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Reefs as contributors to the diversity of epiphytic algal communities in seagrass meadows

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REEFS AS CONTRIBUTORS TO THE DIVERSITY OF EPIPHYTIC ALGAL COMMUNITIES IN SEAGRASS MEADOWS

BY

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the requirements for the award of
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Dr Gary Kendrick, University of Western Australia.

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ABSTRACT

It has recently become dogma that reef systems are a source of diversity to algal epiphyte communities in adjacent seagrass meadows. While this theory had not been tested, it was often cited as the reason for unexpected results in algal studies and marine pollution monitoring. This study examined whether reefs do in fact contribute to the diversity of seagrass epiphytes by testing the effect of distance from reef on seagrass epiphyte communities. The study was conducted in the vicinity of Carnac and Garden Islands and Parmelia Bank, off the coast of Fremantle, Western Australia. Three habitat types were selected as treatments, on reef (0m), seagrass meadow near reef (<20m from reef), and seagrass meadow distant from reef (>3000m from reef), with the experiments replicated at four separate locations.

The study consisted of two experimental components and descriptive sampling of epiphyte communities on natural seagrasses. Each component investigated a different stage in the recruitment process of epiphytes. Propagule availability was examined by collection and culture of propagules to determine their origin and whether reefs contributed algal propagules to seagrass meadows. Community structure was examined by studying the recruitment of epiphytes to artificial seagrass and by sampling communities on natural *Posidonia sinuosa*, to investigate whether distance to reefs influences the post-recruitment processes which determine community composition. Artificial seagrass was used in addition to descriptive sampling to remove the confounding effect of host variability.

The results of this study showed that epiphyte assemblages in seagrasses adjacent to reefs were different to those different from reefs, and that reefs were a source of propagules to seagrass meadows. Propagule availability varied with distance to reef. Epiphyte communities growing on artificial seagrass and natural seagrass also differed. The same trend was evident for propagule availbility, recruitment of epiphytes to artificial seagrass and epiphytes on natural seagrass, where

ordination patterns showed a significant separation of sites adjacent to reef from those distant to reef. The differences intensified post-recruitment, as shown by the tighter clustering patterns and increased spatial distance between habitats evident in ordinations. Biomass was significantly higher for sties adjacent to reef, which confirmed earlier findings that proximity to reef is confounding monitoring programmes.

These differences suggest different pre-recruitment and post-recruitment influences for epiphyte communities near reefs and distant from reefs. Reefs can reasonably be expected to produce changes in environmental factors such as water motion, grazing and nutrients, which affect epiphyte growth. Additionally, reefs provide a source of algal propagules to seagrass meadows which can affect community structure.

DECLARATION

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

Signature.

Date 24 April 1998

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I would like to dedicate this thesis in memory of my father, Dirk Van Elven, who encouraged me to always do my best.

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CHAPTER 1: INTRODUCTION

It has recently become accepted dogma that reef systems are a source of diversity to algal epiphyte communities in adjacent seagrass meadows (Borowitzka & Lethbridge, 1989; West, 1990). While this theory has not been scientifically tested, it is often cited as the reason for unexpected results in algal studies and marine pollution monitoring (Hillman *et al.*, 1994, Kinhill, 1996a, 1996b & 1997). This study examined whether reefs contribute to the diversity of seagrass epiphytes by testing the effect of distance from reef on seagrass epiphyte communities.

1.1 BACKGROUND

There are approximately 1,800 species of marine macroalgae recorded for Australia (Huisman, *et al.*, 1998), with 700 species estimated for Western Australia (Walker, 1991). Macroalgae inhabit a variety of environments, including rocky intertidal and subtidal zones, tropical reefs, salt marshes and seagrasses (Lobban & Harrison, 1994). Those algae which grow on rocky substratum are known as epilithic, while species which occur on seagrasses and other algae are termed epiphytic.

Epiphytic algae are an important component of seagrass ecosystems. They contribute significantly to the productivity of seagrass meadows (Silberstein *et al.*, 1986), while coralline species of epiphyte provide an important source of calcium carbonate to sediments (Walker & Woelkerling, 1988). Many animals feed on algal epiphytes, including shrimps, amphipods, gastropods (Kitting *et al.*, 1984) and leatherjackets (Orth & Van Montrans, 1984). In nutrient enriched waters, overgrowth of epiphytes can cause the decline of seagrass meadows by reducing light penetration to the surface of seagrass leaves (Silberstein *et al.*, 1986).

1.2 DIVERSITY

Biodiversity is currently a matter of scientific and political concern, primarily because of the increase in extinction rates of species caused by human activities (Huston, 1997). Seagrass meadows are one of the many marine ecosystems under threat. In Australia, over 45,000 ha of seagrasses were lost by the early 1990's (Walker & McComb, 1992), while 80% of seagrass meadows in Cockburn Sound were lost by 1978 (Cambridge & McComb, 1984).

Seagrass meadows in Western Australia are the most diverse in the world (Kirkman & Walker, 1989) and contain valuable sources of marine biodiversity. Algal epiphytes, which use seagrasses as a substratum, are an important component of this biodiversity.

Despite the recognition that algal epiphytes are a significant component of biodiversity in seagrass habitats, little is known of the processes influencing epiphyte diversity (Borowitzka & Lethbridge, 1989; Kendrick & Burt, 1997). Understanding the nature of these relationships can aid environmental monitoring, rehabilitation and the selection of appropriate reserves (Fairweather, 1991).

1.3 EPIPHYTE DIVERSITY STUDIES

There has been little research into the processes affecting seagrass epiphyte diversity. However, a small number of descriptive studies of seagrass epiphyte communities have been conducted.

Heijs (1987) compared epiphyte communities of monospecific and mixed seagrass meadows in Papua New Guinea. She recorded 64, 55 and 55 species of epiphytes for *Thalassia hemprichii, Cymodocea serrulata* and *Syringodium isoetifolium* respectively in monospecific meadows and for mixed seagrass beds 45, 43 and 43 species respectively. Most species were not host specific, nor did they show a preference for meadow type. May *et al.*, (1978) examined epiphytic algal communities on *Zostera* spp *and Posidonia australis* in Botany Bay and Jervis

Bay, New South Wales over a two year period, and also found little evidence for host specificity. A total of 57 taxa were recorded, with all except one species, *Gracilaria edulis*, occurring on both seagrass types.

A study of *Amphibolis antarctica* epiphytes in Shark Bay recorded 66 species over three sampling occasions (Kendrick *et al.*, 1988). There was a general dominance in the number of temperate species over those with tropical affinities. Fifty percent of all red algal epiphytes were endemic to temperate Australia, while a higher proportion of brown and green algae were of cosmopolitan distribution. Borowitzka *et al.* (1990) also studied *Amphibolis antarctica* epiphytes, collecting samples from Dongara, Penguin Island and Albany, with over 150 species of algal epiphyte recorded. Total species richness was not reported for each location, however species richness (per $0.25m^2$ quadrat) at Dongara ranged from 15-21 during September and at Penguin Island ranged from 19-26 in July and 36-47 in November.

The only study using the same host seagrass species as this study, *Posidonia sinuosa*, is that of Kendrick and Burt (1997). They compared the differences in epiphyte assemblages with different exposure levels at Success Bank and Owen Anchorage near Fremantle. 51 taxa were identified from both locations over a twelve month period. Species richness varied between season and location, with different peaks in diversity between the two locations. Owen Anchorage, the lower energy site, was typified by filamentous reds from the Rhodomelaceae (*Polysiphonia* spp., *Herposiphonia pectinella*, *Laurencia* sp.), filamentous browns (*Hinksia* sp., *Feldmania* sp., *Sphacelaria* spp.) and green algae. Success Bank, the higher energy site, was represented more by filamentous reds from the Ceramiales (*Antithamnion* spp., *Callithamnion* sp., *Centroceras* sp., *Ceramium* spp.) and articulated and encrusting coralline algae.

The above examples have shown that species richness of algal epiphytes can vary considerably between studies. These differences are a function of different sampling intensities between studies, different sampling seasons, variability of the

host species in terms of morphology and leaf age and different biogeographic locations.

1.4 FACTORS DETERMINING SEAGRASS EPIPHYTE COMMUNITIES

The epiphyte assemblage present in a seagrass meadow at any given time is the result of several simultaneous or sequential processes; propagule release, dispersal, settlement, germination and growth to adult stage (Santelices. 1990). These different stages in life cycle are each important in the subsequent expression of community diversity. Additionally, physical and biological factors act on each of these life cycle stages to determine ultimate community composition (Lobban & Harrison, 1994).

Physical factors include light, temperature, water motion, salinity, and nutrient availability and, as has been hypothesised, proximity to reefs which can affect local hydrodynamics. Biological factors include host interactions, competition, grazing and propagule availability, and many of these factors may also potentially be influenced by proximity to reef. These biological and physical factors can influence epiphytes pre-recruitment (ie before propagule settlement), or post-recruitment (ie after settlement). Figure 1.1 illustrates some of the factors influencing epiphyte assemblages.

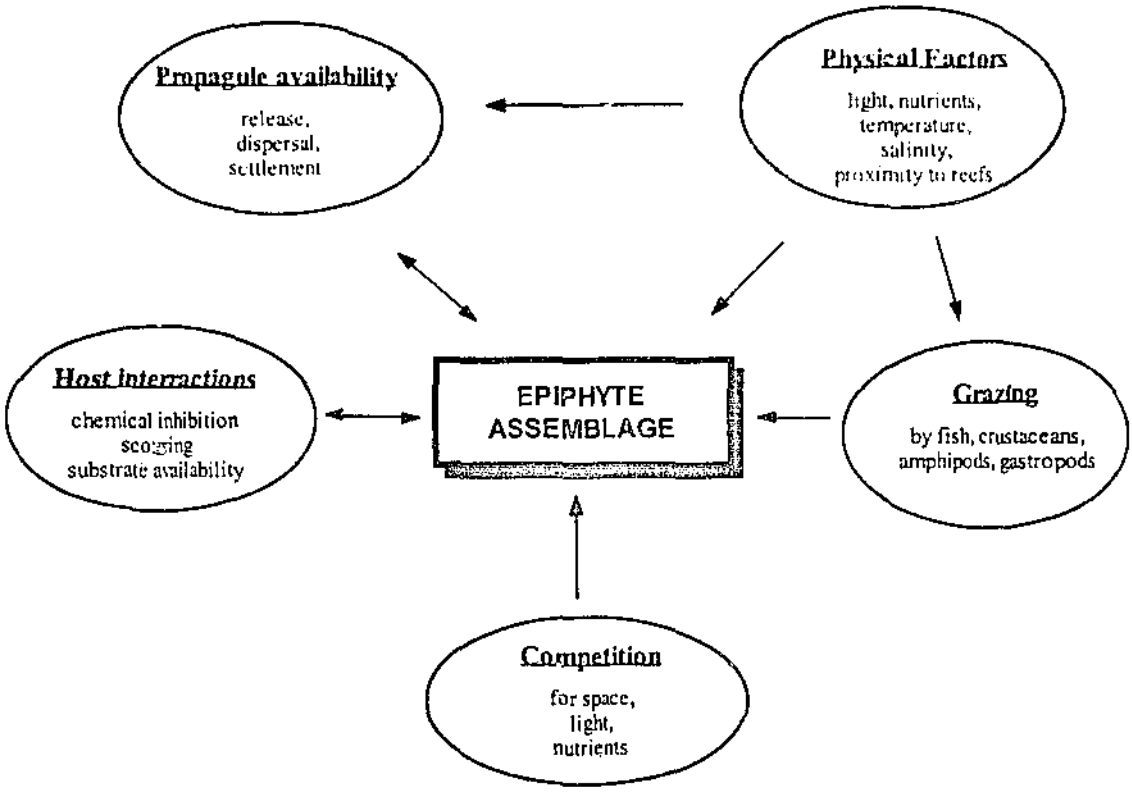


Figure 1.1 Conceptual diagram illustrating some of the processes influencing epiphyte community structure. Arrows indicate direction of influence.

1.5 LOCAL VERSUS REGIONAL PROCESSES

Epiphyte recruitment may be a local or regional process. The source of propagules may be from the seagrass meadow itself (local), hence the epiphyte community is self perpetuating, or propagules arrive from outside the seagrass meadow (regional), from other algal habitats such as adjacent reef systems.

It has become accepted dogma that reef systems contribute to the biodiversity of epiphyte communities in seagrasses, and while this concept has yet to be supported by scientific analysis it has often been cited in scientific literature (Borowitzka & Lethbridge 1989; West 1990). Hillman *et al.* (1994) visually assessed epiphyte assemblages in Perth coastal waters and found no recognisable differences in assemblages due to depth, exposure or distance offshore and suggested that proximity to sources of algal propagules such as reefs may instead determine diversity.

Studies have shown that algal species have limited ranges of propagule dispersal (Hoffman, 1987) and that even if dispersal occurs the chances of a propagule successfully germinating and persisting to adult stage are extremely small. Kendrick & Walker (1995) found that less than 0.0001% of *Sargassum* spp recruits survived for 12 months and their dispersal range was only 1-2m. If this is so then local recruitment processes are likely to be more important in maintaining epiphyte diversity in seagrasses than regional processes. This would suggest that the proximity of reefs may be of minimal significance in determining the epiphyte composition of adjacent seagrass meadows, and would appear to contradict the accepted dogma. This study aims to contribute to our understanding of the sources of algal diversity to seagrass meadows and to test the unproven dogma that reefs provide a source of algal diversity to adjacent seagrass meadows.

1.6 SIGNIFICANCE

An understanding of the processes affecting epiphyte diversity is relevant to environmental management for at least three reasons:

Epiphytes have been used extensively as a tool to measure the impact of point source water pollution. In Western Australia various studies on the effects of coastal sewage outfalls use artificial seagrass or periphyton collectors to measure accumulated periphyton biomass as a biological indicator of nutrient enrichment effects (Hillman *et al.*, 1994; Kinhill, 1997). These studies have encountered problems with higher biomass readings at some sites which are not correlated with nutrient enrichment, thereby reducing the reliability of monitoring results. It is believed that the confounding factor is proximity of monitoring sites to reef, (Hillman *et al.*, 1994, Kinhill, 1996a, 1996b & 1997) though insufficient evidence is available from these studies to determine if this is the cause.

In Western Australia, the Department of Conservation and Land Management is considering considerable expansion of the current system of marine conservation reserves with 13 new reserves proposed (CALM, 1994). If reefs contribute to seagrass epiphyte diversity and the purpose of the reservation is preservation of marine biodiversity, then both reef and seagrass near reef will need to be included within reserve boundaries, in addition to seagrass systems isolated from reef. Current planning for the Jurien Bay Marine Park is relying heavily on locating sources of diversity to delineate exclusion zone boundaries (Burt & Anderton, 1997).

An industry using the nearshore marine environment as a mining resource has proposed mitigation of impacts on seagrasses by planting replacement meadows (Cockburn Cement Ltd, 1994). and has suggested that in restoration it is important to place reef next to meadows to provide a source of propagules. Again, this underlying assumption that reefs will provide a source of propagules to seagrass meadows has never been tested or proven.

1.7 AIMS

This study will contribute to an understanding of the processes affecting algal epiphyte diversity which will have direct relevance to the management of these assemblages in marine ecosystems. The results of this research will help to clarify whether reefs do in fact contribute to seagrass epiphyte diversity and will test experimentally some of the processes influencing epiphyte diversity.

Specific aims were to:

- Determine whether reef systems contribute to algal diversity in adjacent seagrass meadows; and
- Determine whether the availability and composition of epiphyte propagules varies with distance from reef.

To do this, three distinct experiments/descriptive sampling exercises were undertaken. In the first, water samples were collected from sites on, near and distant from reef to see whether the propagules present at these sites differed. This examined pre-recruitment processes acting on epiphyte communities, and was used to determine the origin of propagules (i.e. local or regional sources), and whether reefs provided a source of propagules to seagrass meadows.

Secondly, artificial seagrasses were established on reef, near reef and distant from reef to assess the epiphyte assemblages that actually established, thereby providing an insight into whether distance to reefs influences the early post-recruitment processes which determine community composition. Finally, real seagrasses near and far from reef were sampled to determine whether natural, mature epiphyte communities varied with distance to reef, giving some indication of the recruitment processes acting over the longer term. This study could have been undertaken simply as a descriptive exercise (ie the third task listed above). However, this may have given misleading results because of the uncertainty of natural seagrass leaf age for comparisons, which has been shown to be a primary determinant of epiphyte community structure (Borowitzka & Lethbridge, 1989).

STRUCTURE OF THESIS

This chapter (Chapter 1) introduced the study and its three components, provided a general background on algal epiphytes and the factors influencing their diversity and explained the relevance of this study to environmental management. Chapter 2 will cover the experimental design, the methods used for each component and the justification for those methods where relevant. Chapter 3 presents the results of the propagule availability experiment, the artificial seagrass recruitment experiment and the sampling of natural seagrass epiphytes in turn. Then in the final chapter (Chapter 4) each of the components will be discussed, the potential influence of reefs examined in the light of these findings and the management implications addressed.

CHAPTER 2: METHODS & MATERIALS

2.1 STUDY AREA

The study was conducted off the coast of Fremantle, Western Australia using Parmelia Bank and the island chain to the west of the Bank (Figure 2.1).

Parmelia Bank is an unconsolidated carbonate sand bank which to the south of Owen Anchorage approximately 6km south of Fremantle, extending from the coast offshore to Carnac Island. The bank supports mixed seagrass meadows which are considered to be one of the best examples of this community type on the west coast (CALM, 1994). Common seagrass species occurring there include *Posidonia australis, P. coriacea, P. sinuosa, Amphibolis griffithii, Heterozostera tasmanica* and *Halophila ovalis (*Lord & Assoc., 1995).

