Chapter 19

Epiphytes of Seagrasses

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I. Introduction

In all aquatic environments, available surfaces are rapidly colonized by a variety of organisms. If these organisms grow on plants they are called epiphytes. Seagrasses provide an excellent substratum for epiphytic organisms and these organisms are an integral component of seagrass ecosystems. The ecology and physiology of seagrass epiphytes have been reviewed previously (Harlin, 1980; Borowitzka and Lethbridge, 1989) and this chapter focuses primarily on new developments in our understanding of seagrass epiphyte[1] biology and ecology that have occurred since then.

Seagrasses grow in a wide range of habitats ranging from the intertidal to depths of over 50 m (Long et al., 1996), from estuarine to marine environments, and from temperate regions to the tropics. The different seagrass genera also show a diversity of morphologies ranging from the simple subulate leaves of *Syringodium* and the strap-shaped leaves of *Cymodocea*, *Posidonia*, *Thalassia*, and *Zostera*, to species with upright lignified stems with terminal strap-shaped leaf bundles as in *Amphibolis* providing a structurally diverse range of habitats. The above-ground parts of seagrasses provide a temporary, but continuously renewing, substratum for epiphytic organisms. The life-span of the leaves, stems, and rhizomes upon which epiphytic organisms can grow varies between species, habitats and with season and ranges from about 11 days for *Halophila ovalis* leaves to about 130 days for *Posidonia* leaves and over 2 years for stems of *Amphibolis antarctica* (Fig. 1).

II. The Role of the Epiphytic Organisms

A. Primary Producers

The epiphytic algae of seagrasses are important primary producers in seagrass ecosystems and make a significant contribution to food webs. They can account for over 50% of the standing stock in seagrass meadows. In Florida, USA, epiphytic algae contributed 62, 50, and 44% of primary production for *Syringodium filiforme*, *Thalassia testudinum,* and *Halodule wrightii*, respectively (Wear et al., 1999). In Papua New Guinea, Heijs (1984) determined that the epiphytic algae on *T. hemprichii* contribute from 19 to 37% of the total primary production and

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[1] The term *epiphyte* is variously defined in the literature. In this chapter, we define an *epiphyte* as an organism that grows upon plants. *Periphyton* are the microalgae (diatoms, dinoflagellates, juvenile germlings of larger algae, etc.), bacteria, protozoa, etc. on surfaces such as seagrass leaves.

A. W. D. Larkum et al. (eds.), Seagrass Biology, pp. 1–21.

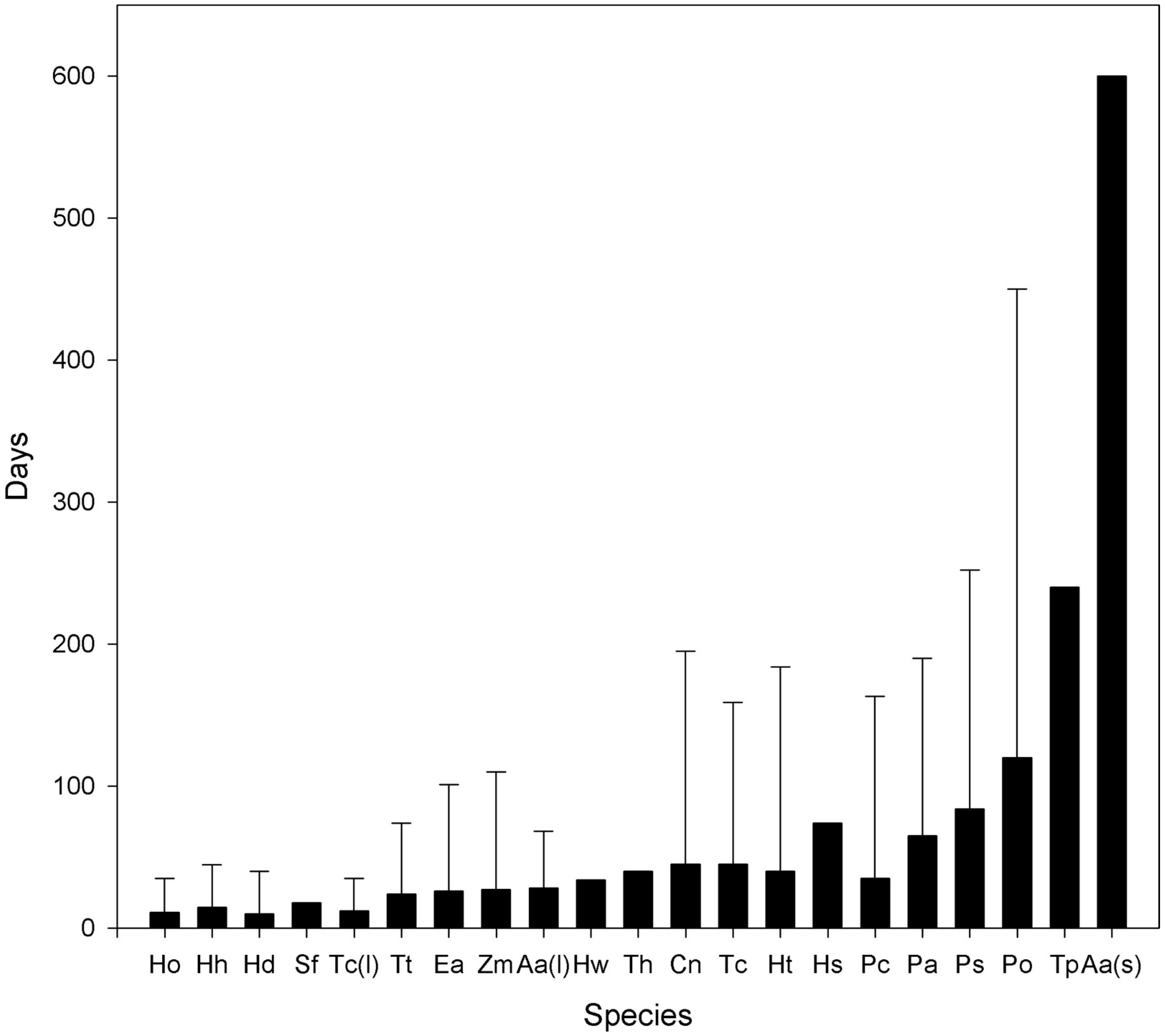

Fig. 1. Minimum and maximum life of seagrass leaves. Separate data for leaves and stems are indicated by (l) and (s), respectively. Aa = *Amphibolis antarctica* (Walker, 1985); Cn = *Cymodocea nodosa* (Reyes et al., 1998); Ea = *Enhalus acaroides* (Johnstone, 1979; Brouns and Heijs, 1986); Ho = *Halophila ovalis* (Hillman, 1987); Hh = *H. hawaiiana* (Herbert, 1986); Hd = *H. decipiens* (Josselyn et al., 1986); Hs = *H. stipulacea* (Wahbeh, 1984); Hw = *Halodule wrightii* (Morgan and Kitting, 1984); Ht = *Heterozostera tasmanica* (Bulthuis and Woelkerling, 1983b); Pa = *Posidonia australis* (West and Larkum, 1979; Silberstein et al., 1986); Pc = *P. coriacea* (Lavery et al., 1999); Po = *P. oceanica* (Ott, 1980; Zupo et al., 1997); Ps = *P. sinuosa* (Walker, 1977; Jernakoff and Nielsen, 1997); Sf = *Syringodium filiforme* (Zieman et al., 1979); Th = *Thalassia hemprichii* (Heijs, 1984); Tt = *T. testudinum* (Patriquin, 1973; Zieman et al., 1979); Tc = *Thalassodendron ciliatum*; Zm = *Zostera marina* (Sfriso and Ghetti, 1998).

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Silberstein et al. (1986) showed that >60% of the total maximum photosynthetic rate of *Posidonia australis* in Cockburn Sound, Western Australia, could be attributed to epiphyte photosynthesis. On the other hand, Brouns and Heijs (1986) estimated that only 2–9% of the total annual mean above-ground production of *Enhalus acaroides* was produced by the epiphytic algae.

