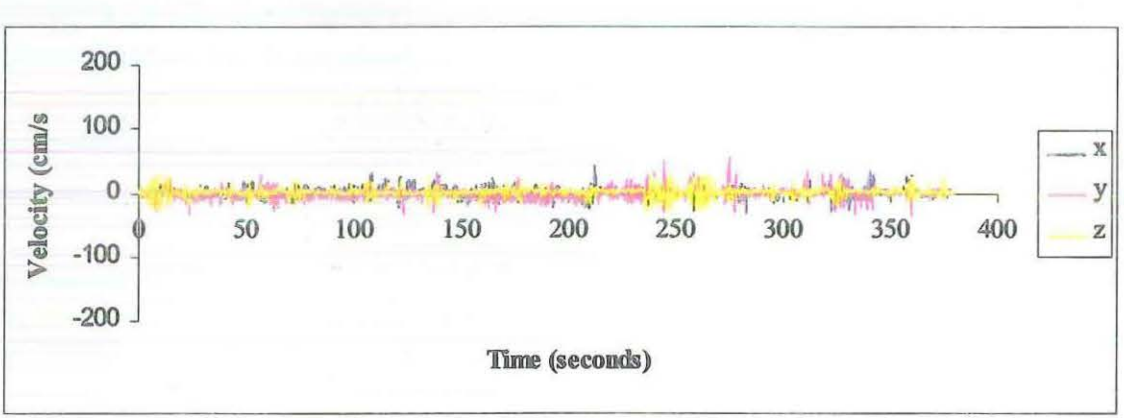
The Acoustic Doppler Velocimeter (ADV) measurements were recorded in three dimensions. These measured the velocity of the backward and forwards motion of the water plus oscillating water motion. Greater water velocities and variability at the exposed sites were recorded using the ADV (Figure 3.6). Water velocity was calculated to be greater at the exposed site, with a mean velocity at the exposed site of 115 cm/s but a mean velocity of only 25 cm/s at the sheltered sites. The range in water velocity was high at the exposed site with maximum recorded velocity peaking at 165 cm/s and a minimum of 15 cm/s. The range was much smaller at the sheltered sites with a peak velocity recorded at only 52 cm/s and a minimum velocity of just 5 cm/s. A higher variability in velocity was exhibited at the exposed site, shown by the consistently higher coefficient of variation on all axes measured at this site (Table 3.7).

Table 3.7. Coefficient of variation measured on three axes (X, Y, Z) at two exposures (sheltered and exposed). Variations are consistently higher on exposed axes.

AXES	COEFFICIENT OF VARIATION	
	Sheltered	**Exposed**
X	87.79	143.43
Y	126.9	163.49
Z	77.19	114.8



a) Exposed: Marmion Marine Park



b) Sheltered: Cockburn Sound

Figure 3.6. Water velocity and movement recorded on 3 axes at the a) exposed site, and b) sheltered site during July-August 2000 in Marmion Marine Park and Cockburn Sound, Western Australia.

3.2.2. Differences in Epiphytic Biomass

ANOVA showed that there was a significant difference in the DW and AFDW between tethered and untethered artificial seagrass units at each site (Table 3.8). There was no significant difference in epiphytic biomass in terms of DW and AFDW between sites (three sheltered and one exposed) for both tethered and untethered artificial seagrass units (Table 3.8), indicating that these variables did not differ between sheltered and exposed sites.

Table 3.8. Results of two factor ANOVA testing differences in biomass variables between sites (1 Exposed and 3 Sheltered) and between two types of artificial seagrass units (Tethered and Untethered) during July-August 2000 in Marmion Marine Park and Cockburn Sound, Western Australia. Data untransformed as Levene's test of homogeneity of variance result of P=0.061 indicated variances were homogeneous).

FACTOR	**ANOVA RESULTS**				
	Effect of Site				
	d.f.	Mean square	F-value	P-value	
Dry Weight	1	0.479	0.167	0.686	NS
Ash Free Dry Weight	1	1.130	0.706	0.409	NS
	Effect of Type of Artificial Seagrass Unit				
	d.f.	Mean square	F-value	P-value	
Dry Weight	1	165.590	57.889	0.000	*
Ash Free Dry Weight	1	54.558	34.091	0.000	*
	*Site * Artificial Seagrass Unit*				
	d.f.	Mean Square	F-value	P-value	
Dry Weight	1	0.278	57.889	0.922	NS
Ash Free Dry Weight	1	0.618	0.386	0.540	NS

NS Not statistically significant ($p > 0.01$)

* Statistically significant ($p < 0.01$)

The mean DW on the tethered artificial seagrass units at the three sheltered sites had a combined mean 5.9 ± 0.6 SE g/10 leaves (Figure 3.7). The mean DW on tethered units at the exposed site was very similar with 4.6 ± 0.9 SE g/10 leaves. Similarly, the mean AFDW at sheltered sites was 0.33 ± 0.03 SE g/10 leaves, and at exposed sites was 0.22 ± 0.07 SE g/10 leaves (Figure 3.8).

The untethered units also showed relatively similar mean DW among the four sites, with 0.7 ± 0.07 SE g/10 leaves combined over the three sheltered sites and 0.5 ± 0.07 SE g/10 leaves at the exposed site (Figure 3.7). This trend was again repeated for mean AFDW (Figure 3.8).