Carnac and Garden Islands are part of a limestone reef/island chain running roughly parallel to the metropolitan coastline and forming part of the westerly boundary of Parmelia Bank. Carnac Island is a Class "A" Nature Reserve, while Garden Island is Commonwealth land, used by the Department of Defence as a naval base. The surrounding waters are used extensively for recreational boating and commercial and recreational fishing (CALM, 1994). Erosion from this geological unit is believed to supply Parmelia Bank with much of its sediment deposition (Lord & Assoc., 1995). Both islands are surrounded by extensive sub-tidal limestone reef systems which support macroalgal communities. Seagrasses occur in sandy patches within the reef systems (CALM, 1994).

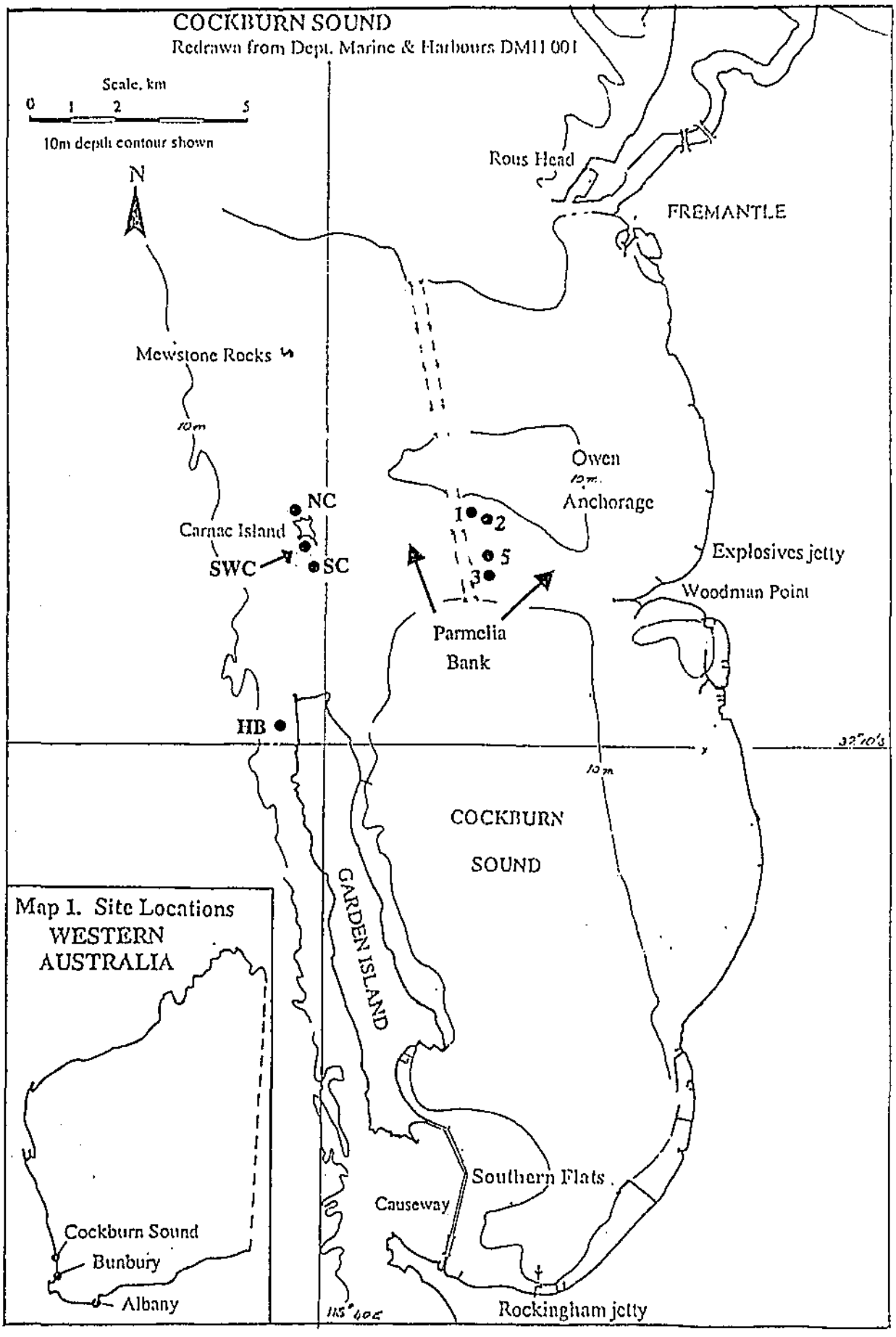


Figure 2.1 Location of study sites shown by black dots. HB=Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, 1,2,3 & 5=Parmelia Bank (Source Clapin, 1996 page 11).

2.2 EXPERIMENTAL DESIGN

The study involved three components, an *in-situ* study of epiphyte recruitment on artificial seagrass, laboratory culture of propagules collected *in-situ* and sampling of natural epiphyte communities.

For the *in-situ* study of epiphyte recruitment onto artificial seagrass, artificial seagrass units were placed in three habitats defined by their proximity to reef; 'On Reef', 'Near Reef' (seagrass meadow within 20m of reef) and 'Away from Reef' (seagrass meadow at least 3km from reef). The experiment was replicated four times giving a total of twelve sites, with four units deployed at each site (n=48). A two factorial nested experimental design was used, the two factors being proximity to reef, and site nested within proximity to reef (Table 2.1). All epiphytic recruits onto the artificial seagrass were recorded and their abundance measured, to test whether proximity to reef influenced the diversity and biomass of epiphyte assemblages.

The propagule culture experiment used the same experimental design however due to time constraints only three samples were collected from each site (n=36). Epiphytes grown in culture were recorded and quantified to determine whether propagule availability and composition varied with distance to reef.

Sampling of natural seagrass was conducted at sites at the time of artificial seagrass deployment. Again, epiphyte composition was determined to test whether patterns of epiphytic recruitment recorded onto the artificial seagrasses were similar to the established epiphyte communities in natural seagrass habitats, and also to provide information on potential sources of propagules grown in culture.

Table 2.1. 2 factor experimental design (distance from reef = main factor, site = nested factor)

Treatment (x3)	On Reef				SG Near Reef				SG Away from Reef			
Site (x4)	1	2	3	4	1	2	3	4	1	2	3	4
Sample No. (x4) for ASG experiment	4	4	4	4	4	4	4	4	4	4	4	4
Sample No (x3) for PC experiment	3	3	3	3	3	3	3	3	3	3	3	3

SG = natural seagrass, ASG = Artificial Seagrass, PC = Propagule Culture (n = 48 for ASG, n=36 for PC)

2.3 SITE SELECTION

Posidonia sinuosa was selected as the target species due to its relatively common occurrence in the region and its presence both near reef and distant from reef. Additionally, whilst epiphyte communities of *Amphibolis* and other *Posidonia* species have received some attention, there has been relatively little study of *Posidonia sinuosa* epiphytes.

2.3.1 On and Near reef sites

Four sites around Carnac Island (North Carnac, South Carnac and South West Carnac) and Garden Island (Herring Bay) were chosen for the on and near reef treatments (Table 2.2). Considerations in final site selection included: presence of high relief reef (>0.5m above ocean floor); presence of patches of *Posidonia sinuosa* meadow within 20m of reef; and shallow water depth (<5m). While attempts were made to select seagrass patches of the same size, this was not always possible due to limitations in availability of the target species (*P. sinuosa*) adjacent to reef (Plate 2.1).

Herring Bay proved to be an anomaly compared to other On Reef and Near Reef sites as results later showed. The bay was surrounded by an extensive reef which provided a sheltering effect from wind driven waves and current swells. In addition, a narrow channel connected the bay to the open ocean hence water movement was restricted.

2.3.2 Away from reef sites

Four sites within Parmelia Bank were chosen for the Away from Reef treatment (Table 2.2). Criteria for site selection included: relatively shallow depth (approx. 4m); presence of patches of *P. sinuosa* of similar density and size; a minimum of 100m between sites; and at least 3km from the nearest known reef (Plate 2.2).

Table 2.2. Australian Map Grid Coordinates and depth (m) of sites.

Site	Coordinates		Depth (m)
N Carnac Island	0373638	6445437	3.5m
SW Carnac Island	0373665	6445007	2m
S Carnac Island	0373943	6444475	3 – 5m
Herring Bay Garden Island	0373467	6440930	1m
Parmelia Bank 1	0377700	6445601	4m
Parmelia Bank 2	0377592	6445604	4m
Parmelia Bank 3	0377615	6445483	4m
Parmelia Bank 5	0377879	6445671	4m

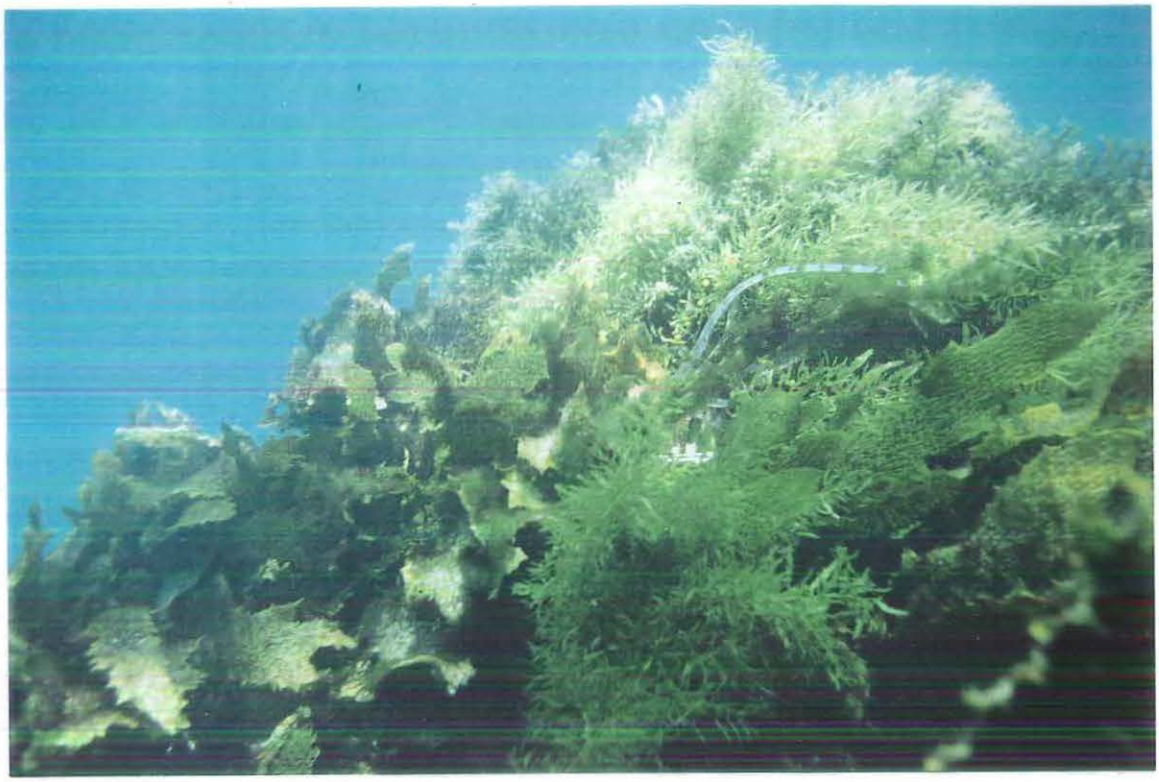


Plate 2.1 Typical On Reef habitat with brown algae *Ecklonia* sp and *Sargassum* sp growing attached to the rocky substratum.

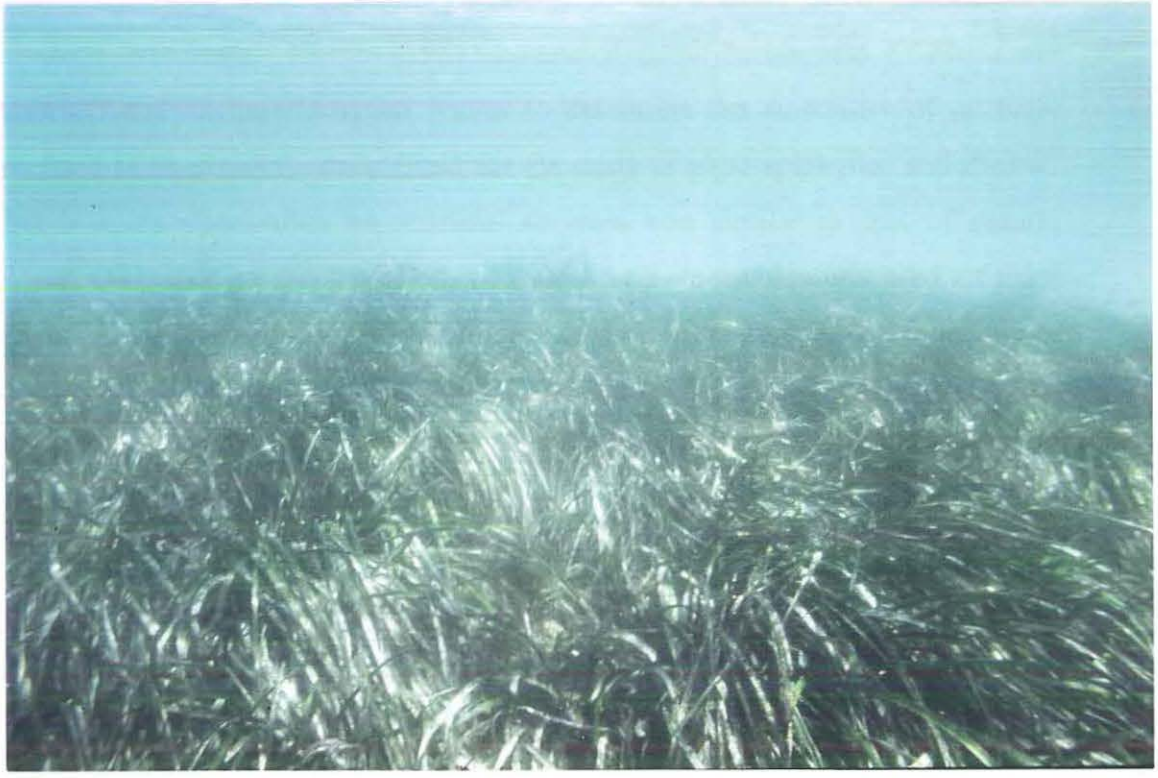


Plate 2.2 Typical Away from Reef habitat with *Posidonia sinuosa* growing in soft sediments.

2.4 RECRUITMENT OF EPIPHYTES ONTO ARTIFICIAL SEAGRASS

The use of artificial substratum is becoming increasingly more common as a research technique in marine science, because it removes the effect of any potential interaction between host and epiphyte, and provides identical habitat and known area for comparison purposes.

Artificial seagrass was chosen over natural seagrass to study epiphyte recruitment, as it was not possible to accurately select *Posidonia sinuosa* of the same leaf age to make accurate comparisons as to the influence of the main effect, namely proximity to reef. There is strong evidence to suggest that it is not the nature of the substratum, but rather the period of availability of that substratum that determines epiphyte communities (Kendrick & Hawkes, 1988; Kendrick & Burt, 1997; Borowitzka *et al.*, 1990).

Artificial seagrasses have been used for a number of epiphyte studies, because of their ability to reduce substrate variability to allow more direct comparisons between treatments. Horner (1987) compared epiphyte biomass of *Posidonia australis* and artificial seagrass leaves to determine the suitability of artificial seagrass as an experimental method for the study of algal epiphytes, and showed that biomass distribution on artificial seagrass was similar to that of natural *Posidonia* leaves. A number of other researchers have successfully used artificial substratum to quantify the effects of nutrient enrichment on epiphyte productivity (Westera and Paling, 1994; Bunbury Dive and Outdoor, 1996; Hillman *et al.*, 1994; Kinhill, 1997).

Lethbridge *et al.* (1988) found at least 36 species of algae growing on *Amphibolis*-like artificial seagrass deployed at Penguin Island, and noted similar species growing on natural *Amphibolis* over the same period. Diversity was lower on artificial seagrasses than natural communities, however the artificial seagrass was only left *in situ* for up to 78 days while natural *Amphibolis* stems may persist for up to two years.

2.4.1 Construction of Artificial Seagrass Units

Artificial seagrass resembling *Posidonia sinuosa* was constructed using a similar method to Westera and Paling (1994). Artificial seagrass shoots made of clear flexible polyethylene 600mm x 10mm x 300μm thick were threaded through and stapled to plastic coated wire grids 150mm x 150mm - aperture 25mm x 25mm. Each shoot consisted of 2 leaves, one 400mm and one 200mm in length. Sixteen shoots were attached to each grid. A plastic information tag was attached to each grid to reduce the potential of inadvertent removal by other divers and swimmers (Plate 2.3).

2.4.2 Deployment/Retrieval of Artificial Seagrass

Grids were deployed over a two week period in October-November 1997 (Table 2.3). Four artificial seagrass units were randomly placed within each target area by SCUBA divers, using distances and compass bearings derived from random number tables. At the location of each grid, underlying plant material was collected and placed in plastic bags for later analysis. Units were then fixed to the substratum using 30cm long tent pegs and 5kg weights.

Grids were checked after 5 weeks to ensure they could be located, were still intact, and that plastic shoots were not weighted down by epiphyte growth.

Grids were retrieved after 8-10 weeks (Plates 2.5 and 2.6). After being brought on board, grids were carefully placed in a bin of seawater to prevent desiccation, weights were removed and each grid placed in a labelled plastic bag containing seawater. Samples were kept on ice for transport to the laboratory where they were processed within 24 hours.