B. Sediment Formers

Calcareous red algae are common epiphytes of seagrasses and these contribute to the production of calcareous sediments. Land (1970) produced the first estimate of epiphytic carbonate production and since then there have been several other studies. Estimates range from 1.9 to 282.7 g $CaCO_3$ m^{-2} $year^{-1}$ for

T. testudinum beds in Florida Bay, USA, and these values are equivalent to the carbonate sediment production by other calcareous organisms in this region such as molluscs and the calcareous algae *Halimeda* and *Penicillus* (Frankovich and Zieman, 1994). Even higher rates have been reported for *T. testudinum* epiphytes in Barbados (2800 g $CaCO_3$ m^{-2} $year^{-1}$; Patriquin, 1972), and for *A. antarctica* in Shark Bay, Western Australia (50–526 g $CaCO_3$ m^{-2} $year^{-1}$; Walker and Woelkerling, 1988).

C. N_2-Fixation and Nutrient Cycling

Seagrass ecosystems show high levels of N_2-fixation and this has been attributed mainly to bacteria in the rhizosphere (Welsh, 2000) although cyanobacterial epiphytes on the seagrass leaves can also make a significant contribution in some systems (Goering and Parke, 1972; Iizumi and Yamamuro, 2000; Pereg-Gerk et al., 2002). In most cases, the main N_2-fixing organisms on the leaves are cyanobacteria and it has been estimated that they can supply 4–38% of the nitrogen needed for primary production in *T. testudinum* beds (Capone and Taylor, 1977). This nitrogen may be made available by grazers feeding on the cyanobacteria thus releasing the nitrogen for uptake by the seagrass (Yamamuro, 1999). Pereg et al. (1994) have also suggested that anaerobic photosynthetic bacteria of the Rhodospirillaceae also contribute to N_2-fixation observed on seagrass leaves.

Seagrass epiphytes are also likely to be nutrient ‘sinks’. It has been estimated that the epiphytes of *T. testudinum* are responsible for about 17% of the total NH_4^+ removed from the water column by the whole seagrass meadow (Cornelisen and Thomas, 2002). However, nothing is known of how much epiphytic algae compete with the seagrass for available nutrients and more studies are needed to assess the importance of seagrass epiphytes to nutrient cycling.

III. Distribution and Abundance of Epiphytic Organisms

The epiphytic organisms found on seagrass leaves, stems, and rhizomes generally show distinct patterns in their distribution.

A. Bacteria, Fungi, and Protozoa

Bacteria, fungi, and protozoa are ubiquitous members of the epiphytic community but remain little studied. The bacterial flora of *Zostera marina* has been the object of several studies (Sieburth and Thomas, 1973; Kirchman et al., 1984; Barnabas, 1992). A bacterial film is discernible on new seagrass leaves within 1 h (Novak, 1984) and young leaves of *Z. marina* and *Posidonia oceanica* have a significantly lower bacterial density than older leaves (Kurilenko et al., 2001), with the bacteria most abundant on the leaf tip. On mature leaves this gradient is reversed and bacterial density is highest at the leaf base (Novak, 1984). Wahbeh and Mahasneh (1984) also observed differences in viable counts of heterotrophic bacteria attached to various parts of *Halophila stipulacea*. Maltas and Borowitzka (unpublished results) have also found distinct seasonality in the abundance and diversity of culturable bacteria on the leaves of *P. australis* and *A. antarctica*.

Bacteria found on seagrass leaves include the genera *Vibrio, Alteromonas*, *Moraxella*, *Pseudomonas*, *Marinobacter*, and *Brochothrix* (Maltas and Borowitzka, unpublished, Kurilenko et al., 2001) as well as several nitrogen fixing bacteria (Pereg et al., 1994). New methodologies such as restriction fragment length polymorphism analysis of 16S rRNA genes (Weidner et al., 1996) will provide further important information on the diversity of the prokaryotic epiphytes of seagrasses and their possible roles.

B. Algae

The most abundant and diverse epiphytic organisms on seagrasses are algae. These range from unicellular diatoms and dinoflagellates found on almost all seagrasses (Kita and Harada, 1962; Buia et al., 1996; Jernakoff and Nielsen, 1997; Mazzella, 1999) to large macrophytes such as *Laurencia* spp., *Metagoniolithon stelliferum*, and *Hypnea* spp. found attached to the stems of *Amphibolis* spp. (Lethbridge et al., 1988). Seagrasses are also host to a wide range of other epiphytes including fungi (Belofsky et al., 1999), protozoa (Aladro-Lubel and Martínez-Murillo, 1999; Saraswati, 2002), sponges, bryozoans, hydroids, and ascidians (see later). Other invertebrates such as crustaceans and molluscs live amongst the sessile epiphytic flora and fauna.

With few exceptions, the diversity and biomass of epiphytic algae is highest on the leaves, especially on the oldest leaf and near the leaf apex (Buia et al., 1985; Cullinane et al., 1985; Borum, 1987; Mazzella et al., 1994; Reyes et al., 1998; Trautman and Borowitzka, 1999; Uku and Bjoerk, 2001). This sort of pattern has been reported for most species with strap-like leaves, including *Z. marina*, *Posidonia sinuosa*, *P. australis, P. oceanica*, *Cymodocea rotundata*, *Thalassodendron ciliatum*, and *Thalassia hemprichii*. A similar apico-basal pattern has also been observed in *Syringodium isoetifolium* (Yamamuro, 1999). Some notable exceptions to these generalizations are species of *Amphibolis* and *Thalassodendron*, and *P. oceanica*. In *Amphibolis*, for example, the majority of epiphytic algae occur on the long-lived stem, with relatively few species and significantly lower biomass on the leaves (Borowitzka et al., 1990; Lavery and Vanderklift, 2002). Interestingly, an apico-basal pattern of epiphyte distribution is not observed on some seaweeds such as *Cystoseira* (Belegratis et al., 1999). The rhizomes of seagrasses generally carry a low epiphyte load compared with the leaves, with the exception of *P. oceanica* where greater species richness and higher biomass on the exposed and long-lived rhizomes has been reported (Piazzi and Cinelli, 2000). The low abundance of epiphytes on rhizomes is probably due to the fact that the rhizomes of almost all seagrasses are buried most of the time.

There are few truly comparative studies of the epiphyte assemblages on different seagrasses (but see Pinckney and Micheli, 1998; Trautman and Borowitzka, 1999; Wear et al., 1999; Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002). In contrast, there are a large number of studies on the biomass and composition of epiphyte assemblages on single seagrass species, usually related to questions about the effect of environmental factors on these assemblages. Comparisons across species are often, therefore, gleaned from the literature. However, this is fraught with difficulty as the studies are performed over different time scales and, as this chapter will show, time scale is a crucial source of variability in epiphyte assemblages.

While we might expect differences in patterns of distribution between seagrasses with markedly different morphologies, subtle differences in morphology can also have significant effects on epiphyte assemblages. For example, *P. sinuosa* and *P. australis* are morphologically similar seagrasses with strap-like leaves; the leaf of *P. sinuosa* is narrower and is concave in transverse section unlike *P. australis,* which is wider and flat. Trautman and Borowitzka (1999) found that the epiphyte assemblage on *P. sinuosa* leaves differed between the two leaf sides, with greater species richness and biomass on the convex surface, including some species restricted to only that side; no differences in species richness or abundance of epiphytes were noted between adaxial and abaxial sides of leaves on *P. australis*. Similar observations were made in respect to epiphytic invertebrates (see below).

Seagrasses with distinct morphological differentiation tend to provide several distinct microhabitats for epiphytes and there are reports of epiphytic algae that are confined to particular plant parts. In *Amphibolis*, for example, few species of epiphyte are common to both stem and leaf, with most on the stem and some showing specificity to a particular part of the stem (Lethbridge et al., 1988; Borowitzka et al., 1990). This within-plant spatial specificity of epiphytes is not confined to seagrass species with long-lived stems. Cullinane et al. (1985) found a similar pattern on *Z. marina*, except that some taxa were confined to different parts of the leaf/sheath structure. In the Mediterranean, Piazzi and Cinelli (2000) noted distinct leaf and rhizome assemblages on *P. oceanica*, with 28 leaf taxa (dominated by encrusting coralline algae and brown algae species) but 56 species on the rhizome (dominated by filamentous Rhodophyta—*Acrothamnion*, *Womersleyella*, and the crustose *Peyssonnelia*); only 13 taxa were common to both niches. Borowitzka et al. (1990) also observed distinct fine-scale patterns in the distribution of epiphytic algae; on *A. griffithii* leaves, for example, plants of the green alga *Bryopsis plumosa* were usually found only on the leaf tips whereas the rhodophyte *Ceramium puberulum* was most common at the base of the leaves near the leaf junctions. These observations suggest that even small differences in turnover rates of plant parts as well as localized variation in hydrodynamics can provide sufficient habitat differentiation to result in distinct epiphytic algal assemblages.