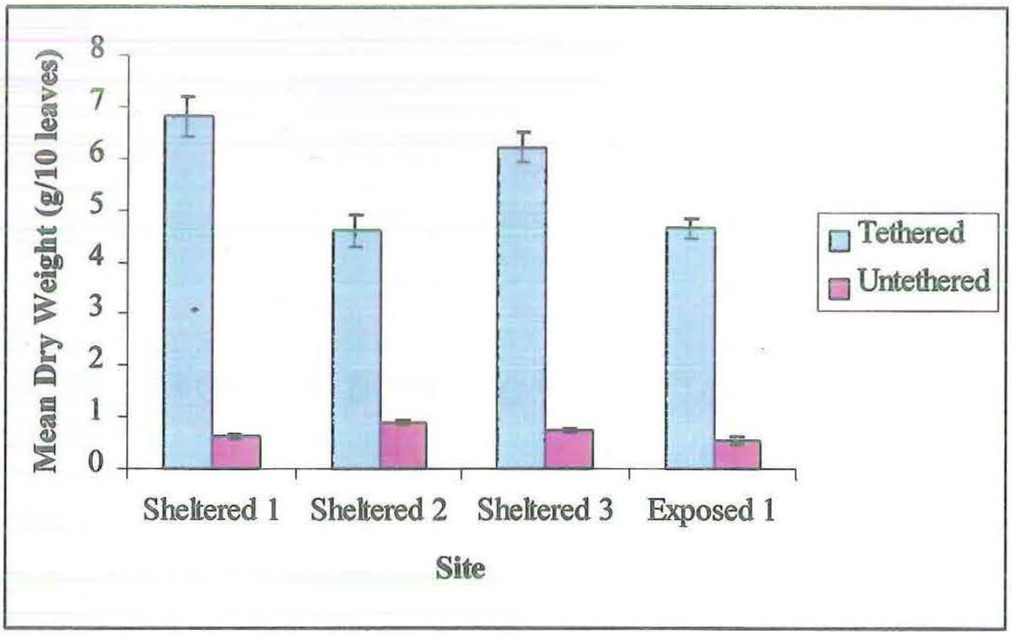


Figure 3.7. Mean dry weight (g) of epiphytic algae (± SE, n = 3) recorded from 10 leaves each on two types of artificial seagrass units (Tethered and Untethered) at four sites (three Sheltered sites in Marmion Marine Park, one Exposed site in Cockburn Sound, Western Australia) during July-August 2000.

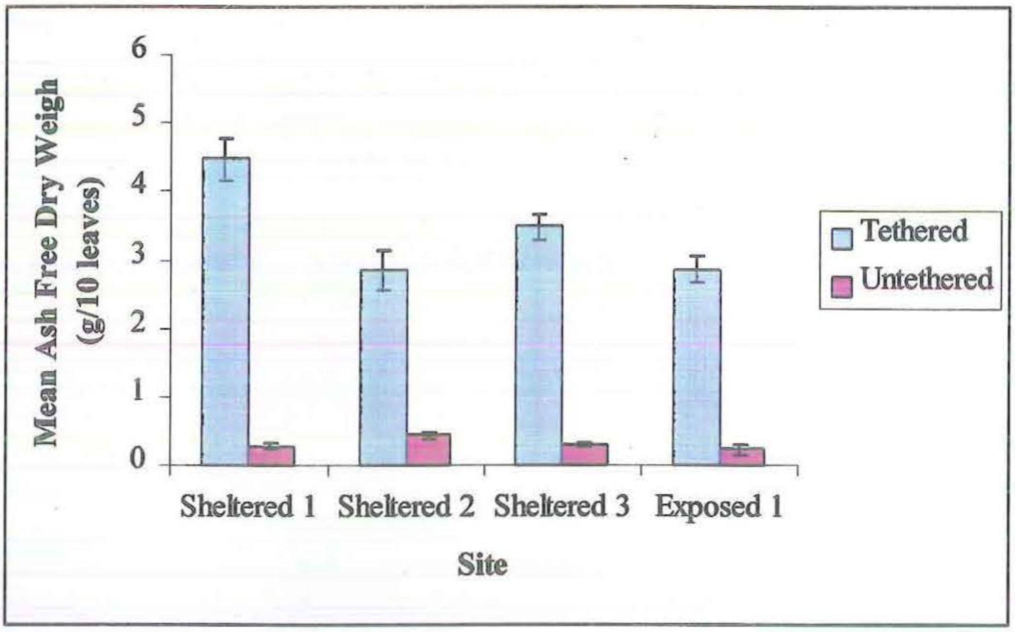


Figure 3.8. Mean ash free dry weight of epiphytic algae (± SE, n = 9) recorded from 10 leaves each on two types of artificial seagrass units (Tethered and Untethered) at four sites (three Sheltered sites in Marmion Marine Park, one Exposed site in Cockburn Sound, Western Australia) during July-August 2000.

3.2. INFLUENCE OF DEPTH ON THE BIOMASS OF ALGAL EPIPHYTES

3.3.1. Differences in Epiphytic Biomass

ANOVA showed that both DW and AFDW of epiphytic biomass differed significantly between depths, while sites nested within depths did not differ significantly (Table 3.9).

Table 3.9. Results of two factor nested ANOVA testing differences in biomass variables between depths (ranging from eight metres in Deep to three metres in Shallow) and between two types of artificial seagrass units (Tethered, Untethered inside and Untethered outside) during July-August 2000 in Marmion Marine Park and Cockburn Sound, Western Australia. Data untransformed because Levene's test of homogeneity of variance result of P = 0.06 indicated variances were homogeneous.

FACTOR	**ANOVA RESULTS**				
	Effect of Depth				
	d.f.	Mean Square	F-value	P-value	
Dry Weight	1	47.804	63.508	0.000	*
Ash Free Dry Weight	1	13.087	35.140	0.000	*
	Effect of Site Nested in Depth				
	d.f.	Mean Square	F-value	P-value	
Dry Weight	4	0.402	0.534	0.712	NS
Ash Free Dry Weight	4	0.509	0.772	0.881	NS
	Effect of Type of Artificial Seagrass Unit				
	d.f.	Mean Square	F-value	P-value	
Dry Weight	2	66.546	88.408	0.000	*
Ash Free Dry Weight	2	21.065	56.564	0.000	*
	*Depth * Artificial Seagrass Unit*				
	d.f.	Mean Square	F-value	P-value	
Dry Weight	2	31.734	48.317	0.000	*
Ash Free Dry Weight	2	10.325	27.724	0.000	*

NS = Not statistically significant ($p > 0.01$)
* = Statistically significant ($p < 0.01$)

The mean DW of epiphytes on the tethered artificial seagrass units was five times higher for those units placed in shallow sites compared to those placed at the deep sites (Figure 3.9). In shallow sites, the mean DW of epiphytes on tethered units ranged from 2.6 ± 1.2 SE to 9.2 ± 1.7 SE g/10 leaves compared to only 1.2 ± 0.1 SE to 1.3 ± 0.6 SE g/10 leaves at deep sites. The mean AFDW of epiphytes again showed similar trends over depth. The mean AFDW of epiphytes accumulated on the tethered artificial seagrass units in shallow sites was twice to eight times higher than those at the deep sites (Figure 3.10). The mean AFDW of tethered units at the shallow sites ranged from 1.6 ± 1.5 SE to 6.1± 3.8 SE g/10 leaves compared to only 0.7 ± 0.2 SE to 0.8 ± 0.5 SE g/10 leaves at the deep sites.

