

A review of epiphyte community development: Surface interactions and settlement on seagrass

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Abstract: A focus of community ecology is the spatial distribution of species assemblages and the interactions among species and abiotic features of the environment. While the ubiquity of species associations is apparent, it is less clear if interactions within a community impart an organizational structure to the community. Do settlement processes in early stages of community development contribute to later community structure? What are the interfacial forces that lead to recruitment and colonization of diverse substrata? This review examines seagrasses as living substrates for epiphyte colonization and the surface interactions which may determine settlement success. These epiphytes include primary producers which contribute to biodiversity and are bioindicators of pollution/nutrient enrichment.

Key words: Epiphytes, Seagrass, Surface interactions

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Introduction

The importance of seagrass ecosystems to near shore environments include habitats for invertebrate and fish nurseries, food sources, stabilization of sediments, centers for biological diversity, preservation of water quality, and commercially viable sources of shellfish and fish. In light of eutrophication, seagrass declines have become a global issue (Costanza, 1997; Orth *et al.*, 2006). Anthropogenic factors potentially contributing to the decline include biological disturbance by the introduction of invasive species, disease, nutrient influx, algal blooms, commercial fishing and aquaculture. Physical disturbance leads to sediment changes and the loss. These factors as well as global warming are considered significant in seagrass decline (Orth *et al.*, 2006).

Seagrass species are commonly epiphytized by micro- as well as macrocolonists. Photosynthetic epiphytes enhance overall primary productivity of the systems (Borowitzka *et al.*, 2006) that can rival or exceed that of cultivated terrestrial ecosystems (Duarte and Chiscano, 1999) and are reported to match or double those of the seagrass hosts (Morgan and Kitting, 1984; Williams and Heck, 2001). The rapid generation times and growth by epiphytic algae, as well as biomass, can lead to other seagrass ecosystem effects including provision of a food source for fauna (Buia *et al.*, 1992; Gambi *et al.*, 1992), formation of sediment, and nutrient cycling (Borowitzka *et al.*, 2006).

Biotic and abiotic factors influence the diversity, distribution and abundance of seagrass epiphytes. Light, temperature, grazing, and/or nutrients are reported to influence epiphyte colonization and

community development (Gil *et al.*, 2006; Lee *et al.*, 2007; Prado *et al.*, 2007). Light intensity and quality influence epiphyte species and productivity (Mazzella and Alberte, 1986; Cambridge and Hocking, 1997; Dalla Via *et al.*, 1998; Robbins and Bell, 2000; Drake *et al.*, 2003). Epiphyte growth, biofouling, and colonization in general are affected by water motion (Kendrick and Burt, 1997; Lavery *et al.*, 2007) and by diversity of algal propagules (Norton, 1992; Beach *et al.*, 1995).

Spatial and temporal variations in epiphyte communities have been the focus of research (Vanderklift and Lavery, 2000; Saunders *et al.*, 2003; Johnson *et al.*, 2005). Nutrient loading is currently the most documented factor influencing epiphyte communities. Distinct increases in epiphyte biomass with increased nutrients have been reported (Borum, 1985; Tomasko and Lapointe, 1991; Moore *et al.*, 1996; Uku and Bjoerk, 2001; Frankovich *et al.*, 2003; Hays, 2005; Gil *et al.*, 2006; Peterson *et al.*, 2007). Because the epiphyte biomass corresponds to changes in nutrient conditions, epiphytes are regarded as sensitive indicators of "natural" and long term environmental variation (Martinez *et al.*, 2006; Richardson, 2006).

Seagrasses are also important indicators of human-induced sources of variation (Pardi *et al.*, 2006). Seagrasses integrate environmental impacts over time (Longstaff and Dennison, 1999; Carruthers *et al.*, 2002). Bricker *et al.* (2003) consider seagrasses to be one of the five sensitive indicators of pollution in the US National Estuarine Eutrophication Assessment. In this paper, we address potential bases for patterns between epiphytes and seagrasses which have been considered a natural model for the study of interactions



between sessile marine algae and invertebrates in select tropical systems (Borowitzka and Lethbridge, 1989).