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The composition of the assemblages of epiphytic algae includes taxa from all the major algal phyla. Generally, red algae dominate the composition and biomass and diatoms are almost ubiquitous. This dominance by rhodophytes reflects the dominance of this phylum in the surrounding environment.

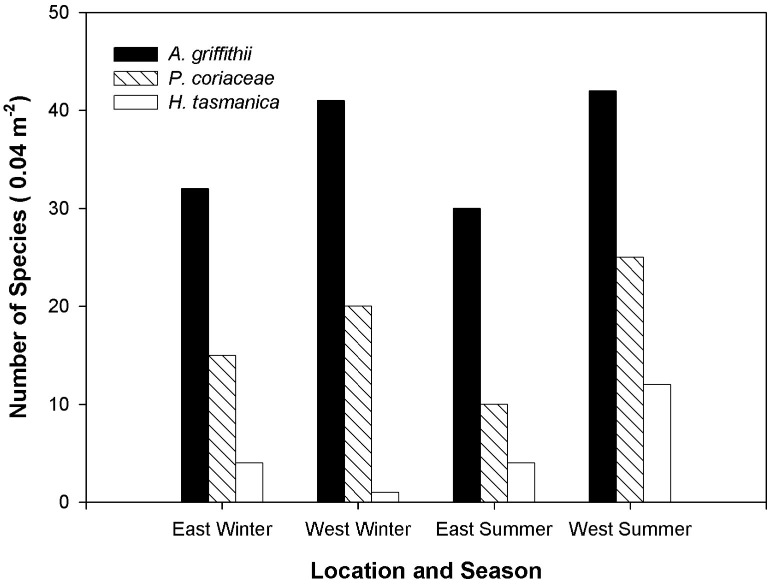

Fig. 2. The mean number of epiphytic algal species present on three seagrasses of differing structural complexity and longevity (*Amphibolis griffithii*, *Posidonia coriacea,* and *Heterozostera tasmanica*) located in the same general location off Perth, Western Australia, at two sites (east and west) and at the same sampling times. Data are means of six 0.04 m^{-2} quadrats (unpublished data).

Where other phyla dominate the seagrass epiphyte flora, there is an implication of unusual environmental conditions, such as nutrient enrichment resulting in an abundance of green algae or cyanobacteria (Coleman and Burkholder, 1994; Ierodiaconou and Laurenson, 2002) or changes in energy levels and depth resulting in shifts between diatoms and cyanobacteria (Pinckney and Micheli, 1998). Consequently, most reports of cyanobacterial or green algal domination suggest these are either transient, or regular but seasonal, coinciding with seasonal nutrient inputs. Alternatively, they are from estuarine seagrass habitats.

The number of species of epiphytic algae found on different seagrass species varies considerably. It should be noted, however, that most studies of the algal epiphytes of seagrasses focus only on the multicellular algae and not the unicells forming part of the periphyton. Unfortunately, there are almost no studies of the diversity and community dynamics of the algal component of the periphyton. However, as Jernakoff and Nielsen (1997) have shown, this community can be very diverse. They found a total of 70 taxa on the leaves of *P. sinuosa* consisting of 62 diatoms, 4 cyanobacteria, 2 dinoflagellates, 1 green alga, and a coralline red alga germling. Similarly, Mazzella et al., have observed a total of 56 species of diatoms, especially members of the Naviculariaceae, on leaves of *P. oceanica* in the Gulf of Naples.

As a very general rule, the more persistent and structurally complex seagrass species tend to have a greater epiphyte biomass as well as more diverse epiphyte assemblages. However, this generalization is based on a range of studies in different locations and over different time scales, so that the very rich assemblages tend to be recorded over more than one annual cycle. At any one point in time, there are considerably fewer taxa present on the seagrass. For example, Borowitzka et al. (1990) recorded over 150 species of epiphytic macroalgae on *A. griffithii* over the 4 year length of their study at several sites in Western Australia, but only up to 47 at any one time and place. Where seagrass species occur in the same region, it is generally accepted that short-lived seagrass species are likely to be relatively depauperate in epiphyte species richness and biomass compared to persistent seagrass species. For example, *A. griffithii* (highly persistent), *P. coriacea* (persistent), and *Heterozostera tasmanica* (short-lived) co-occur on sand banks in SW Australia and have been found to support about 90, 60, and 34 species, respectively, over an annual cycle. This same pattern is observed at any one sampling time and sampling region and is even maintained where *P. coriacea* and *H. tasmanica* co-exist in mixed meadows (Fig. 2).

Rindi et al. (1999) found 20 species of algae epiphytic on *H. stipulacea* leaves in the Mediterranean and considered this ‘remarkably’ scarce compared to *P. oceanica* which has been reported as having up to 90 epiphytic taxa. However, Rindi et al.’s (1999) study was a single sampling occasion and they note that *P. oceanica* sampled at the same time and over a similar depth range at the same time (but a different location) yielded only 38 taxa, comparable to *H. stipulacea*. Alongi et al. (1993), on the other hand, recorded 30 species of epiphytic algae on *H. stipulacea* at a different site in winter. This suggests that while generic models relating epiphyte diversity to seagrass persistence may hold overall, many other site-specific and seasonal factors interact to confound this relationship.

A few studies have assessed macroalgal epiphytes at the functional group level, using Littler and Littler’s (1980) functional groupings. The number of studies is too limited to allow generalizations to be drawn. These studies also do not test which specific functions are of importance making generalizations difficult (cf. Padilla and Allen, 2000). However, the results suggest that patterns found in distribution and abundance of epiphytic algal species may be paralleled, to some extent, in functional groupings, suggesting that the spatial and temporal patterns in epiphytes species assemblages may have functional implications. For example, Saunders et al. (2003) showed that filamentous, corticated filamentous, and coralline functional groups accounted for 99% of epiphyte biomass on *Z. marina*, but that there were significant differences in the abundances of these functional groups among different seagrass beds. Lavery and Vanderklift (2002; and Fig. 3) have compared the functional grouping of epiphytes on two morphologically distinct seagrasses *A. griffithii* and *P. coriacea*. While there were significant differences in the species composition and abundance of epiphytes on the two seagrasses, each supported assemblages that contained a wide range of functional groups. Further, there were distinct regional differences in the abundance of different functional groups, and these patterns mimicked species-level patterns.

Similarly, Bandeira (2002) showed significant between-site differences in the assemblages of epiphytes on *T. ciliatum* stems; in this case only articulated coralline algae occurred at a sandy site but elsewhere articulated coralline, encrusting, corticated filamentous, corticated foliose, and leathery algae were present.

Few studies have examined the variability in composition of epiphytes across spatial scales larger than within plants, despite recognition that the spatial scale is likely to influence the difference between assemblages (Fonseca, 1996). Most information on larger-scale spatial variability has been obtained incidentally, while studying the effects of nutrients or other environmental factors (e.g. Frankovich and Fourquean, 1997; Kendrick and Burt, 1997; Pinckney and Micheli, 1998). However, several recent studies have explicitly examined spatial variation at different scales (Kendrick and Burt, 1997; Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002; Saunders et al., 2003). These studies generally show an increase in dissimilarity of epiphyte assemblages with increasing distance apart. Significant differences occur in assemblages on *P. sinuosa* separated by kilometers on the same shallow coastal bank and across a gradient of wave exposure (Kendrick and Burt, 1997); filamentous browns and reds and cyanobacteria dominated the more inshore site, while articulated and encrusting coralline algae dominated the offshore site. Further, within the filamentous rhodophytes that occurred at each site there were differences; the inshore site was dominated by Rhodomelaceae and the offshore site by Ceramiaceae. Frankovich and Fourqurean (1997) examined epiphyte assemblages across a nutrient gradient and found composition shifts, though these tend to occur rapidly and close to the nutrient source. Bandeira (2002) also observed a great difference in epiphytes in *T. ciliatum* growing on either rocky substrata or sandy substrata at Ithaca Island, Mozambique. He found that the communities at the rocky sites had a diverse epiphytic flora whereas at the sandy site epiphytes were restricted almost completely to the coralline *Jania adhaerens* growing on the stems of the seagrass.