Plate 2.3 Example of an artificial seagrass grid. Grids were made of plastic coated wire mesh with polyethylene strips attached to simulate *Posidonia* shoots.

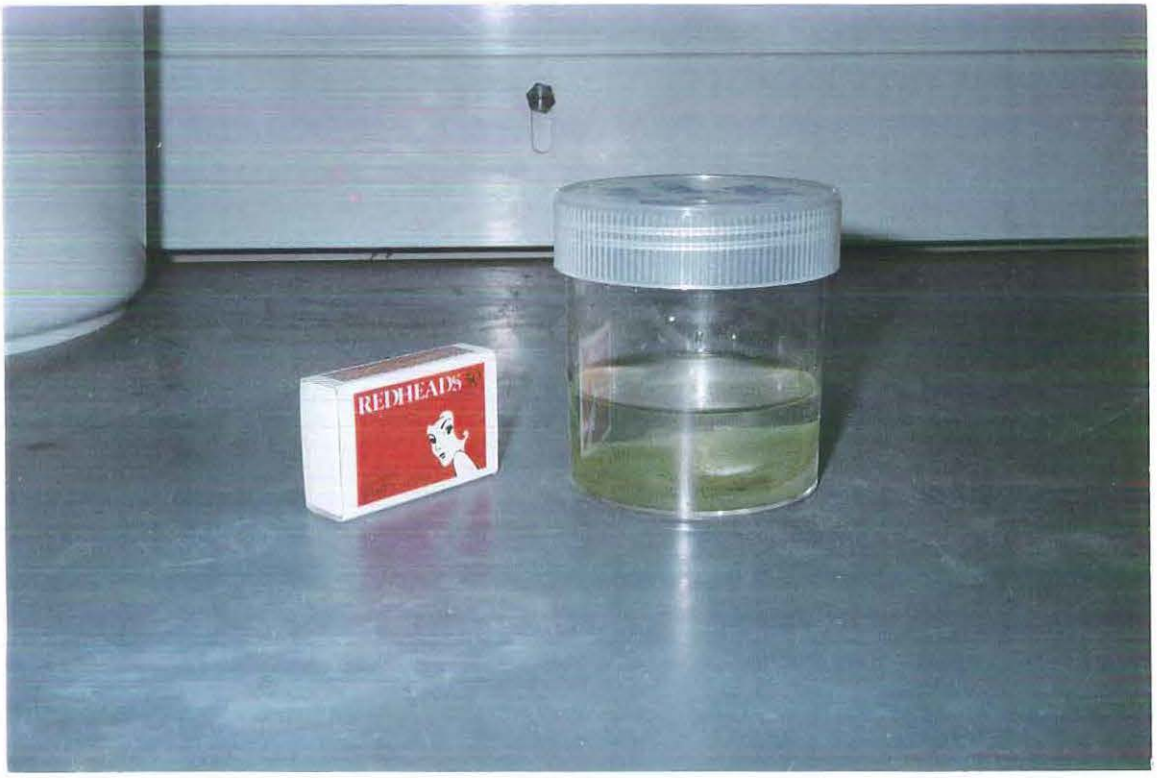


Plate 2.4 Propagule culture jar with polyethylene disk affixed to the bottom with Pterostat. The green fuzz visible on the surface of the plastic disk is algal growth.

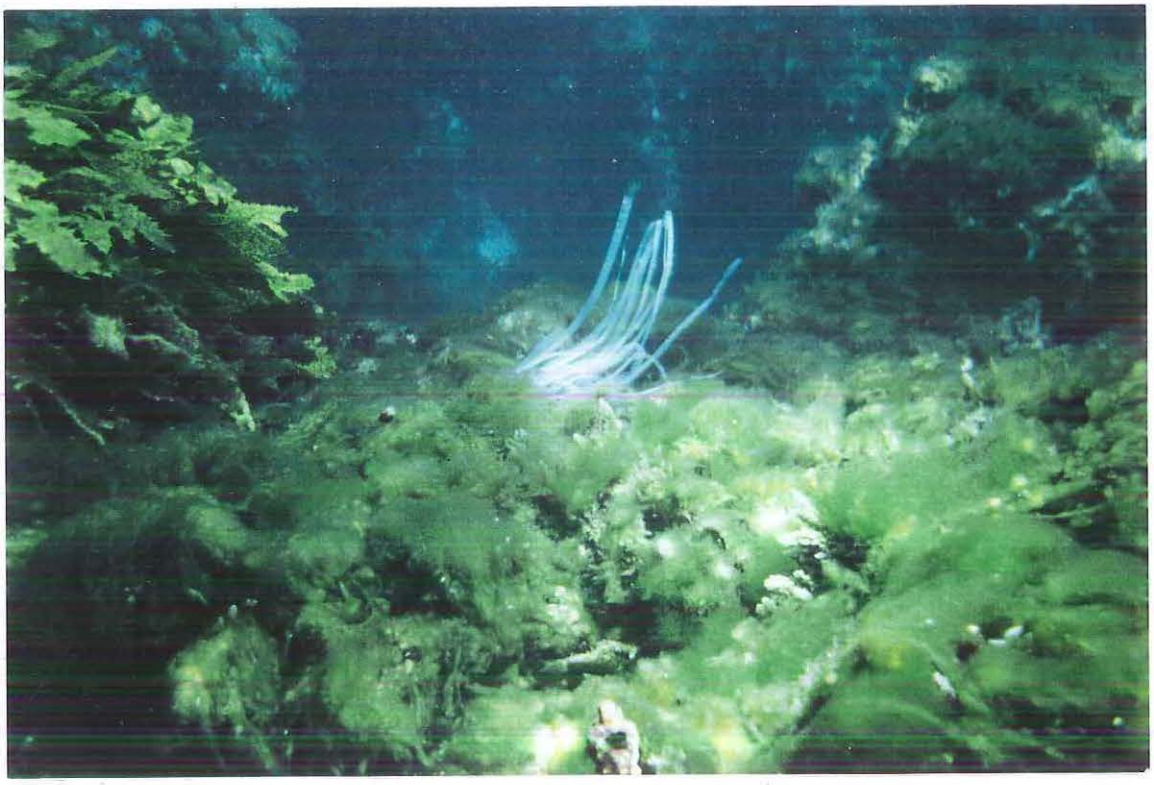


Plate 2.5 Artificial seagrass unit deployed at On Reef habitat.

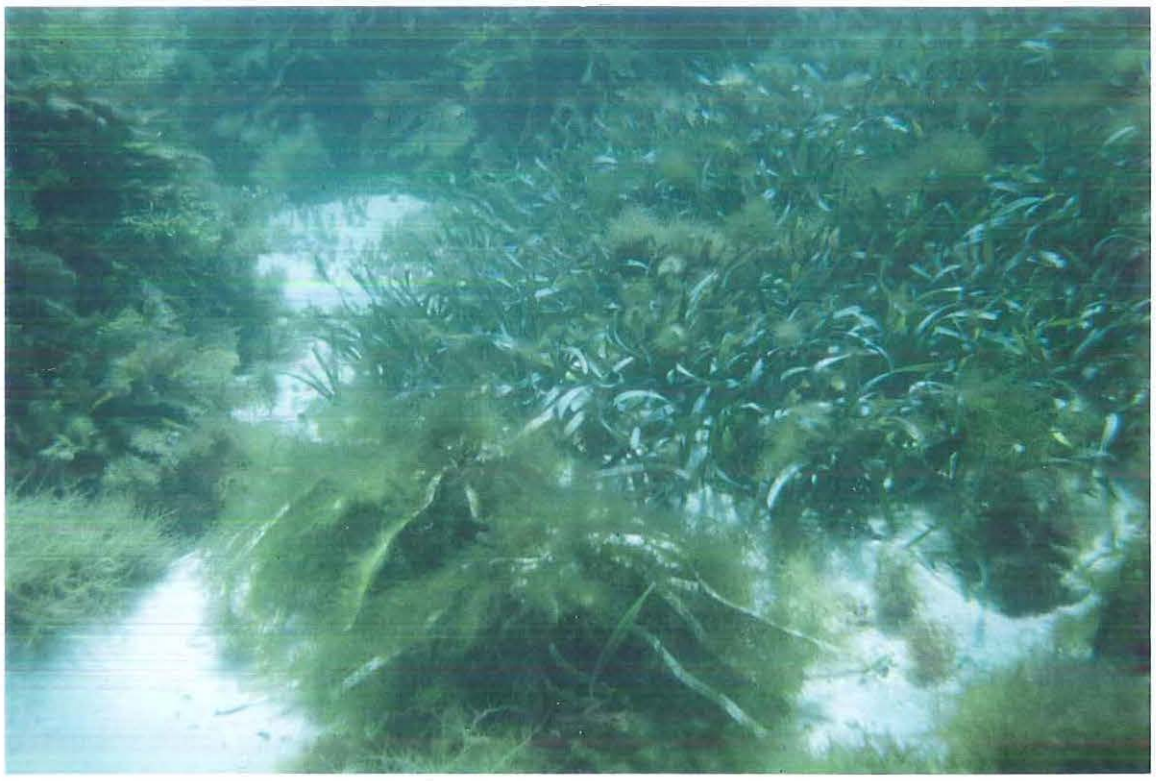


Plate 2.6 Two artificial seagrass grids (bottom centre) ready for transfer to the surface after retrieval from seagrass Near Reef. Note the high amount of epiphyte growth.

Table 2.3 Date of deployment and retrieval of artificial seagrass units for each site and number of days grids were left *in situ*.

Site(s)	Deployed	Retrieved	No. Days *in situ*
North Carnac Reef/Near Reef	22/10/97	18/12/97	57
South Carnac Reef/Near Reef	22/10/97	18/12/97	57
South West Carnac Reef/Near Reef	22/10/97	18/12/97	57
Herring Bay Reef/Near Reef	05/11/97	30/12/97	54
Parmelia Bank 1 Away from Reef	23/10/97	18/12/97	56
Parmelia Bank 2 Away from Reef	23/10/97	30/12/97	68
Parmelia Bank 3 Away from Reef	23/10/97	30/12/97	68
Parmelia Bank 4 Away from Reef	05/11/97	30/12/97	54

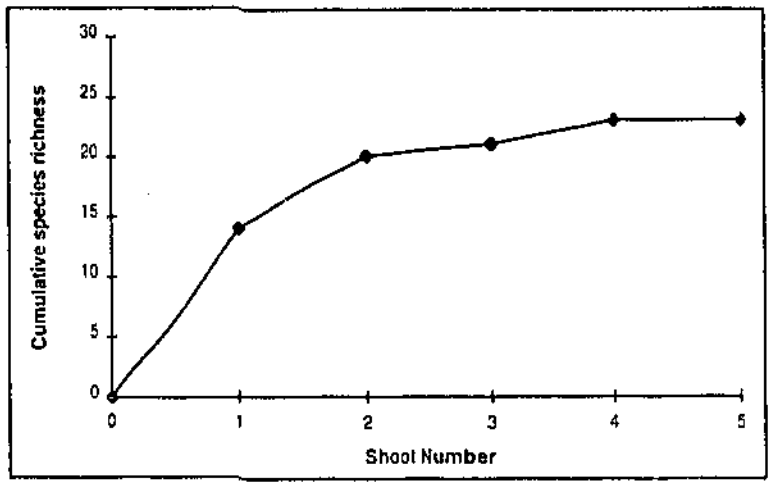
2.4.3 Sample Processing

Grids were processed in trays of seawater to prevent desiccation. Plastic shoots were removed by slicing underneath each wire grid using a one-sided razor blade. Five shoots were randomly selected for analysis of the epiphytic species present and their abundance. These shoots were preserved in 5% seawater-formalin solution. The remaining shoots ($\leq$ 13) were frozen for biomass analysis.

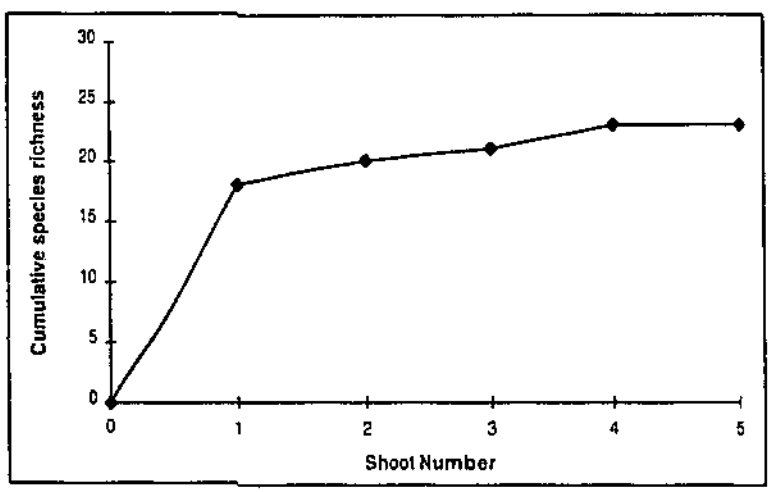
2.4.4 Determining Optimum Sample Size

To determine the optimum number of shoots required for adequate representation of species richness of a sample, epiphytes were identified on 5 artificial seagrass shoots for one sample of each treatment type. Species-area curves were constructed which showed the cumulative number of species recorded with each extra shoot processed. Based on these curves the optimum number of shoots requiring processing was determined, which maximised sampling precision with

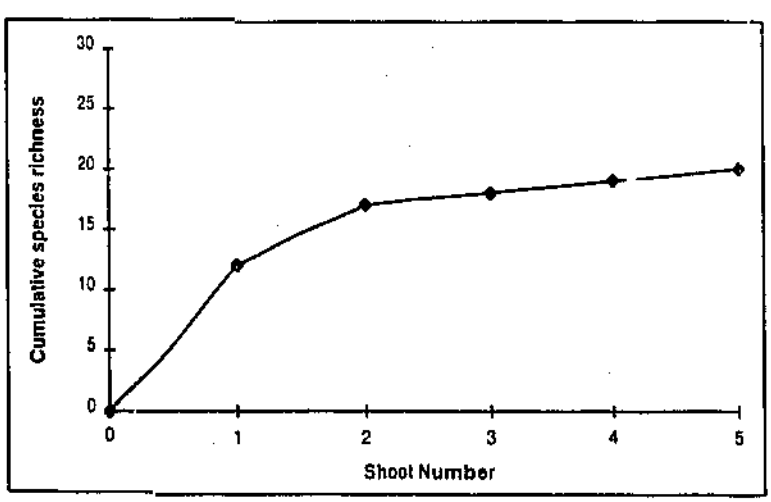
sampling effort. This was particularly important given the time limitations of the study and the time consuming nature of epiphyte identification. Curves were similar for On Reef, Near Reef and Away from Reef, with the curves flattening out after three shoots (Figure 2.2). As only one or two new species were recorded on shoots four and five, a sample size of three shoots was selected.



a) On Reef habitat



b) Near Reef habitat



c) Away from Reef habitat

Figure 2.2. Species-area curves for epiphytes recorded on shoots of artificial seagrass deployed within a) On Reef habitat, b) Near Reef habitat and c) Away from Reef habitat.

2.4.5 Epiphyte Identification

Epiphytes were identified with the aid of a dissecting microscope using the identification keys of Womersley (1984, 1987, 1994, 1996) and Huisman and Walker (1990). Species occurring on each shoot were recorded and percentage cover of each species estimated. Cover values were recorded on a scale from 1 – 6 corresponding with percentage cover (Kendrick *et al.*, 1988) (Table 2.4).

Measurement of epiphyte abundance is problematic due to their small size and the difficulty in determining discrete units. Percentage cover was considered the most appropriate method of measuring epiphyte abundance for this study. Alternatives included measurement of biomass and counts of individuals (Magurran, 1988). However, neither of these were feasible given time constraints. Biomass measurement requires physical separation into species, many of which have such small masses they would fail to register a weight measurement with the equipment available. The growth habit of some epiphytes (e.g., encrusting coralline algae, tufting species) also makes it difficult to determine discrete units. Counts of individuals would therefore be time consuming and not necessarily reflect true abundance.

Permanent specimens of each species were made by preserving, staining and mounting material on microscope slides, following the method of Womersley (1987). The collection is housed within the Environmental Management Department, Edith Cowan University, Joondalup.

Table 2.4 Abundance Categories and equivalent percentage cover used to record epiphyte abundance (percentage range for each category shown in brackets).

Abundance Category	Mid value	Range
1	<1%	(<0-1%)
2	5%	(2-9%)
3	20%	(10-29%)
4	40%	(30-54%)
5	70%	(55-79%)
6	90%	(80-100%)

2.4.6 Epiphyte Biomass

Five plastic shoots of each sample were randomly selected and their combined dry weight, ash free dry weight and calcium carbonate content determined. Approximately 1 cm was cut off the bottom of each shoot to remove staples. Epiphytes were then scraped from shoots using a one sided razorblade and placed in pre-weighed crucibles which had been prefired to 950°C.

Samples were oven dried at 80°C for 48 hours and reweighed to determine dry weight. Ash free dry weight was determined by combustion at 550°C for 1 hour. Calcium Carbonate content was measured combustion of the remaining material at 950°C for 1 hour. Between each step crucibles were cooled in a desiccator for 24 hours. Samples were weighed to 0.1mg using a 4 place balance.

Standards of glycerin (ash free dry weight) and calcium carbonate ($CaCO_3$ content) were used to correct for uneven or incomplete combustion. One gram standards in pre-weighed crucibles were placed at the front, rear and middle of the furnace for each firing. Standards were reweighed after cooling in the desiccator and where standards were not completely burnt off (glycerin) or converted to calcium oxide (CaCO), corrections were made to weights of samples situated in the corresponding third of the furnace.