A community ecology approach to colonization: Theories of marine benthic community organization stress the importance of competition and predation, environmental gradients, disturbance, and early settlement events in community development. Variation in the nature of the propagules and the rate of recruitment can contribute to species diversity, community structure and dynamics (Keough and Downes, 1982). Roughgarden *et al.* (1986) developed a theory of “supply side ecology” that stresses the relationship between potential recruit abundance, resource limitation and competition in select communities. Taxonomic composition of the gene pool, hydrodynamics, disturbance and physical characteristics of the substrate, interact in recruitment and colonization (Palmer, 1988). Physiological variations in propagules contribute to heterogeneity of potential colonists (Beach *et al.*, 1995). The success of settlement, germination and recruitment processes by propagules determines algal establishment and can influence species distribution.

Active and passive mechanisms are involved in recruitment from the water column and colonization of benthic surfaces. The velocity boundary layer, defined as the layer of water near where the current velocity has been reduced by the surface (Lobban *et al.*, 1985), can influence the surface microenvironment for settlement. If a propagule is retained in the boundary layer of a substrate long enough to settle, adhesion may occur.

As living substrates, seagrasses offer unique constraints for colonists as they are spatially and biologically dynamic. Surfaces distal to the meristems are older; young and old blades or regions of blades are exposed to the water column for varied amounts of time. As physiological fluctuations can occur on a leaf, we would expect a mosaic of microhabitats for colonists. Surfaces of these biological hosts then change in physical and chemical characteristics with growth, onset of reproduction, and senescence. Species compositions of epiphytic diatoms appear to be closely related to morphology and lifespan of seagrasses (Chung and Lee, 2008). In seagrasses, the shoot length and density may independently influence ecological processes including epiphyte density, diversity and recruitment (Sirota and Hovel, 2006). Each host may possess specific surface chemistries, as well as microenvironments, that influence recruitment and the distribution of colonists.

Seagrass leaves as host substrates: In a seagrass meadow, the leaves provide spatially uniform surfaces for epiphytic growth in select marine environments (Duarte, 1989). The seagrass leaves interact with water flow and reduce current speeds. This baffle effect is thought to enhance recruitment rates by retaining propagules near the blades and increasing the window of opportunity for settlement (Peterson, 1986). Settlement is generally greater in seagrass meadows compared with surrounding areas (Wilson, 1990). The architecture of the seagrass meadows is influenced by blade density and form. The species with belt-like blades have older distal regions

that are taller or more extended than the young regions. The species with small blades that are spatially separated along rhizomes at regular intervals such that the oldest blades furthest from the meristem; young and older blades are at the same height in the water column.

At the anatomical level, the seagrass leaf epidermis is the site of gas and nutrient exchange as well as photosynthesis and osmoregulation. These cells have “transfer cell” configuration from an invagination of the plasmalemma and may function in cell secretion, and absorption (Gunning, 1977) and osmoregulation (Jagels, 1983). Seagrasses release up to 2% of photosynthetically fixed carbon as dissolved organic molecules (Moriarty *et al.*, 1985). Dissolved organic matter (DOM) secreted by aquatic plants increases the bacterial densities in the phylloplane (Hough and Wetzel, 1975). Laboratory studies with labeled phosphorus have shown that leaves of *Zostera marina* L. excreted one to three percent of the phosphorus absorbed by the roots (Penhale and Thayer, 1980). Phylloplane epiphytes and rhizosphere bacteria capture at least some portion of released nutrients (Moriarty and Iverson, 1986). Harlin (1980) speculated that the effects of rhizosphere nitrogen metabolism may be observed in the phyllosphere via release of nitrogenous compounds exuded by a seagrass.