A small number of studies have attempted to look at spatial patterns in epiphytes that are independent of obvious environmental gradients. Trends across different species appear similar but with some subtle differences. In *Z. marina*, a seagrass of relatively simple structural complexity, epiphyte assemblages showed no differences in composition or abundance at the scales of less than 10 m, but highly significant differences at the kilometer scale (Saunders et al., 2003). Similar observations were made by

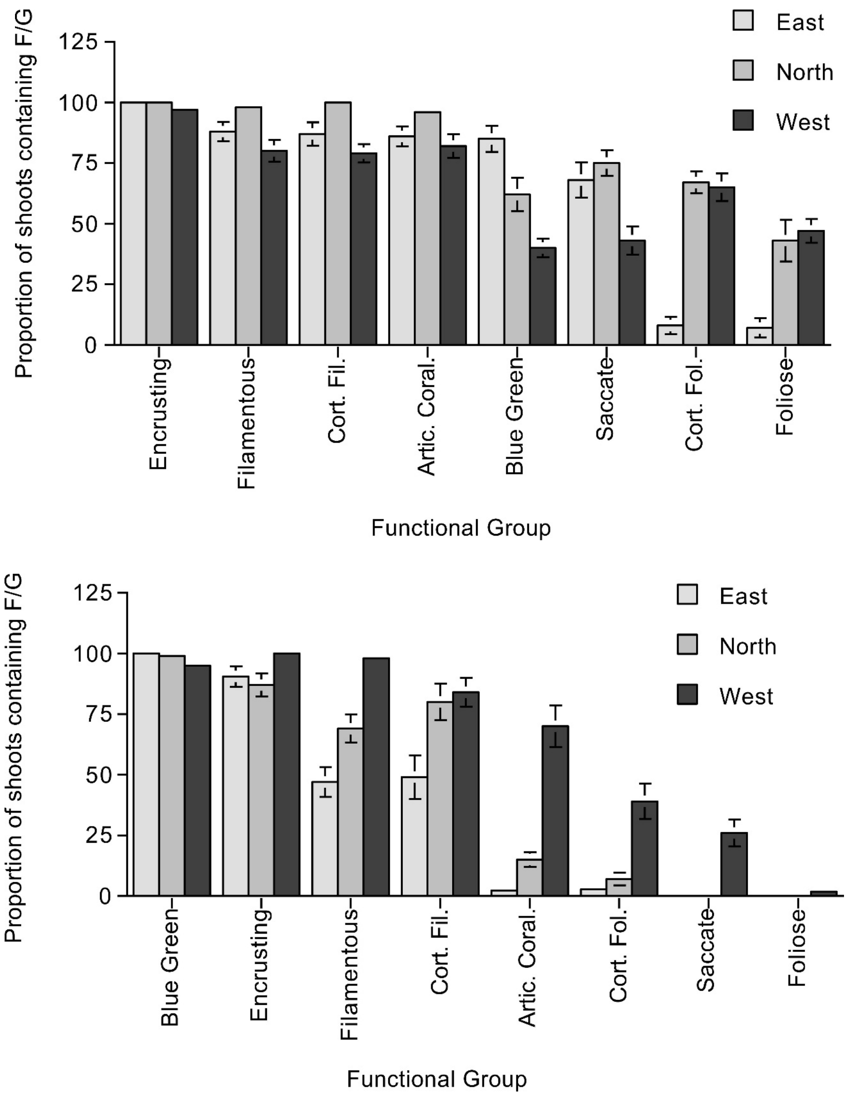

Fig. 3. The proportion of shoots of *Amphibolis griffithii* (top) and *Posidonia coriacea* (bottom) on which different functional groups of epiphytic macroalgae were observed in three different regions separated by 2–3 km (east, west, and north) off Perth, Western Australia. (Data are means ± s.d., $n = 6$).

Cullinane et al. (1985) also working on *Z. marina*; differences in composition were found at the scale of tens of kilometers, with only one species common to six sites separated at this scale. The composition of epiphytes has also been examined on the structurally complex seagrasses *A. griffithii* and *P. coriacea* at scales of tens, hundreds, and thousands of meters (Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002). As with *Z. marina*, there were no differences at very small scales (1 m or less) but, in contrast, differences were apparent at scales as low as one to tens of meters. In *P. coriacea*, where leaf turnover is in the order of 50–100 days, there was a linear increase in dissimilarity of assemblages with distance apart but in *A. griffithii*, with long-lived stems up to 2 years old, the differences in assemblages increased almost exponentially with increasing distance apart. This was attributed to interactions of seagrass and algal life-history timescales. These studies of structurally diverse seagrass species indicate that assemblage structure of epiphytes are likely to be variable between sites separated by as little

Table 1. Relationship between epiphyte biomass and the phenology of the seagrass.

Species	Functional group	Epiphyte biomass ($g\ m^{-2}$)	Epiphyte biomass ($g\ g^{-1}$)	% of above-ground biomass
Western Australia (Lavery, unpublished results)				
Amphibolis griffithii	Persistent; Structurally complex; Slow stem turnover	50–450	0.56	36
Posidonia coriacea	Persistent; Structurally simple; Slow leaf turnover	1–45	0.16	14
Heterozostera tasmanica	Short-lived; Structurally simple; Rapid turnover	0.1–8	0.02	2.3
Florida, USA (Wear et al., 1999)				
Thalassia testudinum	Persistent; Structurally complex; Slow stem turnover	40–125	0.44	31
Syringodium filiforme	Intermediate persistence and turnover; Structurally simple	60–100	0.58	37
Halodule wrightii	Short-lived; Structurally simple; Fast turnover	20–110	0.78	44

as tens of meters and that these differences will be more pronounced as the spatial scale increases. Furthermore, it appears that these differences hold not only at species level but also at the functional group level (Vanderklift and Lavery, 2000; Saunders et al., 2003; Fig. 3). This implies that the differences have the potential to affect the ecological function of the epiphyte assemblages, and therefore the functional attributes of the seagrass habitats separated at these scales.

Epiphyte community structure and biomass also vary over depth for a wide range of seagrasses. Meadows of the Mediterranean seagrass *P. oceanica* supported a more diverse assemblage at shallow sites, but by 30 m depth there were no epiphytic algae. The relative abundance of rhodophytes increased with depth while phaeophyte abundance decreased (Cinelli et al., 1984; Lepoint et al., 1999). These observations both confirm and contrast those of Rindi et al. (1999) who compared the epiphyte composition of the short-lived Mediterranean seagrass *H. stipulacea* at shallow (5 m) and deep (15–25 m) sites and also found compositional shifts over depth. Shifts in composition of *Z. marina* and *H. wrightii* epiphyte assemblages from diatom to cyanobacteria were attributed partially to depth (Pinckney and Micheli, 1998) and effects of depth were observed for more ephemeral seagrass species (*H. tasmanica*, *Zostera muelleri*, and *Ruppia megacarpa*) over a shallow depth range (0–2 m). Epiphyte biomass at 0–0.5 and 0.5–1.0 m, and on a m^{-2} basis, was about 70% higher than at 1.0–1.9 m. When normalized to leaf biomass, the trend is even more dramatic since seagrass biomass was higher at depth. However, there did appear to be a depth by site interaction in this study, suggesting that effects of depth could be over-ridden by other factors.

There are few truly comparative studies of epiphytic algal biomass. Two specific comparative studies have been undertaken, comparing seagrass species with differing morphologies and timescales of persistence (Table 1). One of these compared *A. griffithii*, *P. coriacea*, and *H. tasmanica* which co-occur in Western Australia. Epiphyte biomass in the three seagrasses was highly variable, but was clearly greater in the more persistent and complex species *A. griffithii*, both on an area basis and per gram of seagrass. In another study, Wear et al. (1999) sampled *T. testudinum*, *S. filiforme*, and *H. wrightii*, which also cover a range of seagrass functional types from structurally complex and persistent to simple and ephemeral. In this case, total biomass, expressed per m^2 was comparable on an areal basis, but normalized to seagrass biomass showed the opposite trend to that observed in the Australian study, with the simpler and ephemeral species, *H. wrightii*, having the greater biomass per gram of seagrass. On the basis of these two data sets, it is clear that relative epiphyte biomass does not seem to follow a predictable pattern between seagrass species.