2.5 PROPAGULE CULTURE

2.5.1 Collection of algal propagules

Water samples containing algal propagules were collected over two days on the 17th and 18th November 1997. A boat mounted bilge pump attached to a plastic hose was used to collect three 10 litre samples of seawater from each site. The bilge pump was moved up and down between the surface and just above the bottom in order to sample the entire water column. The water was filtered through a 3 μm phytoplankton net and the concentrate transferred to labelled plastic containers, each with a 6cm diameter polyethylene disk affixed to the bottom of the container using Pterostat™, an inert putty-like substance (Plate 2.4). Samples were stored upright on ice and transported to the laboratory.

Samples were placed in a Thermoline Australia refrigerated seed germination cabinet under 2 fluorescent Grolux lights (F30W/GRO-T8) on a 12-h day/night regime at 20°C (Bellgrove *et al.*, 1997). Propagules were left to settle out onto the polyethylene disks for 48 hours. Then, using sterile technique and a glass hood, the disks were transferred into fresh jars containing 100 ml of autoclaved seawater (110°C for 10 mins) enriched with 2ml Provasoli ES medium. Lids were left loosely closed to facilitate airflow, and samples were returned to the germination cabinet. The water was changed twice weekly using plastic aquarium tubing attached to 100cc syringes, and the position of samples in the cabinet alternated. Equipment was sterilised in ethanol and rinsed in autoclaved seawater to reduce contamination.

Samples were cultured for 24 days, after which microalgal and bacterial blooms began to dominate cultures. Five ml of formalin was added to each culture jar to preserve algal recruits and kill unwanted blooms. After 24 hours the existing formalin-seawater was replaced with fresh autoclaved seawater to reduce loss of colour and damage to cell tissue. Samples were stored in the dark until identified.

The same method employed for identification of artificial seagrass epiphytes was used to identify algae growing in culture, and to record species abundance. Identification was only possible to genus level for many individuals.

2.6 SAMPLING OF NATURAL EPIPHYTE COMMUNITIES

In conjunction with the two experimental components of the study, samples of natural *P. sinuosa* were collected from each away from reef and near reef site at the time artificial seagrass grids were deployed. On Reef samples were not collected as this species does not grow on reef. The purpose of collecting natural material was to help elucidate the source of propagules - the reef, the surrounding seagrass meadow, both or neither. Additionally, comparisons were made between the two communities to test whether any patterns shown by artificial seagrass epiphyte assemblages were similar to those of natural epiphyte assemblages.

Four quadrats of 10cm x 10cm were randomly placed by SCUBA divers within the target area at each treatment site. All above-ground vegetative material was collected from the quadrats and placed in plastic bags whilst underwater using SCUBA equipment. Samples were kept on ice and transported to the laboratory, where they were preserved in 5% formalin in seawater and stored in the dark until processed.

One leaf was randomly selected from each quadrat and epiphyte species and abundance recorded as previously described.

2.7 STATISTICAL ANALYSIS

2.7.1 Univariate analysis

Nested analysis of variance tested differences in mean species richness and biomass between habitats and between sites within habitat for each component of the study using SuperAnova ™ (Abacus Concepts Inc.) software. Data were first tested for homogeneity of variance using the following procedure.

2.7.1.1 Homogeneity of variance

Untransformed datasets were first tested for homogeneity using Levene's Test within SPSS. Where Levene's Test revealed variances between sites were heterogeneous, various transformation methods were explored, square root transformation yielding the more normal distribution of data. Subsequent Levene's homogeneity of variance tests on transformed data still showed variances were heterogeneous between sites, except for calcium carbonate content and species richness of propagules (Table 2.5). As ANOVA is considered to be robust to heterogeneity of variance (Clarke & Warwick, 1994; Chapman, Underwood & Skilleter, 1995) when equal sample sizes are involved (Kendrick, 1991), it was considered appropriate to continue with parametric analyses of data. To compensate for the possibility of an erroneous conclusion, the significance level was set at 0.01 where data failed to conform to homogeneity of variance. If data conformed to homogeneity of variance, the significance level was set at 0.05.

2.7.1.2 Post Hoc Tests

Multiple, pairwise post-hoc comparisons of means were performed to determine which pairs of means were different when significant differences between habitats were detected. The Games-Howell testing procedure (SPSS™ SPSS Inc.) was used because it is robust to unequal sample variances (Chisholm *et al.*, 1997; Abacus Concepts Inc., 1989).

Table 2.5 Results of Levene's Homogeneity of Variance testing differences in mean variances between sites on untransformed and square root transformed biomass data.

VARIABLE	LEVENE'S HOMOGENEITY OF VARIANCE			
	Untransformed data			
	df1 (df2)	Levene Statistic	P Value	Variance Homogeneous
Ash Free Dry Weight	11 (36)	3.889	0.001	NO
Dry Weight	11 (36)	3.330	0.003	NO
Calcium Carbonate	11 (36)	2.112	0.045	NO
Species Richness	11 (36)	2.862	0.008	NO
	Square root transformed data			
	df1 (df2)	Levene Statistic	P Value	Variance Homogeneous
Ash Free Dry Weight	11 (36)	2.839	0.009	NO
Dry Weight	11 (36)	2.639	0.014	NO
Calcium Carbonate	11 (36)	1.732	0.106	YES
Species Richness	11 (36)	2.493	0.019	NO

2.7.2 Multivariate analysis

Multivariate analysis was conducted using the PRIMER (Plymouth Routines In Multivariate Ecological Research) software analysis package to explore patterns in algal epiphyte assemblages, and to determine whether these patterns were linked to proximity to reef.

The full datasets of species abundance data, using untransformed median abundance category values, were used (n=48 for artificial seagrass; n=36 for propagule culture; n=32 for natural seagrass). A similarity matrix of sites was first produced using the Bray-Curtis similarity measure, calculated from the Cluster module in PRIMER using untransformed data. The Bray-Curtis measure was selected as it is the most commonly used association measure in ecological studies, and is robust to non-linear species responses which are typical of ecological data (Faith *et al.*, 1987).

2.7.2.1 Ordinations

Ordinations were performed to visually reveal patterns of similarity among epiphyte assemblages at different sites. The ordinations were performed using PRIMER's MDS module based on the Bray-Curtis similarity matrices, using 2 or 3 dimensional non-metric multidimensional scaling (MDS), and the results for each treatment plotted with the aid of Deltagraph™ graphics package (SPSS Inc.). The plotted graphs provided a visual representation of how similar samples were to each other. Samples that were more similar appeared closer together, while those that were more dissimilar were plotted further apart. Where stress values were relatively high, indicating that the scatter plot was not a good representation of the underlying similarity matrix, 3 dimensional ordinations were used as increasing the number of dimensions gives better results (Clarke & Warwick, 1994). Only the first two dimensions of the 3 dimensional plots were presented. Each ordination was split by habitat to emphasise any patterns of difference between habitats.

2.7.2.2 Analysis of Similarities

Analysis of Similarities (ANOSIM) is a non-parametric test used to determine whether the patterns revealed by ordination are significantly different (Clarke & Warwick, 1994). Using PRIMER, and based on the Bray-Curtis association matrix, a two-way nested ANOSIM was used to test for differences between habitats and between sites within habitats, using a significance level of 0.05. This tested two hypotheses:

There is no difference between sites within habitat; and
There is no difference between habitats.

Where differences were significant, pairwise comparisons were performed to determine which habitats were different, using the procedure available within the ANOSIM module.

2.7.2.3 Simper

To determine which species were responsible for the observed patterns in similarity/dissimilarity between habitats, exploratory analysis using PRIMER's Simper module was conducted. This procedure examines the contribution of individual species by computing the average dissimilarity between all pairs of group samples and then breaking the average down into the separate contributions of each species to the average dissimilarity (Clarke & Warwick, 1994). For consistency, Simper was run on the identical Bray-Curtis matrix produced for the ordination and ANOSIM, using untransformed data.

CHAPTER 3: RESULTS

Proximity to reef significantly influenced algal epiphyte diversity in the seagrass meadows studied. Epiphyte assemblages distant from reef showed lower biomass, lower species richness and different composition to those adjacent to reef. There was considerable variation in epiphyte assemblages within sites, highlighting the local patchiness which is a feature of many marine communities. However, this did not mask the differences between habitat treatments.

3.1 PROPAGULE AVAILABILITY

3.1.1 Species Richness

Laboratory culture of propagules collected from each site produced 14 algal species, 4 Chlorophyta, 6 Phaeophyta, 3 Rhodophyta and 1 cyanobacteria. Of these 14 taxa, 11 were collected from On and Near Reef while only 6 taxa were collected Away from Reef. *Sphacelaria* spp, *Enteromorpha flexuosa, Enteromorpha paradoxa, Hincksia mitchelliae* and *Ulva* spp were common to all three habitats. *Ceramium macilentum* only occurred near reef while encrusting coralline species were only detected in one On Reef sample. A species list showing relative abundance and species occurrence for each habitat is included in Appendix A.

Species richness and abundance was positively correlated with proximity to reef, and the composition of propagules collected On Reef was different to those collected in seagrass meadows distant from reef. Propagules collected from seagrass Near Reef contained elements of both habitat types, ie., On Reef and Away from Reef.

3.1.2 Species Richness comparisons

Mean Species richness was lowest for Away from Reef sites, while On Reef and Near Reef sites were higher and more variable. Herring Bay sites had the highest mean species richness for both On Reef and Near Reef habitats (Figure 3.1). Statistical analysis of variance on untransformed data (homogeneous as confirmed by Levene's test P=0.056) confirmed significant differences between habitats and no significant differences between sites within habitats (Table 3.1). Games-Howell post-hoc testing revealed that species richness of propagules collected Away from Reef was lower than those collected from On and Near Reef.

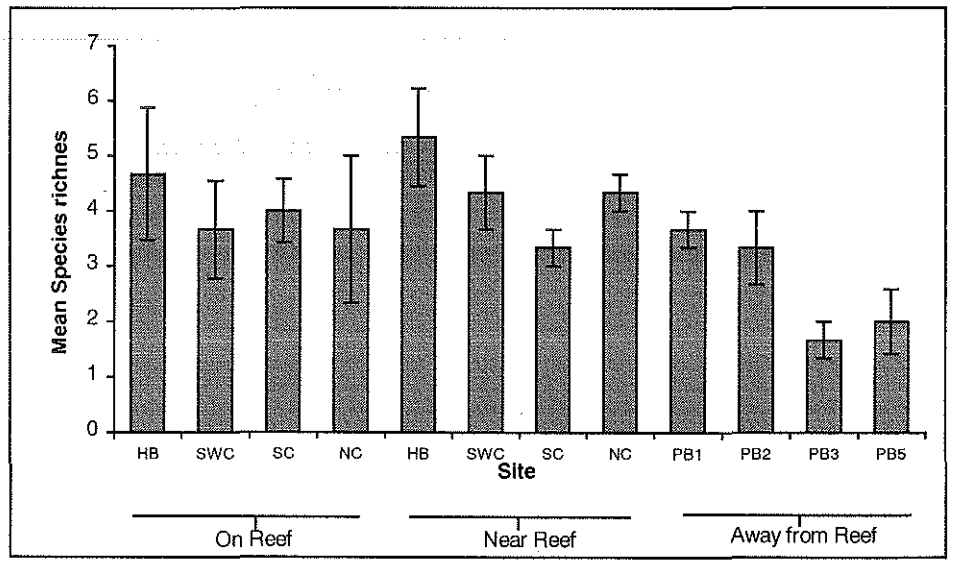


Figure 3.1. Mean species richness (± SE, n=3) recorded from laboratory culture of algal propagules collected from 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). Away from Reef sites had lower species richness than the other two habitats. HB=Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank).

Table 3.1. Results of 2 factor nested ANOVA testing for differences in species richness of propagule culture between habitats and between sites within habitats (data untransformed as Levene's homogeneity of variance result of P=0.056 indicated variances were homogeneous).

FACTOR	2 FACTOR NESTED ANOVA Variable = culture species richness				
	d.f.	Mean Square	F-Value	P-Value	
Between Habitat	2	9.333	5.040	0.0340	*
Between sites within habitat	9	1.852	1.093	0.4038	NS

NS = Not statistically significant
* = Statistically significant ($p<0.05$)

3.1.3 Ordination and Analysis of Similarities

Patterns in the composition of propagules were examined by ordination of the species abundance data. The results of this ordination are presented in Figure 3.2. The ordination gave a good result using 3 dimensions (stress = 0.11), indicating that the scatter plot was representative of the underlying similarity/dissimilarity between samples. Only the first two dimensions of the plot are presented. This figure shows that the composition of propagules was generally different between habitats. On Reef sites separated to the top left of the vertical axis while from Away from reef sites separated to the bottom of the axis. Near Reef sites were clustered more with On Reef sites, however there was some overlap with Away from Reef habitat.

In order to determine whether these differences were statistically significant, analysis of similarities was performed on the Bray-Curtis similarity matrix used for the ordination. This test confirmed that there were significant differences in the composition of propagules collected from each habitat ($p=0.024$), and between sites within habitat ($p=0.001$). Therefore, the null hypotheses of no significant

differences in propagule availability between sites within habitat and between habitats were rejected. Pairwise comparisons revealed that for each combination of habitats, only On Reef and Away from Reef were significantly different to each other ($p=0.029$).

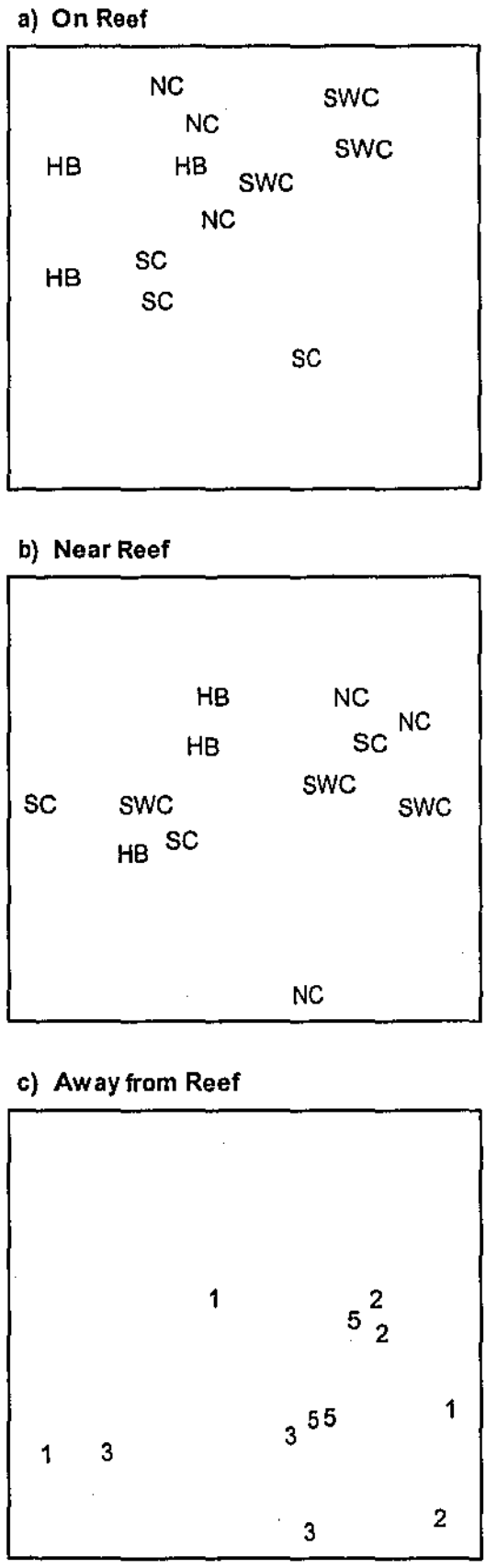


Figure 3.2. First two vectors of 3d non-metric MDS ordination of propagule assemblages (n=36), split into a) On Reef, b) Near Reef and c) Away from Reef sites. Away from reef propagules were different to the other two habitats. HB-Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, 1-5=Parmelia Bank.

3.1.4 Simper

Analysis of the contribution of individual species to the dissimilarity of propagule composition between habitats revealed increasing dissimilarity with increasing distance from reef (Table 3.2). Two species, *Hincksia mitchelliae* and *Ulva spp*, were responsible for 90% of the similarity of Away from Reef sites. The same two species were present On Reef and Near Reef, though their relative contribution to community structure was smaller (Table 3.3).

Table 3.2. Percentage average dissimilarity of propagule composition between habitats. On and Away from Reef propagules was most dissimilar, while On and Near Reef propagules were most similar.

	On Reef	Near Reef	Away from Reef
On Reef	0	53.32%	61.99%
Near Reef	0%		59.02%
Away from Reef			0%

3.1.5 Summary – Propagule Availability

In summary, culture of propagules available in the water column on one occasion during this study showed that there were differences in species richness and composition related to proximity to reef. The differences were most evident between On Reef and Away from Reef habitats, supporting the hypothesis that propagule availability varies with distance from reef.

Table 3.3. Results of SIMPER showing percentage of species contribution to community structure of propagules collected from the water column – cut level 90% (based on untransformed median category values).

ON REEF		NEAR REEF		AWAY FROM REEF	
Species	%	Species	%	Species	%
Ulva juvenile spp	44.20	*Hincksia mitchelliae*	52.89	*Hincksia mitchelliae*	63.93
Enteromorpha paradoxa	17.84	*Ulva* juvenile spp	21.10	*Ulva* juvenile spp	27.43
Hincksia mitchelliae	17.14	*Enteromorpha flexuosa*	10.65		
Enteromorpha flexuosa	16.09	*Sphacelaria* spp	9.91		

3.2 POST RECRUITMENT – ARTIFICIAL SEAGRASS

3.2.1 Biomass

Biomass of epiphytes grown on artificial seagrass was higher in Near Reef habitat than either of the other two habitats. On Reef and Away from Reef habitats both had relatively low biomass. Variability within habitat was low Away from Reef, while Near Reef and On Reef habitats were both much more variable.