Seagrasses provide a physical substratum for bacteria, algae and invertebrates. Attachment to seagrasses can enhance access to irradiance for photosynthetic algae. Hazards for long-lived epiphytes of seagrasses include sloughing of surface layers at the distal ends of strap-like blades (Duarte, 1989) as well as sand scour and whiplash of the leaves (Brawley and Xiugeng, 1987).

Epiphyte communities: Epiphyte assemblages include autotrophic organisms (diatoms, cyanobacteria, macroalgae, encrusting algae), and heterotrophic organisms (bacteria, fungi, invertebrates) (Milchakova, 2000; Uku and Bjoerk, 2001; Garcia-Martinez, 2005; Johnson *et al.*, 2005; Corlett and Jones, 2007; Piazza *et al.*, 2007; Uku *et al.*, 2007; Wilson, 2007). Table 1 refers to epiphytes, their patterns and/or contributions relative to seagrass hosts and abiotic environmental influences. At the seagrass surfaces, transfer of carbon, nitrogen and phosphorus at the leaf surface is likely to enhance primary production by epiphytes (Libes and Boudouresque, 1987). Smit *et al.*, (2005) showed that the major source of carbon for upper trophic levels is the epiphytes rather than the seagrasses which contribute to the sediment level community. Autotrophic and/or heterotrophic epiphyte biomass corresponds to the seasonal nutrient regimes in the water column (Borum, 1985; Tomasko and Lapointe, 1991; Moore *et al.*, 1996; Frankovich *et al.*, 2003; Hays, 2005; Peterson *et al.*, 2007). In addition to nutrients, epiphyte biomass, species richness and diversity are influenced by meadow structure, light and shoot length and grazing (Prado *et al.*, 2007).

Herbivory is a distinct factor in seagrass meadows and includes macroherbivores (*e.g.* fish, turtles and urchins) and micrograzers. The role of specific epiphytes as a target for herbivory, varies with environments (Tomas *et al.*, 2005; Hays, 2005). Epiphyte