Table 2. Contribution of epiphytic algae to total above-ground biomass as a percentage of seagrass + epiphytes in different seagrass meadows.

Seagrass	Range (%)	Source
Posidonia sinuosa	0–16	McMahon et al. (1997)
	10–32	Kirkman and Manning (1993)
Posidonia coriacea	0.3–42	Unpublished
Thalassia hemprichii	29–42	Moncreiff et al. (1992)
	9	Jagtap (1998)
Thalassia testudinum	31–44	Wear et al. (1999)
Amphibolis griffithii	7–75	Unpublished
Amphibolis antarctica	41–47	Kirkman and Manning (1993)
Syringodium isoetifolium	31	Heijs (1985b)
	29–95	Mukai and Ishijima (1995)
Syringodium filiformis	37–41	Wear et al. (1999)
Cymodocea rotundata	44	Heijs (1985b)
Cymodocea serrulate	53	Heijs (1985b)
Heterozostera tasmanica	0–8.2	Unpublished
Zostera marina	1–36	Moncreiff et al. (1992)
Halodule uninervis	49	Heijs (1985b)
Halodule wrightii	19–68	Moncreiff et al. (1992)
Halodule wrightii	44–52	Wear et al. (1999)
Thalassodendron ciliatum	68.5	Bandeira (2002)
Heterozostera tasmanica/Zostera marina/Ruppia megacarpa	49.5	Ierodiaconou and Laurenson (2002)

Epiphytic algae have been shown to contribute to more than 30% of the total above-ground biomass in many seagrass ecosystems (Table 2). Published biomass data must, however, be interpreted with some caution; some authors determine total biomass (dry weight) that includes the $CaCO_3$ of the calcareous epiphytes rather than ash-free dry weight and this inflates the overall biomass figure. The $CaCO_3$ of the coralline algae can account for 40–60% of the total dry weight (Borowitzka et al., 1990; Bandeira, 1997). Epiphyte biomass often represents a significant proportion of the primary producer biomass and it is generally accepted that the epiphytic material is more likely to be consumed by grazers and detritivores than seagrass material.

C. Invertebrates

In comparison to epiphytic macroalgae, there are markedly fewer studies of the distribution and abundance of epiphytic macroinvertebrates. Unlike algal epiphytes where there is no clear evidence that any of the algae are obligate seagrass epiphytes, there are several reports of obligate invertebrate epiphytes of seagrasses (e.g. Hughes et al., 1991a). As with epiphytic algae, there are distinct spatial patterns within plants, such as between the stems and leaves on species of *Amphibolis* spp. (Borowitzka et al., 1990; Edgar and Robertson, 1992) and along leaves in other species such as *P. oceanica* (Casola et al., 1987). There is a general inverse relationship between the abundance of epiphytic invertebrates and algae, with the algae more abundant near the plant apex, whereas the invertebrates are most abundant on the lower parts of the plant leaves or stems. Bryozoans, hydroids, and ascidians tend to be more common as epiphytes on seagrasses with long-lived parts, such as *Amphibolis* spp. or the rhizomes of *P. oceanica* (Colmenero and Lizaso, 1999). On *P. sinuosa* and *P. australis* leaves, hydrozoans were more abundant on the lower part of leaves, other taxa showed no strong trend in distribution along leaves (species of bryozoa, porifera, and foraminifera) and a of spirorbid polychaete was more abundant near the apex (Trautman and Borowitzka, 1999). A similar distributional pattern was observed on *Z. marina* leaves (Nagle, 1968). In addition, some epiphytic invertebrates, as with algae, showed a preference for the concave side of *P. sinuosa* leaves, including a species of porifera, and a hydrozoan. The reasons for these spatial patterns are not clear, but may be related, in some cases, to hydrodynamics around the leaf surface (Trautman and Borowitzka, 1999).

Substratum availability is not the sole determinant of epiphytic invertebrate abundance. The density of tunicates on *Z. marina* is influenced by the particular species of amphipod grazers on seagrasses (Duffy and Harvilicz, 2001). Light availability also has been suggested as a factor negatively influencing the abundance of epiphytic invertebrates. For example, *P. oceanica* assemblages tend to be dominated by epiphytic algae at shallow depth (10 m) but in deeper waters (20–30 m) epiphytic invertebrates dominate, with their contribution to biomass increasing from about one-third to $>50\%$ of the total epiphytic biomass (Lepoint et al., 1999).

The motile epifauna has received much more attention than the attached epiphytic invertebrates. Jernakoff et al. (1996) have reviewed the literature comparing the motile epifauna between different types of seagrass and concluded that there were few differences in the composition of motile epiphytic grazers that could be clearly related to the form of the seagrass host, though there were differences in the abundances. Within a species of seagrass host, density of the seagrass does appear to affect motile epifaunal abundance; for example, Edgar and Robertson (1992) noted that more open stands of *Amphibolis* spp. were relatively depauperate in epiphytic fauna compared with dense stands.

The abundance and distribution of epiphytic macroinvertebrate grazers is strongly influenced by the abundance and distribution of the epiphytic algae or periphyton on which they graze (Bologna and Heck, 1999; Fong et al., 2000). The density of grazers is a function of both seagrass habitat structure and the trophic attraction of the habitat. The relative importance of these two factors appears variable, with different studies weighting each factor differently. Artificial seagrass has been used to examine the relative roles of these two factors and showed that heterogeneity of a habitat was not, alone, the major determinant of epiphytic grazer biomass; trophic attractiveness of the habitat appears to be more important (Bologna and Heck, 1999; Boström and Mattila, 1999). However, it seems that different grazers respond to different factors and a comparison of fauna on *A. griffithii* and *P. sinuosa* found that the abundance of amphipod and gastropod grazers correlated with food availability on *P. sinuosa* and with the biomass of leaves on *A. griffithii*, suggesting that in *A. griffithii* provision of cover was more important (Jernakoff and Nielsen, 1998).

IV. Factors Affecting Distribution and Abundance

The observed diversity, distribution, and abundance of epiphytic organisms on seagrasses are the result of the interaction of a number of factors and processes. A fundamental determinant of potential epiphyte diversity is the availability of propagules to colonize any available seagrass substrata. In order to try to understand the settlement of epiphytic algae and invertebrates one also needs to consider some basic aspects of the reproduction of these organisms. The propagules of red and brown algae as well as diatoms are non-motile and are wholly at the mercy of hydrodynamics. On the other hand, the propagules of green algae such as *Ulva* and *Enteromorpha* and the larvae of invertebrates are motile and therefore can be expected to be able to show greater selectivity as to the site of settlement. Actual settling and attachment to this substratum will be dependent mainly on localized hydrodynamics. Successful recruitment and growth will be a function of light, temperature, nutrients, grazing, and predation as well as other interactions of the organisms with other organisms and their environment. The overall development of the epiphyte community will be limited by the longevity of the seagrass substratum.

A. Succession and Seasonality

The process of colonization of a new seagrass leaf is easily seen by comparing differently aged leaves in a leaf bundle on seagrasses such as *Posidonia*. The earliest colonizers are bacteria and diatoms forming a biofilm, which can be observed on even the youngest leaves (Novak, 1984; Sterrenburg et al., 1995). This is soon followed by a range of algae, especially crustose coralline algae, as well as hydrozoans and bryozoans. In general, organisms once settled and established persist throughout the lifespan of their substratum, the leaf. Settlement is generally greatest at the edge of leaves and near the leaf apex probably because of the higher turbulence in this region which favors the chance of propagules coming in contact with the leaf surface so that they can attach successfully (Jacobs et al., 1983; Trautman and Borowitzka, 1999). Early studies suggested that certain algae such as *Smithora naiadum* and *M. stelliferum* were host specific to particular seagrasses (e.g. Harlin, 1973; Ducker and Knox, 1978).