Mean dry weight was consistently low at the Away from Reef sites, slightly higher and more variable at On Reef sites, and highest but also highly variable at Near Reef sites (Figure 3.3). This trend was repeated for the ash free dry weight and calcium carbonate mass, reflecting relatively constant ratios of the three variables over all sites (Figures 3.4 and 3.5).

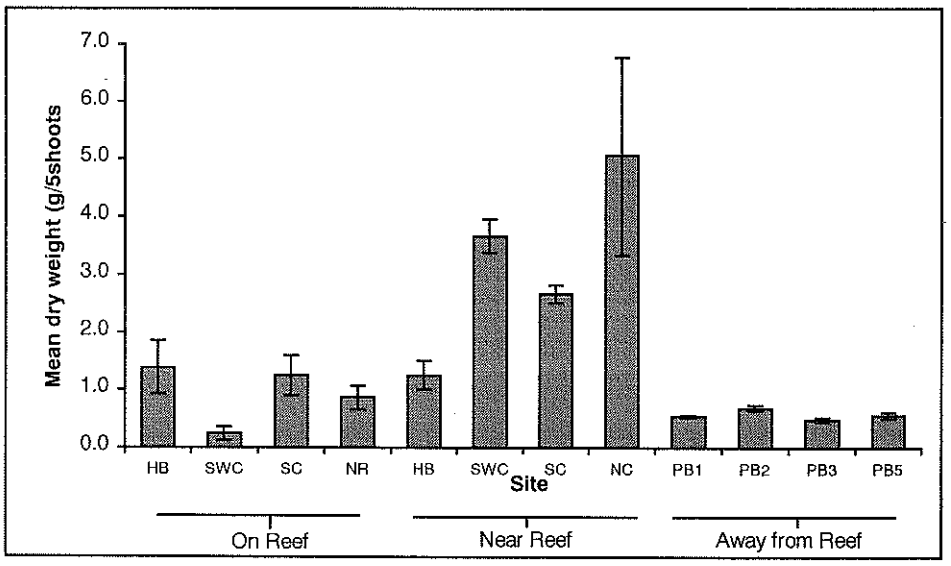


Figure 3.3. Mean dry weight of epiphytic algae (±SE, n=4) recorded on 5 shoots of artificial seagrass at 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). Mean dry weight of near reef sites was significantly higher than other habitats. On Reef and Away from Reef sites were similar though On Reef was more variable. HB=Herring Bay, SWC= South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank.

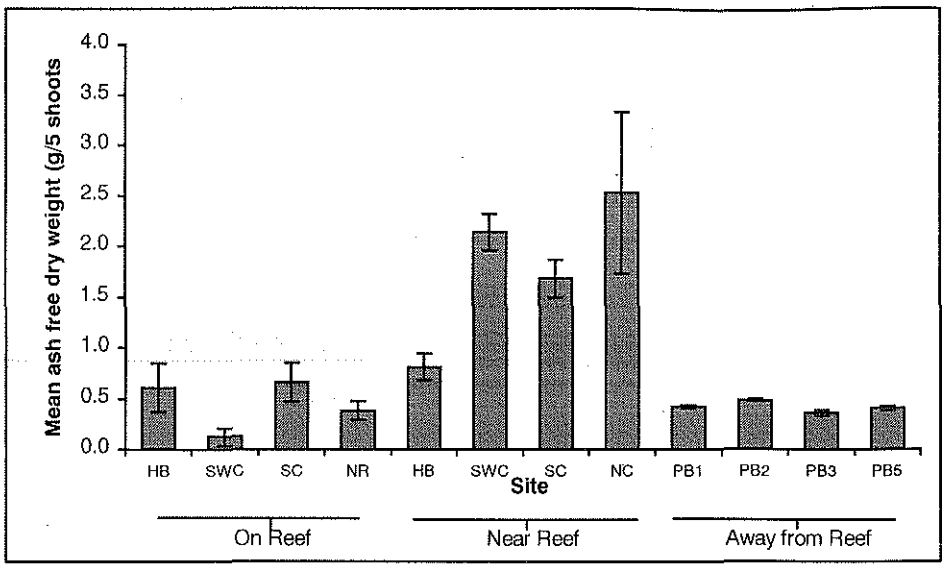


Figure 3.4. Mean ash free dry weight of epiphytic algae (±SE, n=4) recorded on 5 shoots of artificial seagrass at 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). Mean ash free dry weight of near reef sites was significantly higher than other sites, while On Reef and Away from Reef sites were similar though On Reef was more variable. HB=Herring Bay, SWC= South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank.

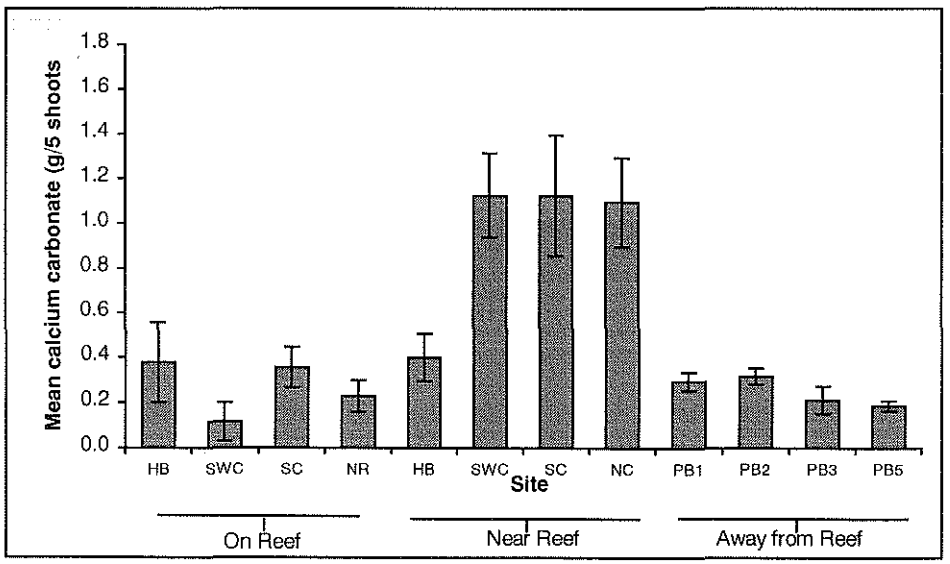


Figure 3.5. Mean calcium carbonate content of epiphytic algae (±SE, n=4) recorded on 5 shoots of artificial seagrass at 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). Mean calcium carbonate content of near reef sites was significantly higher than other habitats. HB=Herring Bay, SWC= South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank.

The higher biomass and calcium carbonate mass for sites Near Reef was confirmed by statistical analysis. Analysis of variance of square root transformed data showed there were significant differences in dry weight, ash free dry weight and calcium carbonate content between habitats. There were also significant differences between sites within habitat for dry weight and ash free dry weight. There was no significant difference in calcium carbonate content between sites within habitats (Table 3.4). Games-Howell post hoc tests revealed that Near Reef sites were significantly higher in biomass than On Reef and Away from Reef sites.

Table 3.4. Results of two factor nested ANOVA testing differences in biomass variables between habitats (On Reef, Near Reef, Away from Reef) and between sites within habitats. All data were square root transformed. Dry Weight, ash free dry weight and calcium carbonate content were all significantly higher Near Reef.

VARIABLE	ANOVA RESULTS				
	Between Habitats				
	d.f.	Mean Square	F-Value	P-Value	
Dry Weight	2	4.189	9.968	0.0052	*
Ash Free Dry Weight	2	2.394	13.571	0.0019	*
$CaCO_3$	2	1.126	11.470	0.0033	*
	Between Sites within Habitats				
	d.f.	Mean Square	F-Value	P-Value	
Dry Weight	9	0.420	3.770	0.0020	*
Ash Free Dry Weight	9	0.176	3.454	0.0037	*
CaCO3	9	0.098	2.873	0.116	NS

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

There were proportionately more calcifying epiphytes in assemblages Away from Reef (Figure 3.6). The mean percentage of calcium carbonate to dry weight was lowest On Reef (20 to 32 percent), higher Near Reef (30 to 41 percent) and highest Away from Reef (34 to 54 percent).

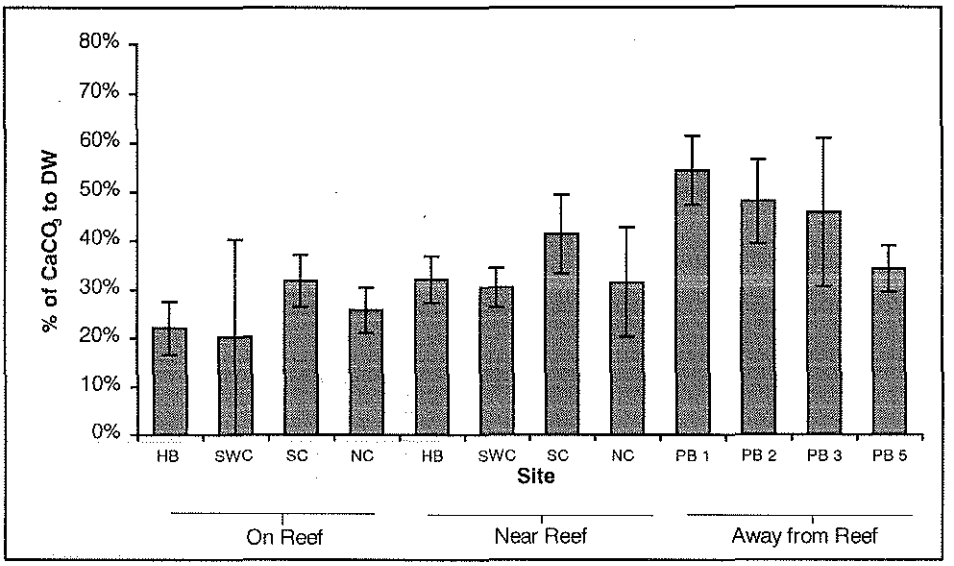


Figure 3.6. Proportion of mean calcium carbonate to mean dry weight of epiphytes on artificial of epiphytic algae (±SE, n=4) recorded on 5 shoots of artificial seagrass at 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). The proportion of calcium carbonate to dry weight was highest for Away from Reef sites. HB=Herring Bay, SWC= South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank.

3.2.2 Species Richness

Sixty-eight epiphytic algal taxa were identified growing on shoots of artificial seagrass across all sites during the study: 10 Chlorophyta, 14 Phaeophyta, 40 Rhodophyta and 4 cyanobacteria. Near Reef habitat recorded the highest number of taxa (53 species), followed by On Reef (44 species) and Away from Reef (37 species) (Figure 3.7). A full list of epiphyte species recorded on artificial seagrass

during the study, together with relative abundance of species for each habitat is provided in Appendix B.

Thirty percent of species recorded were common to all three habitats, while On and Near Reef habitats shared more species with each other than with Away from Reef habitat. Seventeen percent of Away from Reef species were unique to that habitat, compared to 12% for Near Reef and 5% for On Reef (Figure 3.8). Fourteen species occurred at only one of the twelve sites studied.

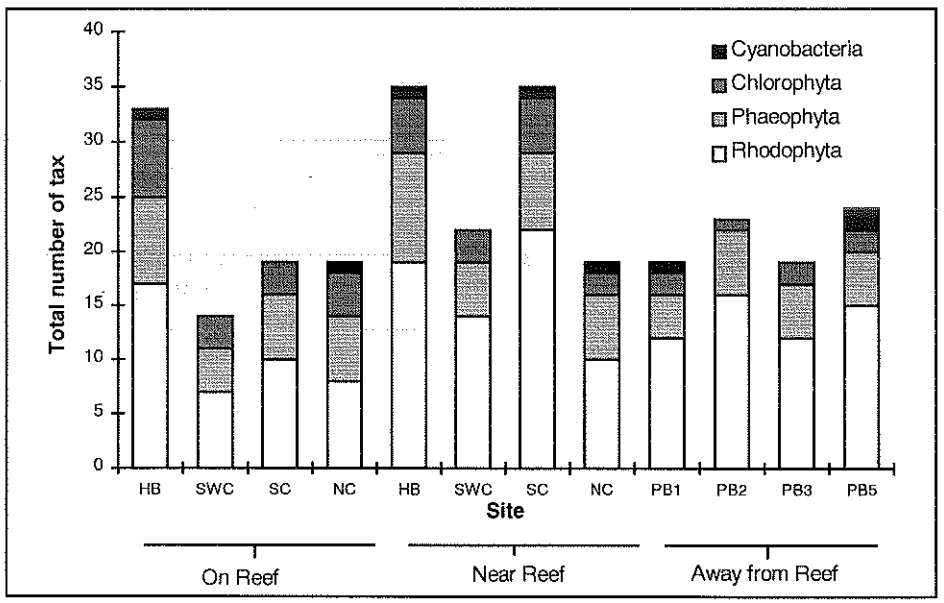


Figure 3.7. Total number of epiphyte taxa and numbers of Chlorophyta, Phaeophyta, Rhodophyta and cyanobacteria recorded on 12 shoots of artificial seagrass at 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). Rhodophyta dominated all sites, followed by Phaeophyta and Chlorophyta, with more taxa of Chlorophyta On and Near Reef than Away from Reef. HB=Herring Bay, SC=South Carnac, SWC=South West Carnac, NC=North Carnac, PB=Parmelia Bank.

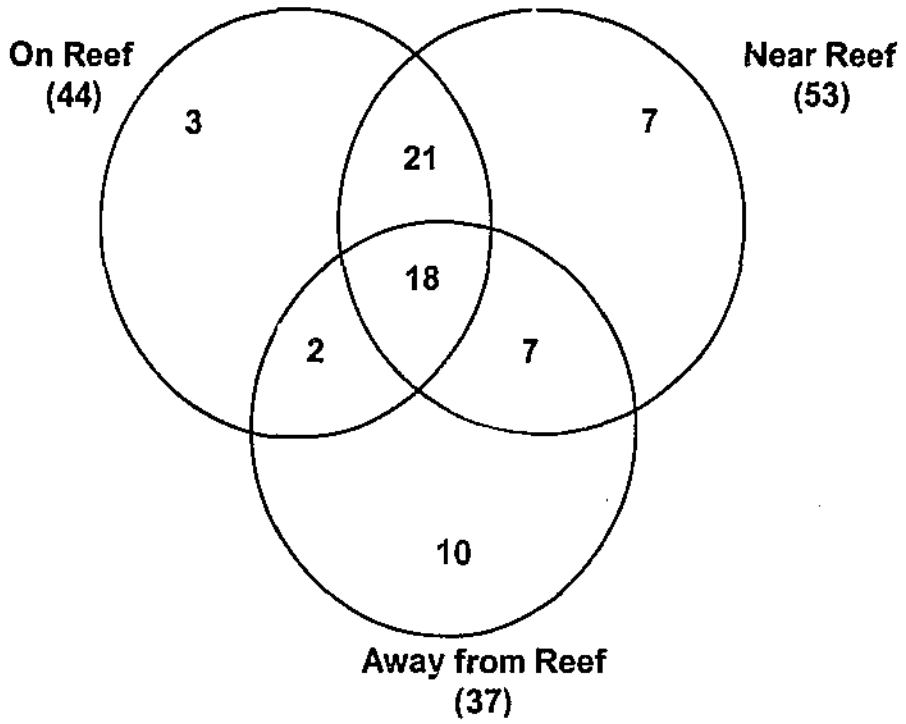


Figure 3.8. Similarity of species composition of epiphytes recruited on artificial seagrass. Number shown within circles indicate the number of species found at that habitat. Where circles overlap species were common to both or all habitats. (i.e. 10 species occurred in Away from Reef habitat only, 18 species occurred in all three habitats and 7 species occurred in both Away from Reef and Near Reef habitats.) Note the large number of species shared between On and Near Reef habitat and also the relatively high proportion of species that only occurred in one habitat.

3.2.3 Species Richness Comparisons

Species richness was highly variable within sites, suggesting small-scale patchiness. This localised patchiness dominated any variation in species richness between habitats. Mean species richness for each site (n=4) was relatively consistent for Away from Reef sites (13 ± 0.854 SE to 15 ± 0.645 SE) and considerably more variable for the other two habitat types (On Reef = 5 ± 1.887 SE to 18 ± 3.326; Near Reef = 11 ± 1.708 SE to 22 ± 2.136 SE) (Figure 3.9). Two factor nested ANOVA analysis confirmed the lack of significant differences in species richness between habitats and significant differences within sites between habitats (Table 3.5).