Table - 1: Seagrass-epiphyte relationships

Seagrass	Site	Epiphyte Focus	Pattern/Community Information	Reference
<i>Amphibolis griffithii</i>	Western Australia	Macroalgae	Macroalgae are the main carbon contributor in trophic transfers	Smit <i>et al.</i> (2005)
<i>Halodule wrightii</i>	Gulf of Mexico	Algal epiphytes in the system	Epiphytic algae are the dominant benthic primary producers	Moncreiff and Sullivan (2001)
<i>Cymodocea rotundata</i> and <i>Thalassodendron ciliatum</i>	Kenya	Rhodophyte dominance, cyanophytes	Nutrients affect epiphyte biomass and composition	Uku and Bjoerk (2001)
<i>Halophila beccarii</i>	South China Sea	Epiphytic algae including diatoms, chlorophytes and cyanophytes	Seagrass and epiphyte biomass fluctuates seasonally	Shamsudin (2002)
<i>P. oceanica</i>	Mediterranean	Epiphytic algae vary relative to biotic and abiotic factors	Biomass, species richness, composition and diversity of seagrass epiphytes are influenced by grazing, nutrients, meadow structure, light and shoot length	Prado <i>et al.</i> (2007)
<i>P. oceanica</i>	Mediterranean	Algal epiphytes from Chlorophyta, Ochrophyta and Rhodophyta with crustose forms dominant	Large scale homogeneity of epiphytes with small scale variation as patches within meadows	Piazzari <i>et al.</i> (2007)
<i>P. oceanica</i>	Mediterranean	Macroalgae and herbivores	Dense epiphytes in exclusion cages without detriment to host	Tomas <i>et al.</i> (2005)
<i>P. oceanica</i>	North East Spain	Epiphytes	Seasonal variation in seagrass shoot size due to solar cycle and local environmental changes, including herbivory, influence epiphyte biomass	Alcoverro <i>et al.</i> (1997)
<i>P. sinuosa</i>	South Australia	Epiphytic algae and invertebrates	Crustose coralline algae dominance is maintained by grazing	Keuskamp (2004)
<i>P. coriacea</i>	Western Australia	Functional groups of algal epiphytes	Temporal and spatial patterns in epiphyte assemblages occur but at a spatial scale of hundreds of metres there was a loss of information using functional group data	Vanderklift and Lavery (2000)
<i>Thalassia testudinum</i>	Gulf of Mexico	Grazers, epiphytes and primary productivity	Grazer intensity reduces epiphytes and benefits seagrass; increased nutrients increased seagrass growth with grazers present	Hays (2005)
<i>T. testudinum</i>	Florida USA	Epiphytes	Nutrients and grazers affect epiphytes and influence leaf turnover rates	Frankovich <i>et al.</i> (2003)
<i>T. testudinum</i>	Florida USA	Autotrophic epiphytes	Epiphyte loads increase with nutrients despite elevated grazer abundances and increased leaf turnover rates	Peterson <i>et al.</i> (2007)
<i>T. testudinum</i> and <i>Halodule wrightii</i>	Florida USA	Algae and epifauna	Proliferation of algal epiphytes is increased by nutrient input and controlled by epifauna	Gil <i>et al.</i> (2006)
<i>T. testudinum</i>	British West Indies	Diatoms, coralline algae and invertebrates	Current baffle effects lead to sedimentation as well as epiphyte diversity	Corlett and Jones (2007)
<i>Zostera japonica</i>	Hong Kong	Gastropods density correlated with epiphytic algae.	Epiphytic growth and grazers enhance seagrass growth and survival	Fong <i>et al.</i> (2000)
<i>Z. japonica</i> , <i>Z. caespitosa</i>	Geoje Island South Korea	Diatoms	Community structure of the diatom varies with seagrass species	Chung and Lee (2008)
<i>Z. marina</i>	Black Sea	Diversity of green and red algal epiphytes	Sessile invertebrates are more abundant than macroalgal epiphytes in eutrophic environment	Milchakova (2000)
<i>Z. marina</i>	Wales	Algal epiphytes	Species richness is related to leaf length	Johnson <i>et al.</i> (2005)



grazing in a nutrient-poor area appears to be limited to the maintenance of an epiphytic assemblage that is free of filamentous algae and dominated by crustose coralline algae (Keuskamp, 2004). Epiphyte grazers are reduced by hydrodynamics which have been shown to enhance epiphyte growth with inhibition of seagrass development (Schanz *et al.*, 2002). Duffy and Emmett (2006) attribute seagrass ecosystem productivity and stability to the epiphyte diversity and state that consumer control is strong.

In addition to herbivory, water motion (Kendrick and Burt, 1997), light quantity and quality (Cambridge and Hocking, 1997), the supply of algal propagules (Norton, 1992) is an important parameter in epiphyte colonization.

Epiphyte influences on hosts: Ducker and Knox (1984) have divided algal epiphytes into two classes based on degree of surface penetration: 1) Those that attach to the outer layers of the host (termed "holo-epiphytes"); 2) and those that anchor deeply in the host tissue (termed "amphi-epiphytes). Complex cytoplasmic connections and altered host metabolism have been described between "parasitic" algae and algal hosts (Goff and Coleman, 1984). Redefining our concepts of "an individual" and "symbiosis" becomes increasingly necessary as information on surface-level interactions increases (Goff, 1982). Cyanobacterial associations with seagrasses can greatly increase ecosystem production in nutrient-poor environments (Capone and Taylor, 1980) via nitrogen fixation on surrogate seagrass leaves (Goering and Parker, 1972). Although this finding has been disputed (McRoy *et al.*, 1973), heterocystic cyanobacteria have been found on leaves as well as in the rhizosphere of seagrasses (Capone and Taylor, 1980). Periphytons benefit the host by acting as a filter to reduce UV-B that reaches the seagrass (Brandt and Koch, 2003).