However, further field observations and studies using artificial seagrasses have shown this not to be the case (Harlin, 1973; Lethbridge et al., 1988). The biofilm which forms on the leaves may, however, be an important factor for the settlement of other organisms, especially invertebrates (Wahl, 1989). The prokaryotic biofilms that are a ubiquitous feature of all surfaces in aquatic environments are complex communities (Stoodley et al., 2002) and this complexity can be seen clearly in published micrographs of seagrass microfilms (e.g. Novak, 1984; Mazzella, 1999). There are many non-seagrass examples showing that marine bacterial and diatom biofilms attract or inhibit settlement and metamorphosis of invertebrate larvae (e.g. Wieczorek and Todd, 1998; Daume et al., 1999; Harder et al., 2002; Steinberg et al., 2002) and the role of such biofilms in structuring the communities of epiphytic invertebrates on seagrass leaves deserves attention.

There appears to be no clear successional pattern in the colonization by macrophytes or invertebrates, rather additional new species recruit to the seagrass over time mainly as a function of propagule availability and local hydrodynamics, leading to increased species richness as the seagrass leaf or stem ages (Bulthuis and Woelkerling, 1983a; Heijs, 1985a,b; Borowitzka et al., 1990). The importance of the availability of propagules is illustrated by the study of Lethbridge et al. (1988) using artificial *Amphibolis*-like seagrasses. They also observed that some algal epiphytes colonized directly by the attachment of larger detached thallus fragments rather than from spores. For example, the hook-like branch tips of the rhodophyte, *Hypnea episcopalis*, entangle with the stems of *Amphibolis* and then form new attachments within a few hours. Similar attachment structures have been observed in *Polysiphonia forfex*, *Dicranema revolutum*, and other algae.

The apico-basal distribution of epiphytic algae observed on the strap-like leaves of seagrasses such as *Posidonia*, *Zostera*, and *Cymodocea* are unlikely to be the result of changes in surface chemistry of the leaves as suggested by Harrison and Durance (1985), but rather are a function of localized differences in turbulence, since exactly the same pattern of settlement is observed on artificial leaves made of plastic tape (Horner, 1987; Trautman and Borowitzka, 1999). Some invertebrates, however, show preferential settlement on to particular parts of the seagrass. For example, the density of newly settled larvae of the spirorbid polychaete *Neodexiospira brasiliensis* were more abundant on the basal part of the leaves of both *Zostera* and *Phyllospadix* (Hamamoto and Mukai, 1999) and this may be the result of a distinct preference for shaded substrata (Saunders and Connell, 2001). On the other hand, the hydroids *Clytia edwardsi* and *Tubularia mesembryantheum* initially settle near the leaf apex of *Z. marina*. *Tubularia* then spread to the lower leaf surface via actinula larvae (Nishihara, 1968). Similarly, the hydroid *Sertularia perpusilla*, an obligate epiphyte of *P. oceanica*, grows downwards on the leaves maximizing the residence time on the leaf and facilitating transfer of hydroids to the short young leaves by stolonization, a method of asexual reproduction (Hughes et al., 1991a,b).

The few long-term studies of seagrass epiphytes show distinct seasonality in both species composition and abundance (e.g. Heijs, 1984; Alcoverro et al., 1997; Reyes et al., 1998; Lepoint et al., 1999; Wear et al., 1999); however, most of these studies are only for a 12-month-period and they therefore provide no information on interannual variation. This seasonality in abundance and diversity appears to be a function of substratum availability (i.e. new seagrass surfaces), substratum stability (i.e. life-time of the seagrass leaf or stem which changes over the year), availability of larvae and propagules of the potential epiphyte, and environmental conditions favoring the growth of the epiphytes. Not surprisingly seagrass epiphytes can be classified into groups based on their seasonal distribution: (a) epiphytes occurring throughout the year, (b) epiphytes with a distinct seasonal pattern in their occurrence, and (c) transient colonizers (Heijs, 1985a). The percent cover and biomass of the epiphytes also shows seasonal variation; however, a distinct pattern is more difficult to determine because the temporal scale of sampling (monthly or quarterly) in many studies is often not well matched to the scale of epiphyte and seagrass leaf turnover.

It has been hypothesized that differences in seagrass growth rate can account for differences in the spatial patterns of epiphyte diversity within seagrass species. A comparison of *A. griffithii* and *P. coriacea* revealed different relationships between epiphyte diversity and the distance apart of the seagrass meadows (Lavery and Vanderklift, 2002). In *A. griffithii* meadows, there was an almost exponential increase in differences between assemblages as distance between sites increased, whereas in *P. coriacea* meadows differences among samples separated by tens or hundreds meters apart were relatively small. This can be explained in terms of the interaction between the lifespan of the host and the reproductive lifespan of the epiphytes (cf. Reyes and Sansón, 1997). Where the host is long-lived, as for *A. griffithii*, local recruitment from existing epiphytes with fast reproductive strategies can continually reinforce the local composition. While this occurs in *P. coriacea*, its faster rate of leaf turnover rate results in a reduction in the influence of the local recruitment but an increase in the relative importance of regional recruitment. The result is less dissimilarity among distant *P. coriacea* assemblages compared to *A. griffithii*.

B. The Physical Environment

1. Light and Temperature

Light clearly has a key influence on the distribution and abundance of algal epiphytes. The widely observed apico-basal distribution of epiphytes on seagrasses largely appears to be determined mainly by the light regime: algal epiphytes can out-compete animal epiphytes near the plant apex where there is more light, and vice versa where there is less light. On a more subtle scale, the distribution on different sides of a leaf as observed in *P. sinuosa* (Trautman and Borowitzka, 1999) may also be determined in part by the light regime, with higher abundances of algal epiphytes recorded on the side that receives more light. On a larger scale, the position of a plant within a meadow or patch can influence the light penetrating the canopy, and hence the epiphyte load observed on it. Edge effects on irradiance penetration into patches of seagrass may play a role in determining epiphyte load and distribution. Carruthers (1994) showed that epiphyte biomass in *Amphibolis* meadows was significantly greater at 50% canopy density than at 100%, suggesting that additional light may play a significant role in determining epiphyte load. However, no edge effects in epiphyte biomass were observed by Saunders et al. (2003) in *Z. marina* beds in Plymouth Sound and this may be a function of the much smaller size and lesser structural complexity of *Zostera* compared to *Amphibolis* as well as the lack of a true, well developed ‘canopy’, which means that there is no marked light gradient. The effect of light availability on epiphyte abundance can also be seen in studies of seagrass epiphytes over a depth gradient (e.g. Buia et al., 1992; Jagtap, 1998; Lepoint et al., 1999).

Not surprisingly, light intensity affects the growth rate of epiphytic algae (e.g. Lewis et al., 2002); however, epiphyte cover also affects seagrass photosynthesis. Dixon (1999) examined the role of epiphytic growth on attenuating light available to leaves of *T. testudinum* and concluded that epiphyte growth attenuated some 33% of PAR at depth. Drake et al. (2003) also observed that epiphytes did not act merely as neutral density filters, but preferentially absorbed light in the blue and red regions thus competing for photons with the underlying leaves. Gallegos et al. (1991) distinguished PUR (photosynthetically useable radiation) from PAR (photosynthetically available radiation), to emphasize the role of epiphytic growth and phytoplankton in the water column in attenuating particular wavelengths of light available to seagrass leaves. Neckles (1993) examined the spectral influence of the epiphyte matrix on attenuated light and concluded that epiphytic growth attenuated light across a broad spectrum. A recent study by Brush and Nixon (2002) showed that epiphytic algae rapidly attenuated light, but that at higher epiphyte densities this attenuation leveled off to a relatively constant value as the epiphytes floated out from the edges of the seagrass blade. They also observed that red algal epiphytes (e.g. *Polysiphonia* sp.) attenuated light faster than green algal epiphytes (e.g. *Cladophora* sp.) highlighting the importance of the morphology of the epiphytic algae. Encrusting algae such as the coralline algae also reduce light more than erect filamentous species (Bulthuis and Woelkerling, 1983a; Cebrian et al., 1999).