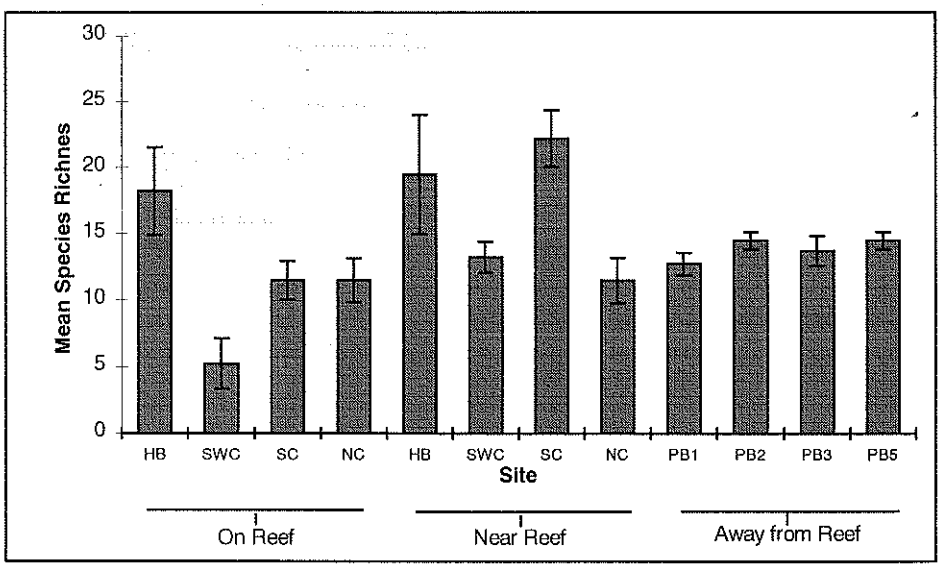


Figure 3.9. Mean Species Richness (± SE, n=4) of epiphytic algae recorded on artificial seagrass at 12 sites within 3 habitats (On Reef, Near Reef, Away from Reef). There was no difference in species richness between habitats, however Away from Reef sites were relatively less variable than other sites. HB=Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank.

Table 3.5. Results of 2 factor nested ANOVA testing for differences in species richness of epiphytes recorded on artificial seagrass between habitats and between sites within habitats (data square root transformed). There was no significant difference in species richness between habitats.

FACTOR	2 FACTOR NESTED ANOVA Variable = Species Richness				
	d.f.	Mean Square	F-Value	P-Value	
Between Habitat	2	2.111	1.435	0.2877	NS
Between sites within habitat	9	1.471	4.184	0.009	*

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

3.2.4 Ordination and Analysis of Similarities

The assemblages of epiphytes which grew on artificial seagrass were different for each habitat as the ordination shows (Figure 3.10). On Reef sites clustered towards the top left of the plot, Near Reef sites towards the bottom left and Away from Reef formed a tight cluster towards the bottom right. Herring Bay sites formed a separate group containing both On and Near Reef, while South West Carnac sites for On Reef formed another separate cluster at the top right. The stress value of 0.13 for the 2 dimensional non-metric MDS was again a fair result, confirming the plot was a reasonable facsimile of the underlying similarity matrix.

Two way nested ANOSIM, with 5775 permutations, confirmed that the patterns of difference visible in the ordination were significant within sites between habitats ($P<0.0001$) and between habitats ($P=0.002$). Therefore, the null hypotheses of no significant differences in epiphytic assemblages recruited on artificial seagrass between sites within habitat and between habitat were rejected.

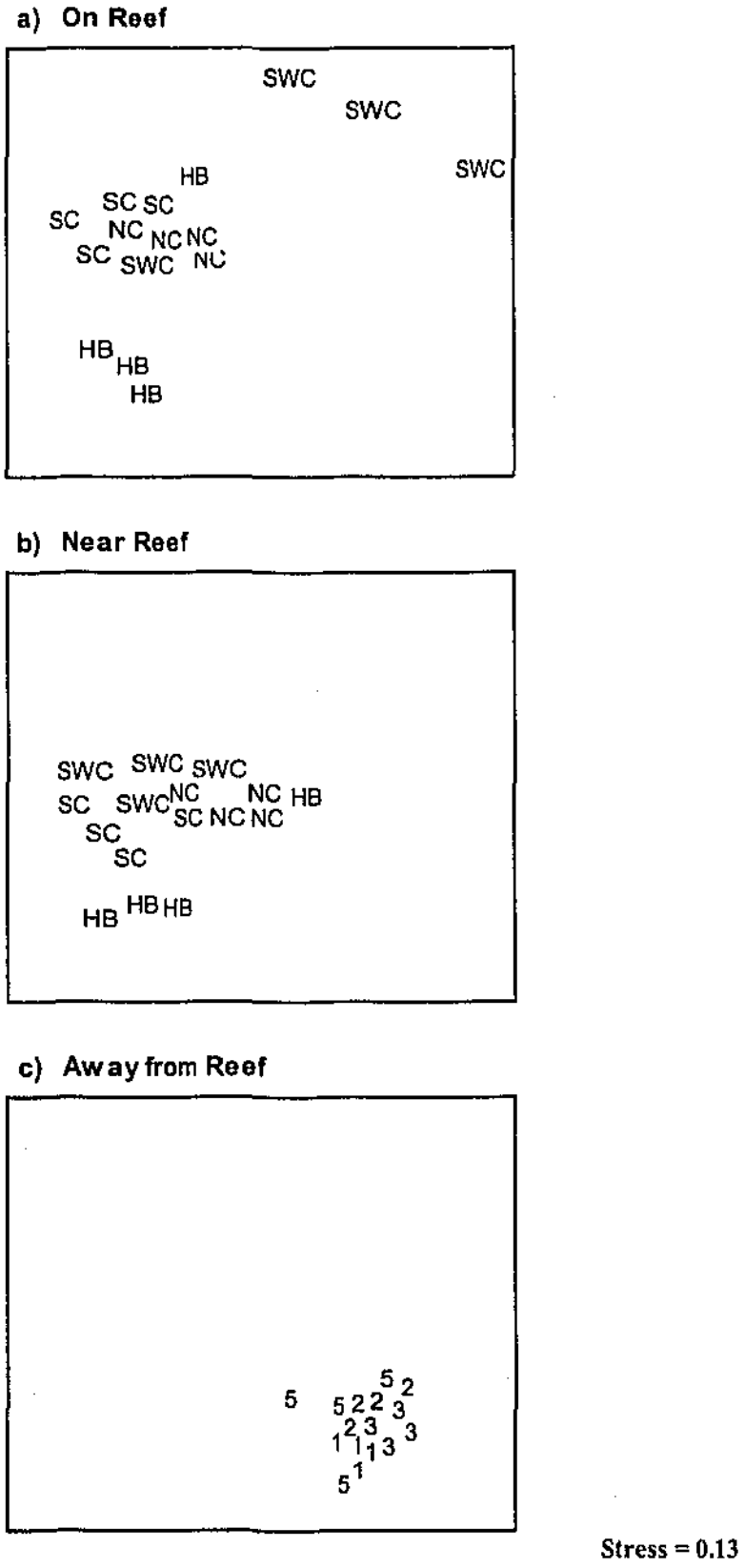


Figure 3.10. Two-dimensional non-metric MDS ordination of artificial seagrass epiphyte assemblages (n=48), split into a) On Reef, b) Near Reef and c) Away from Reef sites. Away from reef assemblages were significantly different to On and Near Reef assemblages. HB=Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, 1-5 = Parmelia Bank sites 1, 2, 3 & 5.

To determine which habitats were different pairwise tests were calculated (Table 3.6). These comparisons showed On and Near Reef were not significantly different to each other (P=0.629) while Away from Reef was significantly different from both (P=0.029).

Table 3.6. Results of ANOSIM pairwise comparisions testing for differences in artificial seagrass epiphyte composition between each habitat. Away from Reef assemblages were significantly different to On Reef and Near Reef assemblages. Group 1 = Near Reef, Group 2 = On Reef, Group 3 = Away from reef.

Groups Used	Statistical Value	Permutations: Possible (Used)	Significant Statistics	P	
1, 2	0.000	35 (35)	15	0.429	NS
1, 3	0.927	35 (35)	1	0.029	*
2, 3	0.917	35 (35)	1	0.029	*

NS = No significant difference (p>0.05)
* = Statistically significant (p<0.05)

3.2.5 Simper

Analysis of the contribution of individual species to observed patterns in the dissimilarity of assemblages between habitat showed that dissimilarity increased with distance from reef (Table 3.7). This pattern was similar to that shown in the propagule availability experiment.

Table 3.7. Percentage Dissimilarity of artificial seagrass epiphyte assemblages between habitats.)

	Near Reef	On Reef	Away from Reef
Near Reef	0%	54.49%	62.61%
On Reef		0%	73.07%
Away from Reef			0%

Nine species accounted for 90% of the community structure of On Reef sites and 10 species for Away from Reef sites. In contrast, 14 species contributed to the same degree for Near Reef. Thus On Reef and Away from Reef sites were dominated by relatively fewer species while Near Reef had a broader and more even distribution of species (Table 3.8).

Table 3.8. Results of SIMPER showing percentage of species contribution to community structure for epiphytes recruiting on artificial seagrass – cut level 90% (based on untransformed median category values).

ON REEF		NEAR REEF		AWAY FROM REEF	
Species	**%**	**Species**	**%**	**Species**	**%**
Coralline encrusting	24.02	*Polycerea nigrescens*	25.17	Coralline encrusting	26.54
Polycerea nigrescens	21.13	Coralline encrusting	25.07	*Giraudia robusta*	11.45
Hincksia mitchelliae	17.97	*Hincksia mitchelliae*	11.13	*Polycerea zostericola*	11.28
Ceramium isogonum	8.33	*Colpomenia sinuosa*	6.22	*Sphacelaria rigidula*	9.90
Colpomenia sinuosa	7.12	*Ceramium isogonum*	5.99	*Haliptilon roseum*	8.06
Polysiphonia mollis	6.35	*Polysiphonia mollis*	4.93	*Myronemia strangulans*	6.37
Polysiphonia forfex	2.50	*Sphacelaria rigidula*	4.15	*Oscillatoria* sp 1	5.39
Enteromorpha paradoxa	2.35	*Wrangelia Plumosa*	1.44	*Ceramium puberlum*	4.47
Sphacelaria rigidula	1.79	*Ceramium macilentum*	1.36	*Laurencia* juvenile spp	4.39
		Centroceras clavulatum	1.33	*Jania minuta*	3.94
		Laurencia juvenile spp	1.09		
		Enteromorpha paradoxa	0.99		
		Champia zostericola	0.98		
		Stictyosiphon soriferus	0.95		

Encrusting coralline algae provided the greatest contribution to community structure within On Reef and Away from Reef sites, and was the second most important algae for Near Reef. There was a positive correlation between percentage contribution of encrusting coralline species and increased distance from reef. This trend was similar to that shown for calcium carbonate biomass,

where there was an increase in the proportion of calcifying to non-calcifying epiphytes with increased distance from reef.

Examination of trends between groups of algae to the contribution of community similarity revealed that coralline (articulated and encrusting) and brown algae were the dominant contributors for each habitat type. Brown algae contributed almost twice as much to community structure for On and Near Reef habitats as coralline species. In contrast, Away from Reef habitat was dominated by coralline species, which contributed more to community structure than brown algae. Green algae featured in On and Near Reef communities, but not in Away from Reef, and red fleshy species featured in Near Reef and Away from Reef, but not On Reef habitats.

3.2.6 Summary – Recruitment of Epiphytes to Artificial Seagrass

In summary, it was found that species composition and biomass of epiphytes recruited to artificial seagrass were different between seagrass habitats. Biomass was substantially higher for sites adjacent to reef. The composition of assemblages on and near reef was relatively similar, while assemblages distant from reef were significantly different. This finding supports the hypothesis that reefs contribute to algal diversity in adjacent seagrass meadows.

3.3 POST-RECRUITMENT: NATURAL EPIPHYTE COMMUNITIES

3.3.1 Species Richness

Fifty nine species of algal epiphytes were identified growing on natural *Posidonia sinuosa* at Near Reef and Away from Reef sites, including 37 Rhodophyta, 14 Phaeophyta and 8 Chlorophyta (Figure 3.11). Thirty-nine species were recorded at each habitat, though only 19 species were common to both (Figure 3.12). A species list detailing species presence/absence and relative abundance is included as Appendix C.

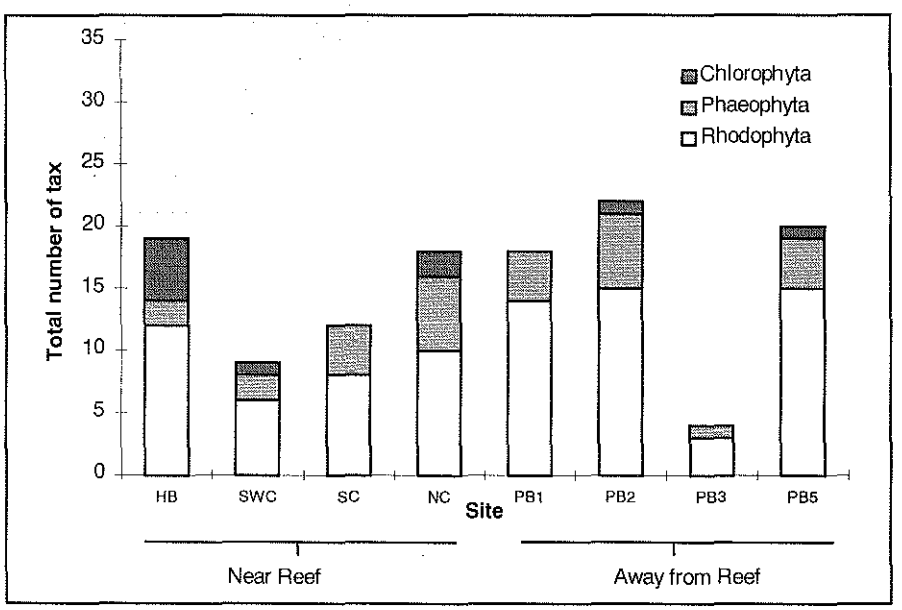


Figure 3.11. Total number of epiphyte taxa and number of Chlorophyta, Phaeophyta and Rhodophyta recorded on 4 *Posidonia sinuosa* leaves at 4 sites of Near Reef and Away from Reef habitat.

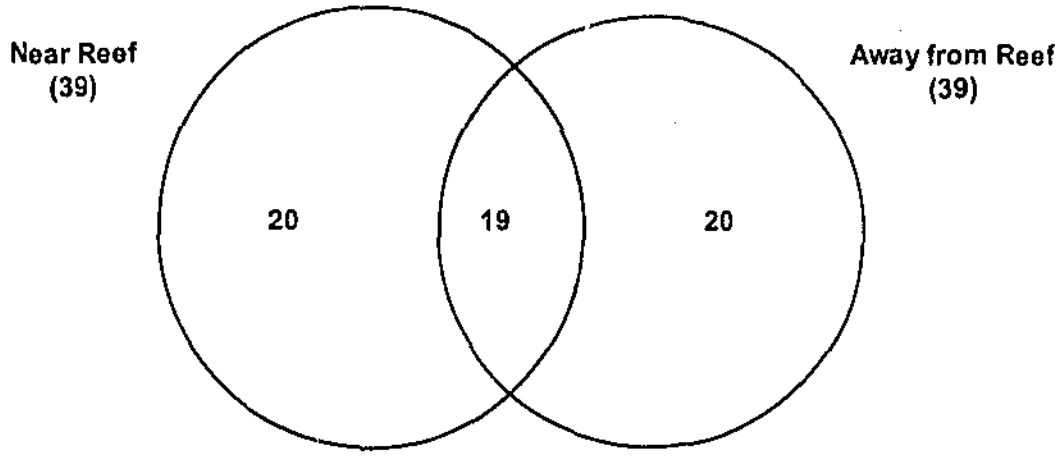


Figure 3.12. Similarity of species composition of epiphytes identified on natural *Posidonia sinuosa* leaves. Number shown in brackets indicate total number of taxa at each habitat. Numbers in circles indicate number of unique and shared species. Where circles overlap species were common to both habitats. Two thirds of all species were present at only one habitat.

3.3.2 Species Richness Comparisons

Species richness of epiphytes occurring on natural *Posidonia sinuosa* was highly variable between sites within habitat and overrode any detectable differences between habitat. Mean species richness varied from 5 ± 1.1 SE to 10 ± 1.95 SE for Near Reef and 2 ± 0.47 SE to 14 ± 0.70 SE for Away from Reef Sites (Figure 3.13). Two factor nested ANOVA confirmed there were no significant differences between Near Reef and Away from Reef habitats and significant differences between sites within habitat (Table 3.9).

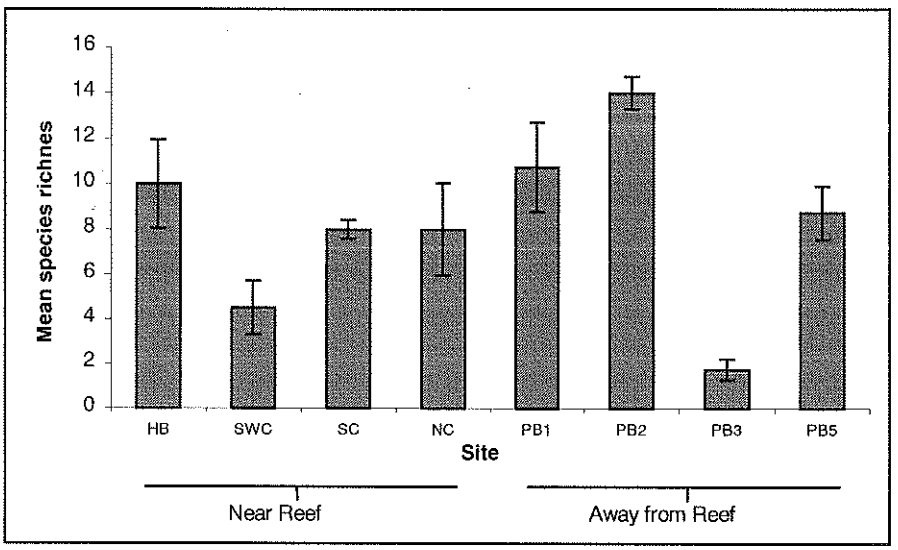


Figure 3.13. Mean Species Richness (± SE, n=4) recorded on natural leaves of *Posidonia sinuosa* for near reef and away from reef habitat. There was no difference in species richness between epiphytes near reef and away from reef. HB=Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, PB=Parmelia Bank.