In contrast to tethered units, epiphytic biomass on untethered units did not vary with depth (Figures 3.9 and 3.10), which resulted in a depth by type of artificial seagrass unit interaction (Table 3.9). The mean DW of untethered inside units ranged from 0.2 ± 0.005 to 0.6 ± 0.09 g/10 leaves and untethered outside units ranged from 0.3 ± 0.07 to 1 ± 0.15 g/10 leaves across both depths. The variability within depths was much higher in epiphytic biomass on the tethered artificial seagrass units compared to the untethered artificial seagrass units, through the shallow tethered units being more than five times higher than deep tethered units. These trends were again very similar for AFDW (Figure 3.10) where untethered units did not vary considerably across depth (Figure 3.10). Again, the variability was much higher in the tethered artificial seagrass units compared to the untethered artificial seagrass units.

ANOVA also confirmed there was a significant difference in epiphytic biomass between tethered and untethered artificial seagrass units (Table 3.9). However, pair-wise comparisons showed that for both mean DW and AFDW, there was no significant difference between untethered units placed inside the meadow and untethered artificial seagrass units placed outside the meadow (P = 1.000).

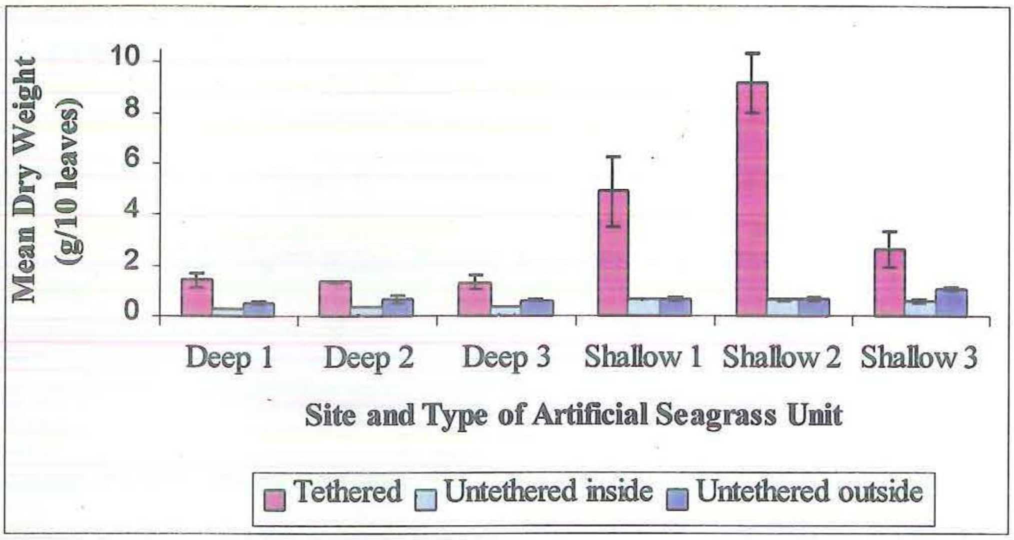


Figure 3.9. Mean dry weight (g) of epiphytic algae (± SE, n = 3) recorded from 10 leaves each on three types of artificial seagrass units (Tethered, Untethered inside meadow and Untethered outside meadow) at two Depths in Cockburn Sound, Western Australia (Deep = 8m, Shallow = 3m) during July-August 2000.

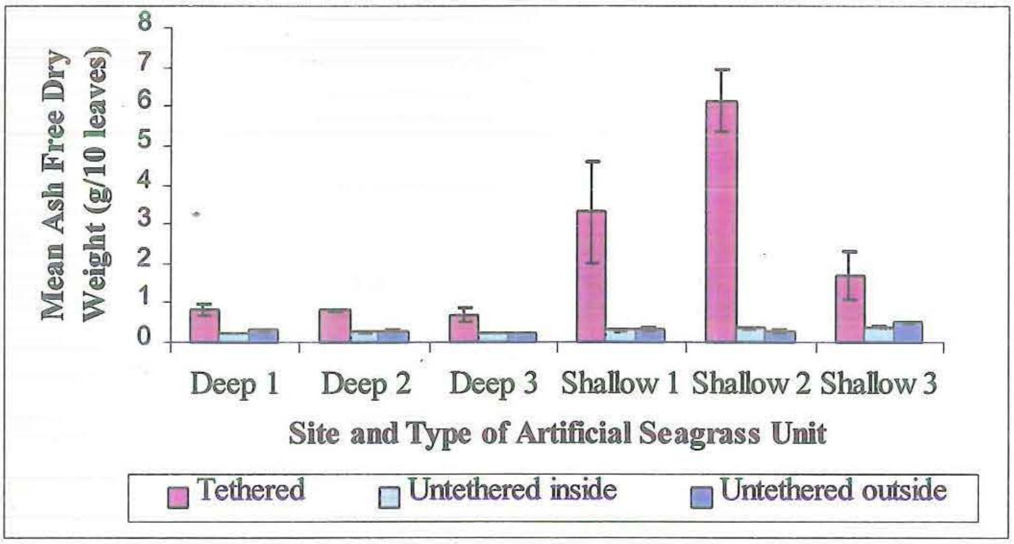


Figure 3.10. Mean ash free dry weight (g) of epiphytic algae (± SE, n = 3) recorded from 10 leaves each on three types of artificial seagrass units (Tethered, Untethered inside meadow and Untethered outside meadow) at two Depths in Cockburn Sound, Western Australia (Deep = 8m, Shallow = 3m) during July-August 2000.

3.4. SUMMARY – EFFECT OF LEAF MOVEMENT ON EPIPHYTES

In summary, it was found that the movement of leaves significantly reduced the accumulation of epiphytic algae. Across all times, exposures and depths, the standing crop of epiphytes on tethered leaves was higher than on untethered leaves, ranging from four to 13 times the untethered biomass. This trend was also seen in epiphytic species composition and species richness, where ordination patterns revealed a clear difference between the tethered and untethered units, and between time intervals.