Advantages to epiphytes are generally clearer than the advantages to the hosts. At an ecological level, epiphytes may impact the hosts via shading (Sand-Jensen, 1977; Howard, 1982; Josselyn and Fonseca, 1986). Epiphytes can alter the flow regime and reduce the diffusion rate of CO₂ and nutrients (Brawley and Xiugeng, 1987), increase the drag force on the blades and increases vulnerability of the host to dislodgement (Borowitzka and Lethbridge, 1989), alter host vulnerability to grazing, and change the potential for metabolic processes that occur at the host surface by altering water movement at the blade boundary layer (Brawley and Adey, 1981). The effects of surface fouling may be so profound as to influence the evolutionary development of high rates of blade turnover (Josselyn and Fonseca, 1986). Seagrass viability may be protected by micrograzer control of epiphyte growth (Howard and Short, 1986; Fong *et al.*, 2000). Effects of invasive algae and invertebrates on seagrass beds have been recently considered; the majority of introductions yielding negative effects that compound with nutrient pollution, reduced herbivory and boating to contribute to seagrass decline (Williams, 2007).

Establishment of seagrass and epiphyte associations: In an early work designed to assess the basis for apparently specific

seagrass and epiphyte associations, Harlin (1980) reported that colonization on artificial substrata and the viable seagrass leaves was similar in composition. While some host and epiphyte associations appear to be specific, the specificity was speculated to be based on the seagrass habitat rather than the host surface (Harlin, 1980). The reducing environment and the wide range of pH (5.8 to 9.4) in sediments of seagrass meadows may exclude some species from seagrass beds (Wood, 1972). Pinckney and Micheli (1998) compared community composition of epiphytes on blades versus artificial substrates and found greater biomass on the seagrass with specific patterns for diatoms and cyanobacteria. They suggest that microenvironment of the blade surface may alter the outcome of competitive interactions between algal groups. Piazzini *et al.* (2007) have shown that at the scale of meadow, epiphyte distribution is homogeneous. Within the meadow however, small scale variation contributes to patches with distinct taxa that presumably reflect microenvironments relative to settlement. The distribution of epiphytes on seagrass blades is not random (Trautman and Borowitzka, 1999). In seagrasses, faunal abundance and species diversity commonly are positively correlated with structural complexity (Sirota and Hovel, 2006).

The pool of propagules that might settle on a leaf determines potential colonists. The rapidity and strength of spore attachment may influence the ultimate composition of an epiphyte flora. Algal propagules could be produced via vegetative cell division (asexual propagules of *Sphacelaria*), thallus fragmentation (*Polysiphonia* and *Ceramium*), or spore formation (diploid or haploid and flagellated or non-flagellated) (Shin, 1995; Shin and Smith, 1996). Variation in adhesive strength and specificity could be expected from diverse propagules and, hypothetically, lead to specific interactions with substrata. Physiological variations in photosynthetic parameters may lead contrasting algae to settle with varied urgency (Beach *et al.*, 1995). The mucilaginous films of bacteria and diatoms are assumed to be significant in the attachment of other organisms (Huang and Boney, 1983). The biofouling literature is rich in information on the effects of biofilms on settlement (Hadfield *et al.*, 1994; Unabia *et al.*, 1999; Zardus *et al.*, 2008).

Colonization of new substrata is one of the most precarious stages in the life history of marine benthic organisms (Fletcher and Baier, 1984). Walters *et al.* (2003) investigated settlement by invertebrates on diverse macrophytes and found that hosts were: 1) toxic to the propagules; 2) chemically deterrent to propagules; or 3) had unacceptable morphologies or surface energies. Substrate characteristics that may influence attachment and settlement of propagules are addressed later in the section on surface properties and modifying films. While some investigators suggest that surfaces in the ocean have been considered neutral to colonists (Blindow, 1987), others have found highly selective in some settlement systems (Maki and Mitchell, 1986; Hadfield *et al.*, 1994; Walters *et al.*, 2003). Underlying bases for patterns in incipient, and perhaps subsequent, stages of community development include the interfacial forces that drive attraction, adhesion, aggregation of cells and settlement (Michael and Smith, 1995).