Table 3.9. Results of 2 factor nested ANOVA testing for differences in species richness of epiphytes recorded on natural *Posidonia sinuosa* between habitats and between sites within habitats (data square root transformed). There was no significant difference between habitats.

FACTOR	2 FACTOR NESTED ANOVA Variable = Species Richness				
	d.f.	Mean Square	F-Value	P-Value	
Between Habitat	1	0.088	0.033	0.8608	NS
Between sites within habitat	6	2.638	10.619	0.0001	*

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

3.3.3 Ordinations and Analysis of Similarities

Epiphytic algal assemblages growing on *Posidonia sinuosa* Near Reef were different to those growing Away from Reef, with the exception of the Herring Bay Near Reef site. The results of the 3d ordination, based on untransformed species-abundance data, are shown in Figure 3.14. Only the first two dimensions are presented. Near Reef sites clustered towards the top left of the scatter plot, while Away from Reef sites clustered towards the bottom left. The exception to this was Herring Bay, a Near Reef site which grouped with the Away from Reef sites. The stress value of the three dimensional ordination was 0.12.

While the ordination showed a pattern of difference between habitats, ANOSIM confirmed that this difference was not statistically significant (p=0.057). Differences between sites within habitat however were significantly different (p<0.001). Therefore, the null hypothesis of no significant difference between habitats was not rejected.

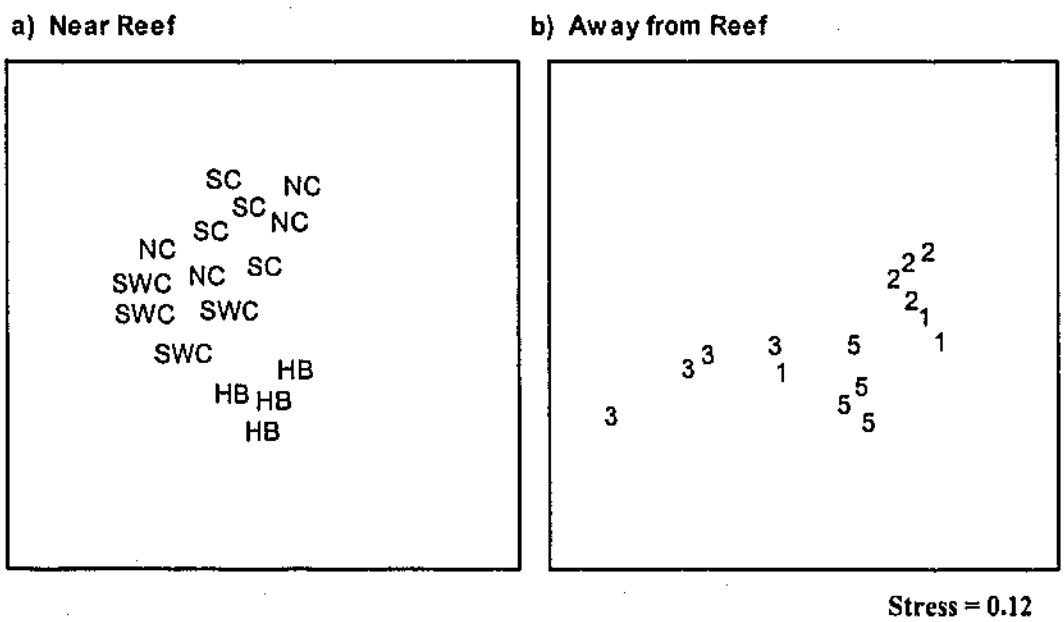


Figure 3.14. Ordination of sites based on natural *Posidonia sinuosa* epiphyte assemblage data. First 2 dimensions of 3d non-metric MDS using untransformed species-abundance data (n=32), split into a) Near reef and b) Away from Reef sites. Epiphyte assemblages were generally different between habitats with the exception of Herring Bay. HB=Herring Bay, SWC=South West Carnac, SC=South Carnac, NC=North Carnac, 1-5=Parmelia Bank sites.

3.3.4 Simper

The average dissimilarity between epiphyte communities found on natural *P. sinuosa* leaves at sites Near Reef and Away from Reef was 66.07%, while the average similarity within these groups was 42.01% and 41.59% respectively. A relatively low proportion of species contributed to 90% of the similarities within habitats (Table 3.10). Encrusting coralline and filamentous brown algae were the dominant algal groups at both locations, while filamentous and fleshy red algae were more conspicuous in Away from Reef habitat.

Table 3.10. Results of SIMPER showing percentage of species contribution to community structure of epiphytes on *Posidonia sinuosa leaves* – cut level 90% (based on untransformed median category values).

NEAR REEF		AWAY FROM REEF	
Species	**%**	**Species**	**%**
Coralline encrusting	68.45	Coralline encrusting	64.55
Ceramium macilentum	5.81	*Sphacelaria rigidula*	7.06
Hincksia mitchelliae	5.79	*Anotrichium liemophora*	6.42
Centroceras clavulatum	3.62	*Ceramium rubrum*	3.83
Sphacelaria rigidula	2.80	*Ceramium puberlum*	3.04
Ceramium puberlum	2.44	*Dasya* sp 1	2.75
Colpomenia sinuosa	2.25	*Laurencia filiformis*	2.29
		Sphacelaria cirrosa	1.61

3.3.5 Summary - Natural Epiphyte Communities

There was no difference in species richness between habitats, however ordination patterns of epiphyte communities growing on natural seagrass were similar to those shown for propagule composition and recruitment to artificial seagrasses, with the separation of sites distant from reef from those adjacent to reef. These differences were not as significant as for the first two components of the study.

CHAPTER 4: DISCUSSION

This study showed that propagule availability, diversity and community structure of seagrass epiphytes were different at sites adjacent to reef compared to those located away from reef. Epiphyte productivity was also higher near reefs. The same trend was evident for each experiment, a separation of away from reef sites for propagule availability, artificial seagrass recruitment and natural epiphyte communities. While it is not possible to determine conclusively that reefs were the cause of these differences, evidence in support of this hypothesis points strongly to reefs as one of the primary agents influencing epiphyte diversity and productivity in adjacent seagrass meadows.

It is possible to explain an influence of reefs in terms of pre-recruitment and post-recruitment processes which proximity to reefs may affect. For example, reefs may affect the type and availability of propagules (pre-recruitment) or they may influence the physico-chemical environment in such a way that only different subsets of the same propagule assemblage manage to express themselves as mature epiphyte communities at different locations (post-recruitment).

In the following sections, the evidence in the results section will be discussed in support of this conclusion. Other explanations for these differences will be suggested.

4.1 PRE-RECRUITMENT PROCESSES

Species richness of propagules was lower, and the composition different, in seagrass meadows away from reef, while sites located on or near reef had higher propagule species richness and composition. Because sites on and near reefs were similar, it can be reasonably assumed that the same sources are providing propagules to these habitats. This also suggests that the source of propagules for sites distant from reefs is either different or is subject to different pre-recruitment processes affecting propagule availability. There is evidence that both of these processes are occurring.

Evidence for local sources of propagules can be found by examining the distribution of propagules in relation to the distribution of adult plants. If local sources alone contributed the propagules, we would expect that those species with adults restricted to near-reef sites would only have propagules in that region, and similarly for those with adults restricted to areas distant from reef. However, it was not possible to determine this from this from the study since, with the exception of two species, all species which were found in the propagule pool were also present as adults at all locations. Despite this, there is evidence that many algal species have limited ranges of propagule dispersal (Hoffman, 1987).

Kendrick & Walker (1995) measured propagule dispersal by staining reproductive *Sargassum* spp thalli and measuring the distance stained propagules settled from the adults. The dispersal shadow of *Sargassum* spp recruits was only 1-2m. Other experiments have shown that dispersal distances of *Macrocystis pyrifera* were approximately 5m and *Colpomenia peregrina* about 2m (Santelices, 1990), while *Hormosira banksii* also has a small dispersal shadow (Bellgrove *et al.*, 1997). While not conclusive, this supports the idea of local sources of propagules for many species of algae.

The distribution of *Ulva* spp and *Enteromorpha flexuosa* provides evidence for regional recruitment. Propagules of *Ulva* spp. and *E. flexuosa* were common in

culture samples at sites away from reef, however no adults of these taxa were found growing on either natural or artificial seagrass in this habitat over the study period. *Ulva* and *Enteromorpha* are reef species (Womersley, 1987), and were common on both natural and artificial seagrass in habitats on and near reef. This suggests that the green algal propagules were not produced locally but had dispersed some distance from reefs in the surrounding region.

Other studies have also recorded green algal propagules some distance from any potential source. In the Northern Hemisphere, *Enteromorpha* spores were found to colonize artificial substratum 35km from the nearest known adult population (Hoffman, 1987), and were also found in water samples taken at sites between 8-24km from the coast (Zechman & Mathieson, 1985). *Ulva* and *Enteromorpha* are ephemeral, opportunistic species and part of their reproductive strategy is to produce vast numbers of propagules. These propagules are positively phototactic and so remain in the water column for long periods of time, enabling them to travel relatively long distances compared to other algal species (Reed *et al.*, 1988). It is therefore feasible that reefs were the source of green algal propagules found in meadows distant from reef.

The distribution of *Ulva* and *Enteromorpha* propagules and adults also hints at the importance of post-recruitment processes in determining the community composition at any point in time. *Ulva* and *Enteromorpha* grow particularly quickly, and are usually one of the first species to colonise vacant substratum. However, they do not persist without disturbances to provide them with vacant patches. It is possible that these green species were present initially, were then replaced by later successional species, and were not able to recolonise due to scarcity of free space. Sousa (1979) studied algal succession of intertidal cobbblestones and demonstrated this succession of colonizing species. The cobblestones that were most frequently overturned held only a few opportunistic species such as *Ulva*. Where rocks were not disturbed, *Gigartina canaliculata*, a slower growing late succession species, dominated. Green algae are a preferred food source for sea urchins, molluscs and many other herbivores (Valiela, 1995),

so it is also possible that selective grazing on these green algae resulted in their local extinction.

Interestingly, there was an extremely low proportion of red algae grown in culture compared to the relative abundance of this type recorded on both artificial and natural seagrasses. Zechman and Mathieson (1985) found similar results in a study of intertidal algae in New Hampshire, USA. The composition of propagules was dominated by green algae, which was different to the composition of *in situ* populations, dominated by red and brown algae. The low occurrence of red algae may have been due to competition for space and nutrients in culture. If red algal propagules were outcompeted in culture, dead germlings would have been visible under the microscope, however none were observed. A more likely explanation for the lack of red algal propagules relates to their specific reproductive strategies.

The concentration and composition of algal propagules available in the water column at a given point in time is a function of the reproductive periodicity of the species involved, differences in the numbers of propagules produced, and the potential dispersal distance of propagules (Hoffman, 1987). Red algae are generally perennial species and expend less effort in the production of propagules compared to growth effort, hence they produce fewer propagules. Also, red algal propagules are known to sink rapidly, reducing the time suspended in the water column and limiting their dispersal capabilities (Amsler & Searles, 1980). These factors, in conjunction with the likelihood that at the time of sampling not many species were releasing propagules into the water column, would explain the lack of red algae in culture compared to their abundance *in situ*.

To reduce potential competition for nutrients a general enrichment medium was added to the seawater. Green algae and filamentous browns respond favourably to nutrient enrichment (Lord & Hillman, 1995), and this may have been why these species were abundant in culture. However, filamentous brown algae such as *Sphacelaria* and *Hincksia* were common at all locations. So again, it is more likely that the presence of these species in culture is simply a reflection of their

relative abundance *in situ*, coupled with high propagule production, as filamentous browns are also known to produce large numbers of propagules (Reed *et al.*, 1988).

While studies have been conducted on macroalgal propagule availability elsewhere in Australia, there has been no other documented study of propagule availability of seagrass epiphytes, nor of macroalgae in Western Australia. A study of intertidal macroalgal propagule availability by Bellgrove *et al.* (1997) in Boags Rocks, Victoria produced eleven different taxa in culture including *Ceramium* spp, filamentous browns, *Enteromorpha* spp and *Ulva* spp. This compares to fourteen species of algae grown in culture in this experiment, with many of the same genera present.

Only a small proportion of the taxa recorded as adults at the sites were also present as propagules collected from the water column at the time of sampling; 14 grew in culture compared to 68 recruited to artificial seagrass and 59 recorded on natural *P. sinuosa*. It must be remembered that the collection of propagules consisted of a one off sampling event. *In situ*, communities are subjected to a continual rain of propagules from different species at different times, depending on their reproductive strategies and seasonal reproductive phases. This rain is an important factor in determining ultimate community composition, as addressed further in the following section on post-recruitment processes.

4.2 POST RECRUITMENT PROCESSES

The artificial seagrass experiment and sampling of natural epiphyte communities gave an indication of the post-recruitment processes operating to determine community diversity. In both experiments, communities near reefs differed from communities located away from reefs.

Sixty-eight species of epiphyte were recorded from artificial seagrass during this experiment, including early colonising species, such as *Ulva* and *Enteromorpha*, and longer lived perennial species, such as *Ceramium* and *Sphacelaria*. Many of these perennial species were reproductive by the completion of the study, suggesting that the time frame selected (8-10 weeks) was sufficient to allow complex, mature communities to develop.

The number of species recruited to artificial seagrass in this study was high compared to other studies. Epiphyte species richness is highly seasonal (Kendrick & Burt, 1997) and the timing of this study may have coincided with periods of peak species richness. It may also have been the result of sampling two distinct community types; those of seagrass meadows and those associated with reef communities. Exposure time is usually positively correlated with species richness, so the different time frames used for each study may affect results, or it may simply may be reflection of greater species richness of the region compared to other areas studied.

Many of the species found on artificial seagrass in this study were relatively uncommon, with two or three species dominating and the rest present in either low abundances or infrequently. This trend follows distribution patterns typical of most groups of organisms (Magurran, 1988). Encrusting coralline species were common to all habitats in relatively high proportions. Near reef communities were dominated by two filamentous brown species, *Polycerea nigrescens* and *Hincksia mitchelliae*, and these species contributed to a substantial amount of the biomass for near reef sites. Filamentous brown epiphytes also dominated away

from reef communities, though in lower densities, and with different species composition, including *Giraudia robusta*, *Polycerea zostericola and Sphacelaria rigidula*. Articulated coralline algae were conspicuous components of away from reef communities, but were absent from near reef communities.

More taxa were recorded at sites close to reef than at sites distant from reef. However, there was considerable small-scale variation in species richness and no significant difference in mean species richness between habitats. Species richness, however, is a one-dimensional view of community structure, and provides no indication of the type or abundance of species that make up the community. Its use in detecting differences between communities is limited. Examination of community structure, based on species occurrence and abundance, provided a more detailed comparison of diversity and showed that communities near reef and away from reef were different, both for communities recruited to artificial seagrass, and for communities occurring on natural *Posidonia sinuosa*.

Comparisons of the ordinations of propagule culture and artificial seagrasses showed that the differences between assemblages distant from reef and near reef intensified post-recruitment. Distances between habitats increased, and clustering patterns within habitats became tighter, particularly for sites distant from reefs. There are three explanations for this intensification of differences between sites. First, the propagule availability experiment involved measuring a one-off stochastic seeding event, while the artificial seagrass units were exposed to a continual rain of propagules over the 8-10 week period. Assuming that the trend of difference in propagule availability between habitats continued, it would be expected that this would intensify the differences in post-recruitment communities. Secondly, different post-recruitment processes, such as grazing, nutrients and water motion, might explain the different communities which managed to establish on both artificial and natural seagrasses. Finally, it is possible that these processes (ongoing pre-recruitment plus some post-recruitment pressures) acted simultaneously to intensify differences in assemblage structure.

While different communities were shown to occur on natural *P. sinuosa* near reefs and away from reefs, the differences were not as conspicuous as those identified between artificial seagrass communities of each habitat. This weaker trend can be explained by closer examination of the ordination of natural seagrass epiphytes found at each habitat. All samples from Herring Bay near reef clustered with sites which were distant from reef rather than with sites from the same habitat type, and it is possible that this reduced the significance of the differences between epiphyte communities near reef and distant to reef. Herring Bay, as explained earlier, was significantly different in terms of geomorphology compared to other near reef sites.

4.3 CAN PROXIMITY TO REEFS EXPLAIN THE DIFFERENCE IN EPIPHYTE COMMUNITY STRUCTURE AND BIOMASS?

The results of this study can reasonably be interpreted as showing that reefs not only influence the diversity but also the productivity of epiphytes of adjacent seagrasses. Production in marine plants is usually related to the availability of key resources such as light and nutrients, while diversity is related to a host of pre-recruitment and post-recruitment factors such as hydrodynamics, nutrient and light conditions, grazing and sources of propagules. If we are to explain the clear differences in epiphyte communities near to and distant from reefs in terms of some influence of the reef, then it is worth considering how reefs may act to positively influence those factors affecting productivity and diversity. While many of these factors were not explicitly measured in this study, it is possible to speculate on how reefs could influence them in a way conducive to creating higher epiphyte biomass and differences in diversity. These factors will be dealt with in turn in the following sections.

4.3.1 Nutrients

Some studies have shown a positive response between nutrient enrichment and epiphyte biomass (Orth and Van Montrans, 1984; Neckles *et al.*, 1993), although others have not (Paling *et al.*, 1994; Lin *et al.*, 1996). Moreover,

the response is not always clear cut, and other factors such as light, temperature, water motion, leaf turnover, grazing and propagule settlement interact to influence the rate at which epiphytes respond to nutrient enrichment (Paling *et al.*, 1994; Neckles *et al.*, 1993).