CHAPTER 4: DISCUSSION

4.1. INFLUENCE OF LEAF MOVEMENT

The effect of leaf movement on the accumulation of epiphytes on seagrass was measured throughout this study by examining the difference in epiphytic biomass between tethered and untethered artificial seagrass leaves. The tethered leaves were designed to remove any effect of leaf movement on epiphytic accumulation while the untethered leaves were designed to mimic free-moving seagrass. The results of this study provide clear evidence that the movement of leaves significantly reduces the accumulation of epiphytic algae. Across all times, exposures and depths used in this study, the standing crops of epiphytes on tethered leaves were higher than on untethered leaves ranging from four to 13 times the untethered biomass. Leaf movement could potentially influence epiphytic biomass accumulation through direct processes such as abrasion caused by physical contact between leaves, or indirectly by influencing the degree of grazing by invertebrates (Hall & Bell, 1988) or settlement of epiphytic propagules (Hoffmann, 1987). The following discussion explores the possible causes of the reduction in epiphyte accumulation of free moving seagrass leaves by expanding on the conceptual model described in section 1.4.

The consistency of the effect of leaf movement across all three experiments, incorporating different times, exposures and depths, suggests that there are several potentially confounding factors, in particular, differences of propagules and regional differences, which may influence the composition of epiphytes. While these factors can not be ignored, the results of this study show that leaf movement is sufficiently dominant so that the same effect is being produced, irrespective of region.

Epiphytic algal species composition and species richness also varied between tethered and untethered leaves. Fewer species were recorded on untethered leaves over both time intervals. The composition of epiphytic algae on tethered leaves was characterised by red corticated terete algae, while untethered leaves were characterised by red filamentous algae. The structure of these algae would suggest that the plants of these two species are not significantly different in their resistance to mechanical stress (Womersley, 1994). So the compositional differences may not be reflecting an abrasional effect, but more likely another effect of leaf movement such as settlement of propagules (see section 4.1.3).

4.1.1. Effect of Leaf Movement on Loss of Epiphytes Through Abrasion

The movement of leaves can cause them to come into contact with neighbouring leaves and physically remove (abrade) accumulated epiphytes. Therefore, it is likely that processes affecting leaf movement will potentially be influencing the amount of epiphytic biomass that is abraded and thus lead to a significant underestimation of the gross biomass produced over the lifespan of the leaves. The degree of water movement, plant morphology and the hydrodynamic functions that are related to both these factors could be expected to influence the degree of abrasion.

Water movement can potentially result in the abrasion of epiphytic material in two ways. Firstly, mechanical stress resulting from water movement will often cause drag on marine plants (Denny *et al.*, 1998), which can result in the removal of plant parts including algal epiphytes (Fonseca & Fisher, 1986). Secondly, water movement can resuspend sediments, which could be carried in solution and erode fine algal epiphytes.

The movement of sediment and the effect of water velocity were evident at the exposed sites where both the tethered and untethered artificial seagrass leaves were destroyed and buried, under almost two metres of sand in the most extreme case. However, the results also indicated that any abrasive effect of leaf movement seemed not to be correlated with regional differences in wave energy, as the differences in tethered *versus* untethered leaves were similar at both the exposed and sheltered sites. One explanation for this is that there may be a form of threshold relationship between water movement and the process of abrasion. That is, even though there were large differences in energy between the sheltered and exposed sites, both exposures may have had sufficient energy to exceed the critical amount needed to produce a maximum abrasional effect. Therefore, from this study the results clearly show that there was a reduction in biomass due to leaf movement shown by the differences in the type of artificial seagrass leaf. As leaf movement can only be caused through water column energy, while the level of exposure did affect the movement of seagrass leaves, both exposures may have had enough leaf movement to produce an abrasional effect. However, the reduction of power from the loss of replicates in this experiment, may have significantly reduced the potential to detect differences if they occurred.

The morphology and size of seagrass and its epiphytes can often affect the ability of those epiphytes to stay attached to seagrass leaves under varying energy conditions. In flowing water, morphology affects how algal epiphytes respond to physical forces (Denny *et al.*, 1998). This may account for the different compositions of algae that were found on different artificial seagrass leaves such as tethered and untethered leaves. This study did show such a difference with red corticated terete epiphytes found only on tethered leaves and red filamentous epiphytes found only on untethered seagrass leaves.

The structure of the seagrass can also influence the movement of leaves within a meadow and thus affect the abrasional loss of epiphytes on the leaves. Under high energy unidirectional flows created by tides and currents, narrow flat blades found in the seagrass genus *Posidonia*, often flap with lower amplitude and collapse together in a streamlined bundle (Koch, 1994) and can experience a low drag per unit area of leaf blade at a given flow velocity (Koehl & Alberte, 1988). Under oscillatory flows resulting from wave energy, the seagrass leaves still collapse together, but flap forwards and backwards (Butler & Jernakoff, 1999). The protection of biomass is more likely to occur in unidirectional flows where leaves within the core of a bundle are protected for the majority of the time (Nowell & Jumars, 1984). In oscillatory flows resulting from wave energy, the leaves may experience less permanent bundling and protection, while suffering more opportunities for contacts between leaves thus allowing abrasion of epiphytes. A high degree of variability in epiphytic biomass would then be expected, depending on the degree of bundling and oscillitary movement. This was seen in the study, particularly in the accumulated epiphytic biomass on leaves in sheltered locations and in shallow locations.

Another morphological factor of the epiphytes that is potentially affected by abrasional processes, is the physical size that the epiphytes can grow to under influences of increased water velocity (Gaylord *et al.*, 1994). Personal observations from this study showed that the epiphytes grew much larger on the tethered leaves than the untethered leaves. This partly accounted for the increased biomass on the tethered leaves. This supports the suggestion that leaf movement was abrading epiphytes that grew beyond a certain size. Physical interactions such as hydrodynamic forces may also set mechanical limits to the size to which exposed animals such as epifauna, or plants such epiphytes, can grow before the probability of being dislodged approaches certainty (Denny *et al.*, 1985). Carrington (1990) has shown that changes in the shape of macroalgae with growth can, in conjunction with drag caused when leaves are moving in relation to the movement of water, form a limit to the size of the plant. This can have consequences to the size that macroalgal epiphytes growing on seagrass leaves can reach, before they are physically removed. This could mean that in an exposed area with high water velocity, such as in the study site within Marmion Marine Park, there might be a size limit to the epiphytes, thus a limit to the total biomass of the standing crop.

The reduction in size of epiphytes and epifauna can be attributed to a number of factors. In the first instance, it could be the process of leaf movement, not the physical removal of epiphytes, limiting the potential to grow to their maximum size. Alternatively, leaf contact could be removing any epiphytes that do grow beyond a certain size, thus reducing the biomass on the leaf through abrasion. However, the reduction in accumulation or loss of epiphytes due to their size in exposed areas will also depend upon their tolerance to exposure and whether the velocity of water experienced reaches their upper tolerance level (Denny *et al.*, 1998). Therefore leaf movement may be having an abrasional influence on the epiphytes in this study, by removing algae above a certain size, especially on the untethered leaves.