Forces of attachment: "Supply-side ecology" (Roughgarden *et al.*, 1986) would argue that the probability of propagules encountering a surface is influenced by their abundance in the water column. Propagules including microorganisms are transported by fluid dynamic forces to the point where physico-chemical forces, such as electrostatic forces and van der Waals (electrodynamic) forces act upon cells near a surface (van Loosdrecht *et al.*, 1989). A cell approaching a surface will first be exposed to these nonspecific interactions (Absolom *et al.*, 1983).

Attachment depends on the ability of the colonizing entity to adhere initially to surfaces. A cell wall adheres by electrostatic (columbic) and van der Waals (dispersion) forces, surface charge and the wettability of the surface. Electrolytes (Ca^{++}) can overcome initial repulsive barriers and so facilitate initial attachment (Decho, 1990). The initial adhesion is sustained by particular attachment mechanisms that may involve complementarity between the microbe and the surface. Adhesive mucilages are secreted by microorganisms and propagules upon contact with surfaces (DiSalvo and Daniels, 1975). Adhesive polymers from the cell bridge the distance of the aqueous layer between a cell and the surface (Decho, 1990). In general, extracellular polymeric substances (EPS) secreted by organisms provide cues and can act as carriers of chemical signals which result from the adsorptive properties of the exudates (Wotton, 2004).

Other interactions in biological systems that affect attachment include: 1) hydrogen bonding (Fletcher, 1988); 2) hydrophobic bonding (Pringle and Fletcher, 1983); 3) coordination with metals or other cations; 4) polar group interactions; 5) steric interferences (Maroudas, 1975); and 6) specific reactions between the substrate and surface functional groups (Dazzo *et al.*, 1976). Microbial adhesion to a substratum may result from: 1) specific surface structures, such as pili (fimbriae) or other appendages (Jones, 1975); 2) cell surface adhesives (Fletcher and Floodgate, 1973); 3) cell-surface plasticity (Corpe, 1970); and 4) hydrophobic areas of the cell surface (Dempsey, 1981). All these surface properties may be involved in propagule to host adhesion.

Physicochemical models for adhesion of bacteria to substrata include both electrokinetics and thermodynamics (Fletcher, 1988). The electrokinetic model is based on charge interactions between the cell and substrate surfaces. At physiological pH most bacteria and potential substrata have a net negative charge. Electrostatic repulsion is proposed to occur between surfaces from an overlap between the electrical double layers of the charged groups on opposing surfaces. Adhesion depends upon overcoming these repulsive forces. According to van Loosdrecht *et al.* (1989), this interaction depends on the surface potentials and the thickness of the electrical double layers. The thickness is inversely proportional to the square root of the ionic strength. At high electrolyte concentration or in the presence of polyvalent counter ions, the electrostatic interaction will be reduced.

In contrast with the electrokinetic model, the thermodynamic model is based on the importance of hydrogen bonding, dipole, and hydrophobic interactions (Pringle and Fletcher, 1983). A relationship between free-energy of a solid's surface and bacterial colonization has been demonstrated (Absolom *et al.*, 1983).

Surface properties and modifying films: Surface characteristics of both substrates and cells play crucial roles in the initial stages of attachment and subsequent settlement (Fletcher and Baier, 1984; Michael and Smith, 1995). Important substrate characteristics that we discuss in the following sections are: 1) surface texture, shape and area; 2) surface tension; 3) surface hydrophobicity; and 4) surface charge. In addition to these interactions, surfaces are modified by macromolecular films and biofilms that alter initial surface characteristics relative to colonization.