Reef algae are highly productive (Valiela, 1995), and the input from decaying reef algae may enhance epiphyte growth in adjacent meadows by providing an additional source of nutrients not available to meadows away from reef. The sites selected for this study were well removed from any potential point source nutrient enrichment, so they should have received similar concentrations of ambient nutrients. The Perth Coastal Waters Study (Lord & Hillman, 1995) determined that the waters in the vicinity of Perth were generally low in nutrients, and even near sewage outfalls benthic plant production was not significantly enhanced. As external sources of nutrients were similar for the region, it is possible that the reefs were providing a natural source of nutrients to adjacent seagrass meadows.

4.3.2 Grazing

Grazing has been implicated in biomass variability. Alcoverro *et al.* (1997), studying the influence of herbivores on *Posidonia oceanica* epiphytes in Spain, showed that epiphyte biomass was controlled primarily by seasonal changes in seagrass shoot size, and secondarily by local environmental changes, the most important of which was herbivory. In this experiment artificial seagrass was used to compare biomass, so shoot size may be discounted as a potential cause of variability. Because of the different habitat that reef provides, and also because seagrass patch size was smaller near reefs, it is possible that different suites of herbivores utilise meadows near reef and away from reef, which in turn may have affected epiphyte biomass and community structure. Selective feeding on particular epiphyte species allows other species to dominate, while the absence of grazing may increase biomass. Grazing on *Posidonia sinuosa* epiphytes by amphipods reduced taxonomic richness by 12%, while the absence of gastropod grazers increased biomass by 44% (Jernakoff & Nielsen, 1997). Clearly then, any

influence of reef on the types of grazers could potentially have significant effects on epiphyte productivity and diversity.

4.3.3 Water Motion

Water motion is also believed to affect epiphyte biomass and community structure. It has been suggested that the proportion of calcifying to non-calcifying species is positively correlated with the degree of disturbance, such as water motion. Phillips, (1996), found articulated coralline species such as *Amphiroa anceps* and *Haliptilon roseum* were more prevalent at high levels of wave energy within Marmion Lagoon. Other studies have noted an increase in the proportion of encrusting coralline species with increased levels of physical disturbance (Westera and Paling; 1994, Dethier, 1994; Kendrick, 1991). In this study, articulated coralline species *Haliptilon roseum* and *Jania minuta* were only found at sites away from reef and there were proportionately more encrusting coralline species away from reef, suggesting that away from reef sites were subjected to stronger water motion.

Generalisations may be made on the different hydrodynamic environments encountered by epiphytes in each habitat. Reefs may serve as a baffle to reduce the effects of current and swell, or alternatively the action of wave pumping may generate large currents in the immediate vicinity of the reefs (Pattiaratchi *et al.*, 1995) depending on reef aspect and the prevailing wind direction. Small-scale hydrodynamics are much more variable on and near reef because of their more complex structure (Sorokin, 1993). This within-site variability in water motion is possibly why on and near reef biomass was much more variable than away from reef biomass. Epiphytes situated away from reef grow in a more uniform hydrodynamic environment. Much of the velocity of wave energy has been dissipated by the offshore reef system by the time it reaches the nearshore environment (Pattiaratchi *et al.*, 1995; Phillips *et al.*, 1997). Epiphytes growing near reef therefore receive different levels of water motion to epiphytes growing away from reef.

Assuming water motion is a factor determining the differences between away from reef and near reef epiphyte communities, the presence of higher biomass near reef suggests that this is a lower energy environment, as water motion increases the physical removal of filamentous and fleshy epiphytes by scouring. Near reef sites had a significantly larger component of filamentous brown algae compared to sites distant from reef, pointing to reduced scouring and hence reduced water motion.

In summary, local scale factors are the most likely causes of differences in biomass and community structure of epiphytes adjacent to reef and distant from reef. These factors include water motion, nutrients and grazing. It is not possible to determine which particular factors are producing the differences between near reef and away from reef communities, however it is probably a combination of factors acting in concert but to varying degrees. It is reasonable to conclude that these factors are influenced by proximity to reef.

Other potential explanations for why away from reef and near reef epiphyte communities were different include, latitudinal/longitudinal differences and the effects of the Leeuwin current, however these can be discounted with respect to this study.

While there is little knowledge of biogeographical variation in marine algae in Australia, the data collected to date suggests that maximum species richness is attained in southern Australia, while the northern part of Australia is relatively species poor (Huisman *et al.*, 1998). Assuming the described gradient of low to high species richness is real and not a function of higher sampling effort in the south, there may have been a latitudinal increase in species richness towards the southern sites of this study. However, the scale over which this biogeographical variation would be expected to operate is far greater than that of this study. Sites were less than 5km of each other, so any latitudinal gradient would not be

apparent at this spatial scale. Also, Parmelia Bank and Carnac Island sites were of similar latitudes.

The Leeuwin current has been shown to have a significant impact on marine fauna, extending the range of tropical species past the limits of their natural southerly distributions (Hutchins, 1991, Hatcher, 1991). This influence however does not generally extend to algal species, with the flora of the southwest being dominated by southern temperate species (Walker, 1991). This is believed to be due to the limited dispersal abilities and relatively short viability of algal propagules. Algal studies of Rottnest Island have shown affinities with temperate southern, rather than tropical taxa, except for the sporadic occurrence of tropical species, which is possibly related to the variable strength of Leeuwin Current (Walker, 1991).

Examination of satellite imagery of the Leeuwin current (Lord & Hillman, 1995) showed that all sites were on the coastal side of the current flow and received similar, relatively low temperatures compared to areas in the path of the current, such as Rottnest Island. Hence the Leeuwin current would be expected to have a minimal effect on epiphyte communities near reef and distant from reef.

4.4 MANAGEMENT IMPLICATIONS

There are a number of environmental management implications based on the outcomes of this study, affecting water quality monitoring, ecosystem health monitoring, restoration of seagrass ecosystems and the selection of marine park reserve areas.

Epiphyte productivity is used extensively as a biological indicator of the negative impacts of nutrient enrichment on marine communities. This study showed that while there was considerable variability within sites, epiphyte biomass was significantly higher on seagrasses near reefs. This concurs with observations of

researchers utilising epiphytes as indicators of nutrient enrichment in the Perth coastal waters, (Hillman *et al.*, 1994, Kinhill, 1996a, 1996b & 1997) who found higher epiphyte biomass in areas near reef which were not correlated with nutrient enrichment. This study confirms the suspicions of these other authors that proximity to reef is confounding monitoring programs and has important ramifications for current monitoring methods. In order to improve the ability of monitoring to detect any real effects of nutrient enrichment, it is necessary to eliminate the confounding effect that reefs have on epiphyte biomass. This may be achieved by either incorporating treatment controls for reef in addition to controls for the effect of nutrient enrichment, or alternatively by improving site selection so distance from reef is similar for each monitoring station.

Epiphyte composition is also used to monitor ecosystem health in Perth coastal waters. The Ocean Reef wastewater outlet discharges into the Marmion Marine Park, and to protect the environmental values of the Park various water quality criteria have been determined. These include a measure of the epiphyte carbonate content as a percentage of dry weight. Between 22-40% indicates a healthy ecosystem, 15-20% a mildly degraded ecosystem, 10-15% a moderately degraded system and <10% a grossly degraded system (Lord & Hillman, 1995). Reduced carbonate content indicates a shift from calcifying species to fleshy and filamentous algae, which is often an indicator of eutrophication. The proportion of calcium carbonate to dry weight in this study varied from between 30-41% for sites near reef to 34-50% for sites distant from reef, suggesting all sites were 'healthy'. However, these data illustrate how proximity to reef can influence calcium carbonate content. At least at the locations used in this study, sites proximate to reef are more likely to have lower proportion of calcifying species, hence the use of these criteria may incorrectly conclude that systems near reef are degraded, when in fact this is probably just a response to different environmental factors.

Some managers have implicated proximity to reef as an important aspect of environmental impact mitigation measures. Restoration of impacted seagrass

meadows involves not only the replacement of seagrasses, but also their associated communities. It has been suggested that artificial reefs may be used to provide a source of algal propagules to regenerate seagrass epiphytes (Cockburn Cement Ltd., 1996). Reefs do provide a source of algal propagules to seagrass meadows, hence artificial reefs may have the potential to aid in seagrass restoration. Mature algal communities will develop on artificial reefs (Ohno *et al.*, 1990). However, the species that colonize are determined by the availability of propagules from other sources. As many species of algae have limited dispersal abilities, the composition of species that colonize reefs to eventually provide a source of propagules to adjacent meadows may differ from those of the original seagrass communities. To speed up colonization rates, increase diversity and facilitate the colonization of species with limited dispersal capabilities, it is recommended that artificial reef development include manual seeding of algae by transplanting a diverse range of reproductive algae from the surrounding region.

The findings of this study are also relevant to marine park management. The Department of Conservation and Land Management (CALM) is currently expanding it's marine park reserve system, and have indicated that it is interested in locating sources of biodiversity to help delineate reserve boundaries (Burt & Anderton, 1997). This study has shown that reefs provide a source of biodiversity to seagrass meadows. Thus, to conserve seagrass epiphyte biodiversity and protect sources of biodiversity for seagrass meadows, both reef and adjacent seagrasses should be included within marine parks and boundaries drawn accordingly.

Seagrass meadows near reefs contain different epiphyte communities to those distant from reef, and has important ramifications in their conservation. The selection of 'representative' areas for marine parks, containing as many elements of biodiversity as possible, has been proposed by the state government (CALM, 1994). If the goal of conservation is to incorporate the full scope of epiphyte biodiversity in these 'representative' areas, both meadows near reef and distant from reef need to be included within the state marine park reserve system.

4.5 SUMMARY

This study found that seagrass meadows near reefs contained different epiphyte assemblages to those distant from reef, and epiphytes near reef had significantly higher levels of biomass. Propagule availability varied with distance from reef, and mature epiphyte communities that developed both on artificial seagrass and on natural *Posidonia sinuosa* were also different, suggesting different pre-recruitment and post-recruitment influences for epiphyte communities near reefs and distant from reefs.

I have concluded that reefs are a likely source of variability in respect to epiphyte diversity and biomass. Reefs can reasonably be expected to produce changes in environmental factors such as water motion, grazing and nutrients, which have been shown to affect epiphyte biomass and diversity. Additionally, reefs provide a source of propagules to seagrass meadows.

These findings have clear implications for the management of marine systems, including monitoring design, conservation of seagrass meadows and the mitigation of environmental impacts

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APPENDIX A

List of Propagules grown in culture

Appendix A. Species list of algae grown in laboratory culture for each habitat (December 1997). Relative abundance is the number of times a species was present in culture samples within that habitat type. Maximum relative abundance = 12.

	Relative Abundance		
	On	**Near**	**Away**
Away from Reef only			
Colpomenia juvenile spp	0	0	1
Near Reef only			
Ceramium macilentum	0	3	0
On Reef only			
Sphacelaria rigidula	2	0	0
Coralline encrusting	1	0	0
Common to Near Reef and Away From Reef			
Unknown *Dasyaceae*	0	1	2
Common to On Reef and Near Reef			
Colpomenia sinuosa	1	1	0
Green filamentous	1	1	0
Ectocarpu s spp	2	1	0
Scytonema sp 1	5	3	0
Common to all 3 habitats			
Sphacelaria juvenile spp	1	4	2
Enteromorpha flexuosa	8	6	4
Enteromorpha paradoxa	9	6	3
Hincksia mitchelliae	9	12	11
Ulva juvenile spp	12	8	8
Total abundance value	**51**	**46**	**31**
Total species richness	**11**	**11**	**7**

APPENDIX B

Epiphytes recorded on artificial seagrass

Appendix B. Species list of epiphytic algae recorded on artificial seagrass across each habitat during the study (November-December 1997). Relative abundance is the number of times a species was recorded on a grid located within that habitat type. Maximum relative abundance = 16.

	Relative Abundance		
	On	Near	Away
Away from Reef only			
Aglaothamnion sp 1	0	0	8
Blue Green single celled colonial	0	0	1
Craspedocarpus venosus	0	0	1
Dasya sp 1	0	0	1
Derbesia sp 1	0	0	1
Jania minuta	0	0	12
Myronemia strangulans	0	0	12
Oscillatoria sp 2	0	0	7
Platysiphonia miniata	0	0	3
Polysiphonia amphibolis	0	0	3
Near Reef only			
Brongniartella sp 1	0	2	0
Cladophora dalmatica	0	2	0
Cladophora sp 1	0	1	0
Dasyclonium sp 1	0	2	0
Sargassum sp 1	0	1	0
Scytosiphon lomentaria	0	1	0
Spyridia filamentosa	0	5	0
On Reef only			
Cladisiphon sp 2	1	0	0
Laurencia sp 3	1	0	0
Polycerea zostericola	3	0	0
Common to Near Reef and Away from Reef			
Anotrichium liemophora	0	1	1
Antithamnion hanowiodes	0	1	4
Dipterosiphonia sp 1	0	2	3
Dipterosiphonia sp 2	0	1	1
Herposiphonia tenella	0	1	3
Laurencia filiformis	0	3	3
Laurencia juvenile spp	0	7	13
Common to On Reef and Away from Reef			
Bornetia binderiana	1	0	1
Cladophora lehmanniana	1	0	1

	Relative Abundance		
Common to On Reef and Near Reef	On	Near	Away
Amphiplexia hymenocladiodes	1	3	0
Anotrichium tenue	3	3	0
Asparagopsis sp 1	3	3	0
Bryopsis australis	1	2	0
Centroceras clavulatum	6	8	0
Champia zostericola	3	6	0
Chondria curdeiana	5	5	0
Cladophora sp 2	1	2	0
Colpomenia sinuosa	13	15	0
Enteromorpha flexuosa	6	1	0
Griffithsia ovalis	1	6	0
Laurencia majuscela	2	2	0
Metagoniolithon steliferum	2	1	0
Polysiphonia forfex	7	4	0
Polysiphonia infestans	1	2	0
Ralfsia verrucosa	1	2	0
Semnocarpa minuta	2	5	0
Stictyosiphon soriferus	4	7	0
Ulva sp 1	1	1	0
Ulva sp 2	6	5	0
Wrangelia plumosa	3	8	0
Common to all 3 habitats			
Callithamnion sp 1	3	4	1
Ceramium isogonum	12	11	2
Ceramium macilentum	3	8	4
Ceramium puberlum	2	6	13
Ceramium rubrum	1	1	4
Champia viridis	4	6	2
Coralline encrusting	16	16	16
Enteromorpha paradoxa	8	7	2
Giraudia robusta	1	4	15
Giraudia sphacelaroides	3	7	1
Haliptilon roseum	2	5	16
Hincksia mitchelliae	14	16	9
Hypnea sp 1	1	3	3
Oscillatoria sp 1	1	5	14
Polycerea nigrescens	15	16	16
Polysiphonia mollis	11	13	2
Sphacelaria rigidula	7	12	16
Stigonema (cf)	3	5	7
Total Abundance Values	**186**	**266**	**212**
Total Species Richness	**44**	**53**	**34**

APPENDIX C

Epiphytes recorded on *Posidonia Sinuosa*

Appendix C. Occurrence and relative abundance of epiphyte species on shoots of natural *Posidonia Sinuosa* for 4 shoots at 4 sites (maximum n =16). Collected October-November 1997.

	Near Reef	Away from Reef
Present Away from Reef only		
Antithamnion hanowiodes	0	1
Callithamnion sp 1	0	1
Cladophora sp 1	0	1
Haliptilon roseum	0	1
Heterosiphonia calothamnii	0	1
Heterosiphonia sp 1	0	1
Jania minuta	0	1
Polysiphonia amphibolis	0	1
red fleshy c.f. *Chondria*	0	1
Scytosiphon lomentaria	0	1
Colpomenia peregrina	0	2
Dictyota sp 1	0	2
Laurencia majuscela	0	2
Spyridia filamentosa	0	3
Dipterosiphonia sp 1	0	4
Giraudia robusta	0	4
Sphacelaria cirrosa	0	4
Laurencia filiformis	0	6
Dasya sp 1	0	7
Ceramium rubrum	0	9
Present Near Reef only		
Amphiplexia hymenocladiodes	1	0
Anotrichium tenue	1	0
Chondria juvenile spp	1	0
Chondria sp 1	1	0
Enteromorpha flexuosa	1	0
Hypnea sp 1	1	0
Ulva sp 1	1	0
Unknown brown uniseriate	1	0
Unknown red	1	0
Chaetomorpha sp 1	2	0
Champia viridis	2	0
Polysiphonia forfex	2	0
Semnocarpa minuta	2	0
Ulva sp 3	2	0
Ceramium isogonum	3	0
Enteromorpha paradoxa	4	0
Polycerea zostericola	4	0
Acrosorium sp 1	5	0
Colpomenia sinuosa	7	0
Hincksia mitchelliae	7	0

Common to Both habitats

	Near Reef	Away from Reef
Bornetia binderiana	1	1
Bryopsis australis	1	1
Chondria curdeiana	1	3
Laurencia juvenile spp	1	3
Asperoccocus bullosus	1	4
Giraudia sphacelaroides	1	5
Aglaothamnion sp 1	1	6
Herposiphonia tenella	1	6
Cladisiphon sp 1	2	1
Cladophora dalmatica	3	1
Polycerea nigrescens	3	1
Anotrichium liemophora	3	11
Polysiphonia mollis	4	1
Sphacelaria rigidula	4	9
Griffithsia ovalis	6	3
Ceramium puberlum	7	8
Centroceras clavulatum	8	3
Ceramium macilentum	9	4
Coralline encrusting	16	16
Total species richness	39	39