4.1.2. Abrasional Loss of Epiphytes Through Grazing

In this study, grazing epifauna had the potential to reduce the standing crop of epiphytes on the seagrass leaves. Epiphytic algae form part of the main diets of many grazing epifauna in seagrass meadows (Alongi, 1998). Feeding experiments have shown that epiphytic algae is grazed heavily (Klumpp *et al.*, 1989) and that this grazing can be a major determinant of epiphytic biomass (Alcoverra, 1997). Jernakoff & Nielson (1998) determined that grazing by amphipods often reduced taxonomic richness by up to 12% on *Posidonia sinuosa* leaves, whereas the absence of gastropod grazers often increased the standing crop of biomass by up to 44%. A recent study by Schanz *et al.*, (2000) confirmed that the abundance of grazers was very likely influenced by the degree of leaf movement within a seagrass meadow. If this is the case, grazers could be important in accounting for the different standing crops on the tethered and untethered leaves in the present study. Grazers will also experience similar hydrodynamical forces to epiphytes under influence of exposure (Eckman & Duggins, 1983). Increasing exposure will limit the size that the grazing fauna can attain (Denny *et al.*, 1985), and thus reduce the epiphytic biomass they can potentially consume. However, *in situ* observations of artificial seagrass leaves, did not confirm an abundance of grazers or grazing scars on either type of artificial leaves. There was however, a multitude of grazers found inhabiting the weights used to anchor the units to the benthic substrate. These observations therefore suggest that grazers were unlikely to be contributing to significant loss of epiphytes on untethered seagrass leaves.

The time of sampling may also influence the incidence of epiphytic grazing on seagrass leaves. Kendrick & Burt (1997) noted that mollusc-grazing scars were observed to be more prominent on seagrass leaves sampled during late winter to early summer (August to January). Sampling in this study, took place in winter (June – early August), which may naturally be a period of reduced grazing pressure.

The fact that grazers were only seen on the tethered leaves, albeit in low abundances, suggests the potential for further underestimation of the gross epiphytic biomass on seagrass leaves. If grazers are reducing the standing crop of tethered leaves, the difference between the tethered leaves and the untethered leaves is likely to be more prominent. This may then increase the difference between the net production and gross production of epiphytes that could result in an even bigger underestimation of epiphytic productivity if measured through net production of the standing crop. Therefore, if leaf movement is potentially affecting the epiphytic standing crop through a reduction in grazing pressure, any effect of leaf movement on reducing standing crop is more likely to be through other mechanisms.

4.1.3. Inhibition of Propagule Settlement

While leaf movement causing epiphytic abrasion could be the fundamental cause of the difference in epiphytic biomass, leaf movement could also potentially affect settlement of epiphytic propagules onto the seagrass leaves. Other studies have shown that the nature of the substrate can affect the settlement of algal propagules. These can include the surface properties of the substrate (Lobban & Harrison, 1994), and the size and structure of the propagule's attachment organ or basal disc (Orth & van Montrans, 1984). An algal epiphyte with a small basal disc is able to colonise a greater variety of substrates than algae with larger discs (Orth & van Montrans, 1984; Lobban & Harrison, 1994). It would therefore also stand to reason that the larger the surface area of leaf available, the higher potential for colonisation by epiphytes. However, in this study the same artificial substrate was used or each type of artificial seagrass unit, so any influence of substrate type was removed. Therefore, it is likely that it is perhaps the dispersal of the propagules or the leaf movement itself that is limiting the colonisation and accumulation of epiphytes.

Both forms of artificial seagrass leaves, under all sets of experimental conditions, were in close proximity to each other throughout the experiments, so it could be assumed that the same sources were providing propagules to the artificial seagrass leaves. The type and availability of epiphytic algal propagules in the water column at any given point in time is a combined function of a number of factors, such as the period of reproduction of the species involved, the differences in the quantity of propagules released and also the potential dispersal distance of these propagules (Hoffmann, 1987).

Dispersal of algal propagules can be effected by the morphology of the propagule, how long it can remain viable in the water column and other effects such as currents (Lobban & Harrison, 1994). For example, certain species of green algae have been known to colonise on substrates over 35 kilometres away from its original source, while some brown algae can only disperse and colonise within metres from its source (Hoffmann, 1987). However, most marine algae have quite small dispersal ranges (Zechman & Mathieson, 1985; Hoffmann, 1987), and often settle and recruit within metres of their sources (Kendrick & Walker, 1991, 1995). Red algal propagules have also been known to sink rapidly, which reduces the time spent suspended in the water column, thus limiting their dispersal capabilities (Amsler & Searles, 1980), as red algal species were found in abundance on the artificial seagrass leaves in this study, whereas green algal propagules were not common, it could be reasonably assumed that these propagules were released from a local source. Previous studies also have shown that epiphytic assemblage structure can vary significantly at scales of only a few metres apart, and this may indicate that even at this scale, recruiting propagules may be from different sources (Vanderklift & Lavery, 2000). Thus these spatial studies suggest that only samples within half a metre of each other can be described as homogeneous. None of the replicates used in this study were placed within five metres of each other, suggesting that the variability within replicates also had the potential to be high. However, because the effect of removing leaf movement on standing crop was consistent, it is likely that other factors related to leaf movement are more influential than variability in propagule sources in reducing the potential for untethered leaves to accumulate epiphytes.

There is a lack of literature defining the influence of the movement of seagrass leaves on the recruitment of algal epiphytes. The results of this study show that this influence could have a large effect on epiphytic biomass. It may also influence the species that are able to colonise on a moving substrate. However, as seagrass leaves do move naturally with water flow, colonisation may be influenced by the degree of leaf movement such as in highly exposed areas.

In a relevant study, Nowell & Jumars (1984) found that the orientation of a substrate, determined the type of algae colonising, and the rate that the algal propagules established themselves onto the substrate. Even though the study measured algal recruitment on glass plates, it still has implications to the current study. As a seagrass leaf moves with relation to water flow, it can be reasonably assumed that the leaf's orientation relative to the water flow will vary with time (Denny, 1988). Therefore, the opportunity for colonisation of algal propagules on a moving leaf may well vary depending on its relative orientation at any given time. This might explain some of the differences in epiphytic biomass observed in this study between the tethered and untethered leaves.