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Temperature will also exert a significant effect on the growth of epiphytic organisms and for algae temperature effects would be expected to interact strongly with light availability. There have been no explicit studies of the effect of temperature on seagrass epiphytes; however, there is indirect evidence from seasonal studies which show that epiphyte biomass increases with increasing light and temperature (e.g. Alcoverro et al., 1997; Lepoint et al., 1999; Toyohara et al., 1999). Other factors, such as nutrient availability, however, will interact with these effects. For example, Jacobs et al. (1983) and Borum (1985) demonstrated that epiphytic algal abundance could be either maximal or minimal in summer depending on the degree of nutrient enrichment in the water body.

2. Water Motion

Water motion influences almost every aspect of epiphyte growth (see also Chapter 8). Unfortunately, the study of hydrodynamics as it applies to seagrass epiphyte communities is in a primitive state, and requires considerably more attention. The following outlines some of the major issues.

The supply of propagules of algae and invertebrates is controlled by water motion. The reduction of water flow by seagrass canopies might be expected to assist in the trapping of spores within the seagrass bed; however, very dense canopies may in fact act more as a solid surface, forming an artificial boundary layer and redirecting spores over the top of the canopy. van Keulen (1998) measured apparent increases in water velocity over the surface of seagrass canopies, and postulated this was a form of 'skimming flow'. The structure of seagrass plants has been shown to influence the water velocity profile through the canopy. *Amphibolis* plants have a leafy, dense canopy with relatively bare stems; this permits higher water velocities to penetrate into the sub-canopy region than might be expected for strap-leaved seagrasses, such as *Posidonia* spp. (van Keulen and Borowitzka, 2000, 2002). While the dense growths of epiphytes commonly observed on stems of *Amphibolis* have usually been explained by the long-lived nature of these stems, it is possible that the increased penetration of spores into the sub-canopy layer of *Amphibolis* may also contribute. Ackerman (1986) showed that *Z. marina* plants modified their flow environment to trap pollen during flowering and similar observations have been made for *Amphibolis* (Verduin, 1996). It is likely that morphological roughness also enhances the recruitment of epiphyte spores into the canopy. Many algal spores, by virtue of their small size, may be accommodated within the boundary layer surrounding underwater surfaces (Charters et al., 1973), including seagrass leaves. While this would increase the chances of spore adhesion once within close proximity of the substratum, by permitting the spore to settle in the slower water flow, there would also be some resistance to penetrating the boundary layer as a result of 'skimming flow', whereby ambient water flow is redirected over the top of the boundary layer. Consequently, surface roughness and small-scale turbulence may be important factors in determining final settlement.

Water motion also will influence the supply of food for filter-feeding epiphytes; this may be of particular significance in species such as *Amphibolis* which has a sparse sub-canopy biomass that permits enhanced penetration of water flow into the meadow.

Rates of nutrient uptake for algae and seagrasses have been shown to be dependent on water velocity in several studies (e.g. Thomas et al., 2000) and Cornelisen and Thomas (2002) have demonstrated that ammonium uptake by the epiphytes of *T. testudinum* increased by an order of magnitude over the range of water velocity (0.02–0.20 m s^{-1}) observed in the field. Water motion may play a role in pumping nutrients out of the sediment, making it available for epiphytes in the canopy (Koch and Huettel, 2000). Flushing of a meadow will also enhance gas exchange, permitting supply of inorganic carbon (CO_2), and flushing out waste products (O_2).

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Physical damage is a clear result of water motion, and is responsible for clearing old growth out of the canopy at the end of summer. The high wave energies experienced during winter storms also remove excess epiphyte growth that has accumulated during the peak growth periods of summer (unpublished results).

Recently, Schanz et al. (2002) highlighted the possibility for complex physical–chemical–biological interactions affecting epiphyte biomass. They showed in both observational and experimental studies that differences in flow regime can affect epiphyte biomass. Their data are consistent with a 'cascading' effect of water movement that is negatively correlated with grazer abundance and positively correlated with epiphyte abundance. At high flow rates gastropod grazers are dislodged from seagrass leaves and so grazing pressure is reduced, leading, in turn, to higher epiphyte biomass and diversity. The role of enhanced flow rates on nutrient provision to the epiphytes was not explicitly tested, but there is little doubt that a large amount of the response they observed was related to the effect on grazers. Other studies have also reported on the interaction between hydrodynamics and leaf fouling (e.g. Fonseca et al., 1982; Jacobs et al., 1983; Kendrick and Burt, 1997) and together these studies emphasize the need to consider factors other than grazing, habitat complexity, and nutrients as the prime determinants of epiphytic algal assemblages.

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3. Nutrients

The common wisdom on the effect of nutrients on seagrasses is that increasing nutrient supply results in the overgrowth of seagrasses by epiphytes and, in extreme cases, the death of the seagrasses (Duarte, 1995). Fundamental in developing this paradigm have been some early studies (e.g. Orth and Moore, 1983; Cambridge et al., 1986) which have been cited regularly in the literature and repeatedly ‘confirmed’ with statements that nutrient enrichment stimulated the growth of epiphytic algae (e.g. Wear et al., 1999; Moore and Wetzel, 2000). Observational and experimental studies have, indeed, reported increases in epiphyte biomass in response to nutrient loading (e.g. Silberstein et al., 1986; Tomasko and Lapointe, 1991; Lapointe et al., 1994), while others have demonstrated shifts in composition of epiphytes under nutrient loading (Wear et al., 1999). This has led, implicitly, to the assumption that epiphytes could be a useful indicator of environmental conditions and, in particular, of nutrient concentrations or loads at seagrass sites. However, Lin et al. (1996) found that nutrient addition (NO_3, NH_4, PO_4, either alone or in combination) did not result in greater epiphyte abundance on *Z. marina* in their mesocosms. They argue that this was a result of their mesocosms containing not only various grazers and omnivorous fish, but also almost all plant components (seagrasses, seaweeds, phytoplankton, benthic microalgae, and epiphytes) found in coastal lagoon ecosystems which competed for light, nutrients, and inorganic carbon. These communities respond in a complex manner to nutrient addition, which in turn does not necessarily lead to an increase in the biomass of seagrass epiphytes. Lin et al. (loc. cit.) did, however, observe changes in species composition. In spring, diatoms were dominant in the controls, PO_4 and NO_3 treatment; whereas green algae and cyanobacteria were dominant in the combined nutrient treatments. In mid-summer the dominant group in the control and PO_4 treatment shifted to green algae, in the NO_3 treatment the shift was to cyanobacteria, and in the combined nutrient treatments diatoms dominated. Seasonal influences on the response of epiphytic algae to nutrient therefore increases appear to be important. For example, increased epiphyte load on *Z. marina* due to high nitrogen loading occurred only in summer at Cape Cod, USA, and coincided with the summer phytoplankton bloom (Hauxwell et al., 2003).

The literature reviewed in this chapter provides ample evidence that epiphyte biomass and/or composition responds significantly to nutrient concentration, grazer abundance, hydrodynamic conditions, depth, and light, and that interactions among these factors make it difficult to deduce the cause of shifts in epiphyte biomass or composition. We also reiterate the earliest observations that it is more likely shifts in both the biomass and than the types of epiphytes, not just the biomass, that can result in seagrass loss. This proposition was put forward by authors such as Cambridge et al. (1986) but has become simplified to the paradigm that it is shifts in epiphyte abundance alone that cause seagrass loss.

C. Organismal Interactions

1. Grazing and Predation

Seagrass epiphytes are a food source for a range of grazers and predators and these, in turn, influence the distribution, diversity, and abundance of the epiphytic organisms. Grazers control epiphytic algal biomass in at least two ways: directly through the removal of biomass and indirectly through removal of host substrate. Grazer–epiphyte interactions have been reviewed in detail by Jernakoff et al. (1996). It is abundantly clear from the literature that invertebrate and vertebrate grazers can influence epiphytic algal abundance (Phillipart, 1995; Alcoverro et al., 1997; Fong et al., 2000; Heck et al., 2000), with estimates that up to 40% of epiphytic algal production may be lost to grazers (Peduzzi, 1987). The effect of grazing on epiphyte composition is less clear, though recent studies do hint at grazing as a possible structuring force.