Similarly, another study examined the potential time restrictions for adheration of algal propagules to a substrate (Zechman & Mathieson, 1985). They suggested that the initial adheration of algal propagules onto a substrate is only effective for a short time. If a seagrass leaf is moving, especially in relation to the hydrodynamical water processes as described earlier, leaf movement may be restricting the epiphytic biomass accumulating on a seagrass leaf. Therefore the process of leaf movement limiting the settlement of epiphytic algae, is just as likely to be causing the differences between the tethered and untethered leaves seen in this study.

4.1.4. Other Factors Influenced by Leaf Movement

Any leaf movement, especially that causing bundling of leaves, may affect epiphytes by altering the availability of resources essential for growth, either positively or negatively. In a bundled situation such as when the seagrass leaves in meadow collapse together, epiphytes may experience limitation such as light (Koehl & Alberte, 1988). Shading of epiphytes in a bundle will limit the production of the epiphytes and their biomass (Fitzpatrick & Kirkman, 1995). Therefore, there is likely to be a balance between reducing drag and reducing self-shading. This balance could explain why the untethered leaves that could bundle together in response to water movement, had a similar epiphytic biomass.

Leaf movement within seagrass meadows may be contributing to self-shading, and thus reducing the production of epiphytic biomass on the leaves. A variety of factors influence the amount of light reaching epiphytic algae (Williams & Dennison, 1990). Depth is known to affect the attenuation of light that is available for epiphytes to use for growth and development (Duarte, 1991). The availability of light will also depend on the turbidity of the water column that can affect the attenuation of light available for epiphytic use (Carruthers & Walker, 1997). Thus the deeper a leaf is situated, the less light will be available for its use. It would be expected therefore, that the seagrass leaves in the deep locations would have had smaller epiphytic biomass than the seagrass leaves at the shallow locations. This was not the case in this study as the epiphytic biomass on untethered units was similar regardless of depth. An increased velocity and turbulence above a given threshold can result in suspended material reducing light available for growth (Alongi, 1998). This can often result in a decrease in the rate of production (Koch, 1994), thus limiting epiphytic biomass. Therefore it is likely that a factor relating to leaf movement superseded the effect of light available for epiphytic use.

Leaf bundling and other leaf movement processes may also influence nutrient availability, especially through its effect on boundary layers, which are liable to reduce that rate of nutrient exchange between the water column and the algae (Hurd, 2000). When a fluid moves past a solid object, the layer of fluid immediately next to the solid surface does not slip with respect to that surface (Nowell & Jumars, 1984). Therefore, a shear gradient, known as a boundary layer, develops in the fluid between the surface of the object and the mainstream flow (Koehl & Alberte, 1988). A boundary layer is thus protecting some of the layer of epiphytes on the seagrass leaves. The boundary layer prevents the water adjacent to the algal surface being replenished and increases the possibility of nutrient depletion (Denny *et al.*, 1998). The boundary layer will become thinner (Alongi, 1998) permitting greater diffusive exchange of nutrient molecules (Mann & Lazier, 1996). Those epiphytes that are capable of withstanding increased water motion will potentially have better access to nutrients through increased rates of replenishment (Koch, 1994). However, the increase in turbulence simultaneously increases the loss of the standing crop of epiphytic algae attached to the seagrass leaves through abrasive processes. Again, determining the balance of these two competing processes on epiphytic standing crop was beyond the scope of this project, but is worthy of further investigation.

4.2. HOW DOES EXPOSURE AND DEPTH MODIFY THE INFLUENCE OF LEAF MOVEMENT

Only the tethered form of artificial seagrass leaves varied between exposure and depth, reflecting a difference only in the absence of leaf movement. The untethered leaves maintained an almost constant epiphytic biomass and species richness over time, and an almost constant biomass over exposure and depth. The degree of exposure did not significantly alter the influence of leaf movement on epiphytic biomass. That is, even though the biomass on tethered leaves was slightly higher in the more sheltered sites, the percentage reduction in biomass due to leaf movement was similar at both exposures.

Degree of exposure and depth could reasonably be expected to affect the degree to which leaf movement reduces the standing crop of epiphytes, as the increased water velocity and hydrodynamical forces would be expected to increase leaf movement and any associated effect on epiphytes. The degree of exposure has been shown to influence the composition of algal assemblages in reef ecosystems (Littler, 1973; Hatcher, 1989; Dethier, 1994; Phillips *et al.*, 1997). Yet, in this study, exposure did not appear to affect the difference of epiphytic biomass on the untethered leaves due to leaf movement. While this was considered unusual, the lack of difference on the untethered leaves between exposures could again be explained by both exposures surpassing the threshold of energy necessary to cause an effect. However, as this experiment lost power due to lack of replication from storm events, any differences between the epiphytic biomass between sheltered and exposed locations may not have been detected. The difference in tethered leaves between depths, like over time, was very pronounced. All of these differences were caused through various contributing factors that can occur in the recruitment and post recruitment stages. For example, these factors may influence the recruitment of epiphytes through release, dispersal and settlement of algal propagules colonising the seagrass leaf substrate (recruitment). Alternatively, they may influence the physical environment in such a way that only a certain biomass of epiphytes can be maintained on a seagrass leaf (post-recruitment). If leaf movement is affecting epiphytic composition and biomass in seagrass meadows, there could also be a potential for underestimation of carbonate production by epiphytes, if abrasive processes are removing these epiphytes from the standing crop.

The depth that a seagrass is situated will have implications on the seagrass itself (Duarte, 1991). The standing crop of epiphytes on untethered seagrass leaves was similar in depths of 3m and 8m, whereas epiphytic biomass on tethered leaves was significantly higher in shallow areas. The effect of the standing crop of epiphytes in terms of light reduction to the seagrass leaf would be far more significant at the deep sites, as the seagrasses are receiving less light in these deeper areas. Therefore it would be expected that there would be a higher epiphytic biomass at deeper sites when water movement is reduced, however, this may be counteracted by reduced light in the deeper sites leading to decreased production. Again, however, what was expected was not confirmed by this study's results. The different biomass on the tethered leaves between the deep and shallow sites would suggest that in the absence of leaf movement, other factors must limit epiphyte production. However, untethered leaves that were influenced by leaf movement showed no differences between deep and shallow sites. This could suggest that despite the effect of light and any other limitation which varies over depth, the effect of leaf movement could be so profound that differences due to these other factors are overwhelmed (*i.e.* factors due to leaf movement are the primary limiting factors to epiphyte accumulation).

The greater epiphytic biomass on the tethered leaves in the shallow sites could also have been influenced by nutrients. The effects of nutrients, such as through runoff from the land or from surrounding reefs, have the potential to cause excessive epiphytic loads, or enhanced growth of free-living macroalgae, which can compete with the seagrasses and its epiphytes for nutrients and light (Cambridge *et al.*, 1986). The sources for potential nutrient enrichment in this study could have come from the nearby reefs in all the study sites. Additionally, there was a potential for nutrient runoff from Garden Island itself. Any of these factors could have affected the production of epiphytic biomass on the artificial seagrass leaves. Thus the closer proximity of the shallow sites to the potential source of nutrients such as the nearby reef or Garden Island may have lead to greater biomass of epiphytes in the shallow areas. However, the deep and shallow sites may have been too close to each other for this to be a reasonable influence.

4.3. MANAGEMENT IMPLICATIONS

The results of this study show that there is a potential to underestimate gross epiphytic biomass and thus productivity estimates, if the assumption is made that the standing crop on a leaf is a reasonable reflection of the gross epiphytic biomass to have been present on that leaf over its life. This study clearly shows that movement of seagrass leaves is causing leaves to have less biomass than they would without movement. The potential for underestimation of gross epiphytic biomass raises implications to the management of our seagrass ecosystems, whereas there are limited management applications if the difference in epiphytic biomass is caused through limitation of propagule settlement. The importance of epiphytes is well documented in the literature (Section 1.1), and thus the contribution of seagrass meadows to the productivity of the Australian coastline could be significantly underestimated if in fact leaf movement is resulting in an abrasional loss of epiphytes.

These underestimations of epiphytic biomass have the potential to influence the management decisions relating to our seagrass meadows. Directly affecting these decisions is the extensive loss of seagrass meadows worldwide (Walker & McComb, 1992). The seagrass losses in Australia have been caused through a variety of processes, mainly through anthropogenic impacts, either directly through mining for shell sands (Hegge *et al.*, 1998), coastal developments which involve land reclamation or dredging expanses of meadow, or indirectly through slower processes such as interruption of light quality and/or quantity to seagrass leaves (Cambridge *et al.*, 1986), or increased pollution and nutrient enrichment (Silberstein *et al.*, 1986).

The evidence provided by this research shows that the net and gross productions of epiphytic biomass on a leaf over its life are not equal. Calculations show that the production of epiphytes at the studied sites have the potential to be underestimated by at least a third. This means that the total production of epiphytic biomass may be at least three times the amount previously estimated, if abrasion of epiphytes is the primary cause of difference in epiphytic biomass. If leaf movement is primarily reducing the settlement of epiphytic biomass, rather than abrasion causing a loss of epiphytic biomass, then the underestimations of productivity are not likely to be as large or perhaps not even significant at all.

A relevant and highly illustrative example of the significance of this finding can be found in the work of (Hegge *et al.*, 1998). These authors attempted to estimate the *in situ* production of calcium carbonate by calcified epiphytic algae in seagrass meadows of Success Bank, Western Australia. The study was intended to clarify the significance of seagrass meadows for the formation of carbonate sands in the region. That calculated that the *in situ* carbonate production of epiphytes in that region accounted for less than 15% of the volume of shell sands at Success Bank, and that seagrass meadows were insignificant in forming the sediment of the Bank compared with the erosion and transport of the adjacent Pleistocene reefs from the Garden Island Ridge. It appears that this calculation was made essentially from the net production of epiphytic biomass. That is, only the standing crop of epiphytes on the leaf was sampled. They multiplied the measured standing crop by the leaf turnover rate (*i.e.* the number of leaves per year that drop off the plant and contribute to sediment production) to estimate the annual contribution from epiphytes. Extrapolation and use the predicted gross biomass production in the calculation, may result in the total contribution being closer to 50%. However, this will depend on the percentage of calcareous epiphytes on the seagrass leaves. If this is the case, then the seagrass meadows in that region could be significant in producing sediments on Success Bank. However, if the inhibition of epiphytic accumulation on seagrass leaves were the primary effect of leaf movement, rather than abrasional losses, then again this underestimation would not likely be as significant.

4.4. FUTURE STUDIES

The results of this study have shown that it is difficult to determine with any certainty, whether leaf movement of seagrass leaves is fundamentally causing the abrasion and loss of recruited epiphytes, or if the movement of seagrass leaves is essentially inhibiting the establishment of epiphytes onto the leaves.

An example of the sorts of further studies, which would be appropriate in investigation into these processes, could involve an *in situ* experiment again involving artificial seagrass leaves. As this study has already established a difference in epiphytic biomass between tethered and untethered leaves, it is proposed that two forms of untethered leaves be designed to specifically examine whether the effects of leaf movement in the absence of contacts between leaves still produces an effect on epiphytic biomass. This could be achieved by using two forms of untethered artificial seagrass leaves, one using high leaf densities, where seagrass leaves have the potential to not only move freely, but also have the potential to come into contact with surrounding leaves. The alternate form would use freely moving leaves, at much lower densities where the leaves could not come into contact with neighbouring leaves. This could determine with a higher degree of certainty, which process of leaf movement is more influential in determining the differences in epiphytic standing crop on seagrass leaves.