Copepods, isopods, and amphipods have been recorded as significant grazers on seagrass epiphytes, especially the periphyton. For example, they reduce the accumulation of epiphytic algae on *Z. marina* (Duffy et al., 2001), and may also influence species composition. In microcosm experiments, Duffy and Harvilicz (2001) showed that seagrass exposed to grazing by the amphipod *Gammarus mucronatus* became overgrown by the red alga *Polysiphonia harveyi* compared to ungrazed controls that became heavily fouled with periphyton and tunicates. In contrast, grazing by the amphithoids *Cymadusa compta* and *Amphithoe longimana* removed virtually all fouling material. Jernakoff and Nielsen

(1997) also noted that grazing by amphipods appeared to favor crustose coralline algae over diatoms.

Gastropods consume a wide range of algal epiphytes including the calcareous crustose coralline algae (Padilla, 1985; Nielsen and Lethbridge, 1989) and grazing by gastropods also has been shown to exert a direct control of epiphytic algal biomass on a wide variety of seagrasses and under a range of conditions (Hootsmans and Vermaat, 1985; Phillipart, 1995; Jernakoff and Nielsen, 1997). However, the release of grazing pressure may provide only a temporary increase in epiphytic algal biomass. Controlled experiments showed that the absence of grazers results in dramatic increases of epiphytes on *Zostera japonica* but that shortly after the biomass returns to control values (on a per m^2 basis) due to the increased sloughing of leaves which were (presumed to be) weakened by the epiphytic loads (Fong et al., 2000). This demonstrates the complex interplay of factors, including negative feedback loops that control epiphytic biomass.

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Fish grazers have been implicated in direct control of epiphytic algal biomass. The pinfish *Logodon rhomboides* and black mullet *Mugil cephalus* were experimentally shown to reduce epiphyte biomass through grazing, but only at times of the year when the epiphytes were fleshy chlorophytes (Gacia et al., 1999). At other times of the year, when red algae dominate, the exclusion of fish from seagrass plots makes no differences to epiphyte biomass. Elsewhere the same fish species (*L. rhomboides*) was shown to exert a direct control on total epiphyte biomass through grazing (Heck et al., 2000), though this study did not specify the composition of the epiphytic assemblage. Ruiz et al. (2001) also provide evidence that the reduced epiphyte load in *P. oceanica* leaves near fish farms is due to increased grazing.

Grazers can also influence epiphytic algal biomass indirectly through the removal of the seagrass substratum. Urchins can consume 50–90% of *T. testudinum* production (Valentine et al., 1997) and small vertebrate grazers have been shown to remove almost all seagrass production at other *T. testudinum* sites (Kirsch et al., 2002). It may well be that this indirect control mechanism on epiphyte biomass may not be consistent over time, since earlier studies showed that the effect of grazing by urchins on seagrass was highly seasonal (Valentine and Heck, 1991). This indirect control can be so significant that it overcomes nutrient-related effects on epiphytes and can, conceivably, result in indirect control of epiphytes through changes in their host substratum. For example, the presence of grazers in seagrass meadows produced higher densities of short shoots (Valentine et al., 1997). The significance of these sorts of morphological changes for epiphytic algal abundance and distribution is unclear, and is worth investigating as another mechanism by which grazing influences epiphytic assemblages.

Grazers can also influence epiphytic assemblage structure (both species composition and abundance) by selective feeding or by the removal of competitive dominants. Evidence for this has been reviewed by Jernakoff et al. (1996), and van Montfrans et al. (1982) demonstrated the role of selective grazing by a gastropod grazer in the removal of loosely attached diatoms and the subsequent domination by more strongly adhering diatom species. Two other studies suggest that grazing can not only control the biomass and composition of epiphytic algae, but also seasonality in composition. Fish grazing was shown to control the biomass of algae on *Z. japonica*, but only when the algal assemblage was dominated by green algal epiphytes and not more grazing-resistant red algae (Fong et al., 2000). Nielsen and Lethbridge (1989) showed seasonal differences in the gut content of invertebrate grazers that they explained in terms of an active preference being demonstrated by grazers rather than a seasonal pattern in food availability. Together, these results indicate a clear ability for grazers to influence not only the composition of epiphytic algal assemblages but also temporal patterns in composition.

A large body of work has clearly demonstrated the potential for 'top–down' controls, in the form of macroinvertebrate grazers, to over-ride 'bottom–up' controls, such as nutrient enrichment effects, on epiphytic biomass. Heck et al. (2000) combined nutrient enrichment and top predator experiments. They noted few significant effects of nutrient additions on epiphyte assemblages but many effects of fish, including a reduction in epiphyte biomass. They attributed this to a combination of direct grazing of epiphytes by the fish and the remaining mesograzers that had avoided predation by the fish. Peterson and Heck (2001) performed a similar experiment, but added mussel surrogates instead of fish. Again, the result was that nutrient additions had little effect on epiphyte biomass but the abundance was reduced in treatments containing the mussel surrogates. This was explained in terms of the surrogates providing structure that afforded protection from predation for the mesograzers and resulted in more intense grazing pressure. These and other results (e.g. Moore and Wetzel, 2000) emphasize that any implied relationships between nutrient enrichment and epiphytic biomass may well be over-simplifications if the role of top–down controls are not also considered.

Filter feeders in seagrass beds can also influence the epiphyte population. For example, Peterson and Heck (2001) found that the presence of the mussel *Modiolus americanus* increased the growth of *T. testudinum* and reduced the epiphyte load on the seagrass leaves. This was attributed to the increased growth rate of the leaves resulting from increased nutrient availability and/or the reduction in the availability of epiphyte propagules due to the filtering of the mussels. Seagrass beds support a high density of filter feeding organisms and preliminary estimates by Lemmens et al. (1996) indicate that the filter-feeders, especially the epiphytic species, associated with *Posidonia* and *Amphibolis* meadows are potentially able to filter the overlying water column daily.

2. Interactions Between Other Biota and Seagrass Epiphytes

The potential exists for interactions between biota other than the epiphyte and host to affect seagrass epiphytes. This has been clearly demonstrated in terms of grazers affecting epiphyte biomass and composition (see above). However, other forms of interaction have been reported including competition between algae and indirect interactions between fauna and epiphytes. Piazzi and Cinelli (2000) described different algal assemblages on the leaves and rhizomes of *P. oceanica* in the western Mediterranean. They found the leaves to support 28 species of macroalgae, compared with 51 associated with the rhizomes with the rhizomes dominated by the turf-forming red algal species *Acrothamnion preissii* and *Womersleyella setacea*, both introduced species. In a later study, Piazzi et al. (2002) looked at the rhizome assemblage in more detail and found that the functional diversity of the rhizome assemblage was low (mainly filamentous species) at sites where these introduced species were present and diverse when they were absent. The authors also attributed the absence of seasonal changes in the rhizome assemblages to the presence of these introduced species. They conclude that a competition between the introduced and native species plays an important role in structuring the rhizome algal assemblages and their spatial and temporal patterns. Peterson and Heck (2001) reported quite a different interaction. They introduced mussel mimics into a seagrass meadow and observed an increase in grazer density and decrease in epiphyte biomass. They suggest that the mussel shells provide shelter for epibenthic grazers, thereby creating greater grazing pressure on the epiphytes.

V. Conclusions

The seagrass epiphytes are an integral, complex, and dynamic component of seagrass ecosystems. They can make up a significant proportion of the total primary production of these ecosystems and are generally the primary food source for the associated fauna as well as contributing to detrital food webs. Epiphytes also provide shelter for many species. Normally, the seagrass epiphytes do not seem to have a detrimental effect on their seagrass host; however, under certain conditions that lead to a 'bloom' in the epiphytic algae they may contribute to the decline of the seagrass.

A lack of knowledge about the physiology of epiphytic algae also limits our ability to predict how they will respond to changes in nutrient availability and changes in the light environment. For example, and existing models of seagrass ecosystems need to make some major assumptions about the responses of epiphytic algae to changes in the environment (e.g. Plus et al., 2003). Furthermore, our understanding of the factors controlling seagrass epiphyte diversity and abundance is still limited by the nature of the complex interactions between physical factors (e.g. light, temperature, water movement, nutrients) and biological interactions (competition for space, grazing, and predation). Variability in the growth rate and longevity of the seagrass substratum further complicates experimental studies and data interpretation. The use of artificial seagrasses is one approach to reduce some of this variability and combined with well-designed natural and manipulative field experiments will lead to greater understanding of these communities.

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