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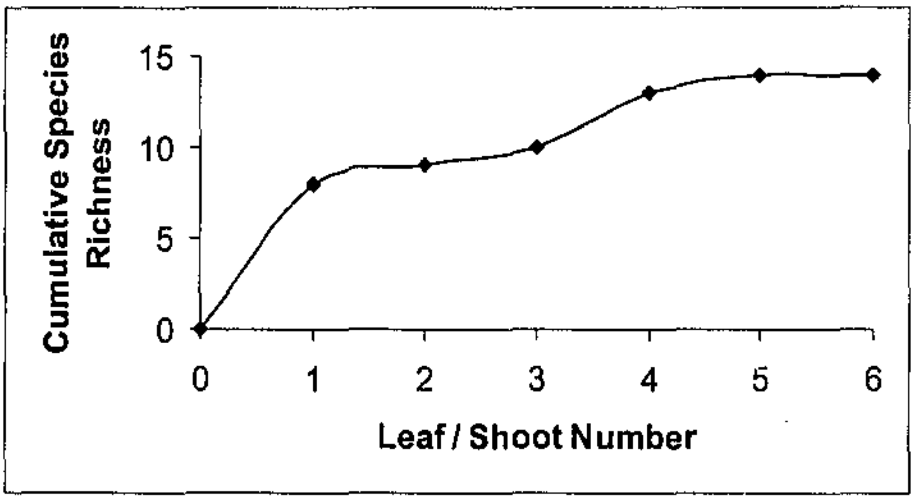
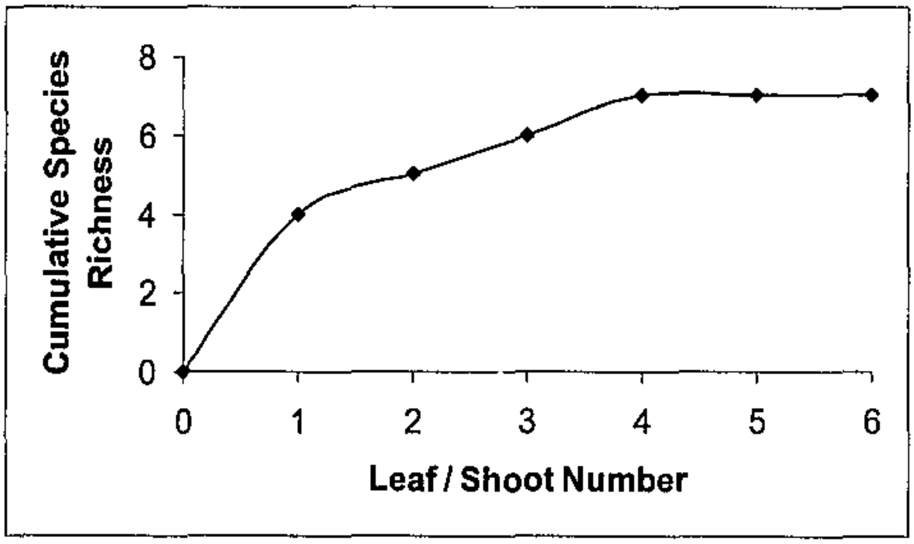
APPENDIX A

Pilot study determination of sample size

Appendix A. Pilot study determination of sample size. Species area curves and biomass curves for tethered and untethered artificial seagrass units (July, 1999).



A) Tethered artificial seagrass unit



(b) Untethered artificial seagrass unit

Figure A1: Species-area curves for epiphytes recorded on shoots of two types of artificial seagrass unit a) Tethered, b) Untethered.

To determine the optimum number of artificial leaves required to get an accurate representation of the species richness of the sites, epiphytes were identified on five artificial seagrass shoots for one sample of both artificial seagrass units (Figure A1). Species-area curves were then constructed which showed the cumulative number of epiphyte species recorded with each extra artificial leaf processed. Based on these curves the optimum number of leaves that required processing was determined which optimised sampling precision with sampling effort. This was very important due to the time limitations of the study and the very time consuming nature of epiphytic algae identification. The curves were very similar for Tethered and Untethered with the curves flattening out after 3 leaves had been processed (Figure A1). As only one and two new species was recorded on leaves four and five, a sample size of five leaves was selected.

APPENDIX B

Epiphytes recorded on artificial seagrass units

Appendix B. Species list of epiphytic algae recorded on tethered and untethered artificial seagrass units over two time intervals, four weeks and eight weeks, (June-July 2000, Marmion Marine Park, Western Australia).

Artificial Seagrass Unit and Time Interval		Species
Tethered Four Weeks	30	Chlorophyta sp 1
	38	*Dictoya* sp 2
	44	*Hirsutithallia* sp 1
	45	*Ceramium filiculum*
	50	*Heterosiphonia* sp1
	55	*Elachista* sp 2
	60	Rhodophyta sp 1
	67	*Elachista* sp 1
	69	*Antithamnion* sp 4
	17	*Antithamnion* sp 1
	3	*Giffordia* sp 1
	36	*Bryopsis* sp 1
	32	*Ceramium faccidium*
	29	*Ceramium isogonum*
	18	*Ceramium puberbulum*
	28	*Champia zostericola*
	48	*Cladophora* sp 1
	2	Phaeophyta sp 2
	61	*Colpomenia peregrina*
	23	*Dasya* sp 1
	1	*Encrusting coralline*
	71	*Enteromorpha* sp 1
	51	*Heterosiphonia* sp 2
	24	*Laurencia* sp 2
	49	*Polysiphonia forfex*
	52	*Polycerea zostericola*
	68	*Polysiphonia* sp 1
	65	Rhodophyta sp 2
	25	*Semnocarpa minuta*
	62	*Dictoya* sp 1
	53	Chlorophyta sp 2
	70	*Ulva* sp 1
Untethered Four Weeks	1	*Encrusting coralline*
	2	Phaeophyta sp 2
	3	*Giffordia* sp 1
	71	*Enteromorpha* sp 1
	52	*Polycerea zostericola*

Tethered Eight Weeks	16	Rhodophyta sp 3
	20	Phaeophyta sp 3
	30	Chlorophyta sp 1
	35	*Glossophora* sp 1
	37	*Antithamnion* sp 2
	44	*Hirsutithallia* sp 1
	45	*Ceramium filiculum*
	17	*Antithamnion* sp 1
	34	*Antithamnion* sp 3
	39	*Bromneatella* sp 1
	41	*Caulerpa distichophylla*
	32	*Ceramium faccidium*
	29	*Ceramium isogonum*
	18	*Ceramium puberbulum*
	28	*Champia zostericola*
	48	*Cladophora* sp 1
	23	*Dasya* sp 1
	27	*Griffithsia australe*
	42	*Hypnea* sp 1
	46	*Hypnea* sp 2
	21	*Laurencia* sp 1
	47	*Mychodea* sp 1
	49	*Polysiphonia forfex*
	25	*Semnocarpa minuta*
	1	*Encrusting coralline*
	2	Phaeophyta sp 2
Untethered Eight Weeks	10	*Cladophora* sp 3
	11	*Cladophora* sp 2
	12	Phaeophyta sp 4
	14	*Dasya* sp 2
	19	*Ectocarpus* sp 2
	4	Rhodophyta sp 4
	5	*Giffordia* sp 2
	6	Rhodophyta sp 5
	8	Phaeophyta sp 5
	9	*Giffordia* sp 3
	17	*Antithamnion* sp 1
	3	*Giffordia* sp 1
	7	*Ectocarpus* sp 1
	13	Phaeophyta sp 6
	18	*Ceramium puberbulum*
	1	*Encrusting coralline*
	2	Phaeophyta sp 2
	28	*Champia zostericola*