Surface texture: The rugosity of a substrate defines, in part, the microhabitat for any potential colonist. The rougher or more uneven the solid surface, the more susceptible it generally is to the attachment of foreign molecules and micro-organisms (Zobell, 1972). Adsorption rates were predicted to be higher for cells arriving at "microrough" surfaces. A decreasing desorption rate occurs as the absorbed cells are sheltered from shear forces; this increases the surface area for cell-to-substratum contact (Characklis, 1990). Interstitial spaces may enhance settlement of spores in two ways. Trapped organic constituents may give local electrical charges to the surface; interstitial texture reduces local water velocities thereby increasing the residence time of spores in the local area (Harlin and Lindbergh, 1977). Irregularly contoured surfaces typically support greater diversity of benthic organisms than do flat surfaces (Hixon and Brostoff, 1985). Spatial heterogeneity generally promotes co-existence of species (May, 1986).

Hydrophobic surface properties: Surface hydrophobicity functions in adhesion by removal of the water film between interacting surfaces, enabling specific short-range interactions to occur (Busscher and Weerkamp, 1987). Hydrophobicity may be the most important factor in the nonspecific adhesion of bacteria to interfaces; the outer surface layers of benthic cyanobacteria are consistently hydrophobic while the surfaces of planktonic cyanobacteria are hydrophilic (Fattom and Shilo, 1984).

Specific molecules impart a hydrophobic/hydrophilic character to cell surfaces. Cell wall proteins and lipids are capable of presenting hydrophobic areas by adopting particular conformations and orientations at the cell surface. Some polysaccharides present surfaces that are essentially non-polar while others (*e.g.* cellulose), have fixed conformations with all the sugar hydroxyl groups forming a polar surface.

Surface modifications: Surface coatings are ubiquitous in marine systems. They modify many chemical and physical surface properties including adsorption, charge (Characklis, 1990), hydrophobicity, and surface tension (Baier, 1975). The duration of submergence,

the characteristics of the substrate, as well as the chemical, physical, and biological properties of the surrounding water determine the kinds and quantities of film-forming materials that attach to submerged substrata (Zobell, 1972).

Baier (1973) proposed that the initial coating, the "conditioning film", is glycoprotein from the water column and that it functions as a surface for bonding with the mucopolysaccharides exuded from the first biotic colonizers. This conditioning film precedes attachment of microbes and the development of microbial biofilms. Biofilms consist of macromolecular, subcellular and microbial components. The bacterial glycocalyx forms the matrix of the biofilm. Microbial flora within certain biofilms exist as groups of physiological units rather than as a random assortment of species embedded within an exopolymer matrix (Costerton, 1984). The bacteria construct the matrix, which has precise structure, chemistry and physiology that is based on the resident bacteria. Depending on the bacterial source, the biofilm can be both hydrophobic and hydrophilic. This component of surfaces can add heterogeneity to the settling surface (Brandt *et al.*, 2005). Microbes within biofilms have patchy distributions. This patchiness produces steep redox gradients within the biofilm, and promotes diffusive exchange of metabolites, gases and nutrients.

Community development on a surface may be mediated by these microbial consortia as they metabolically interact, and as their extracellular polysaccharides enhance microbial binding to the biofilm surface. The identification of microbial consortia in biofilms was an "interesting new development in microbial ecology" in 1988 (White, 1988). Biofilms containing specific organisms and chemistry can influence patterns in settlement by providing cues for surface recognition in the forms of glycan-containing molecules that form chemically heterogeneous surfaces to colonists (Michael and Smith, 1995). Bacterial films have been shown to be important in the settlement and metamorphosis of invertebrate larvae (Crisp, 1973; Unabia *et al.*, 1999).

Glycoprotein-mediate cell surface interactions: In order for adhesion of microbes and/or propagules to occur, the cells must reside near the surface with adequate time for attachment and the cell surface must have a mechanism for recognition and attachment. The mechanism of attachment may involve lectins, a class of proteinaceous compounds that bind carbohydrates specifically and non-covalently. Lectins bond specifically with glycoconjugates (glycoproteins, glycolipids and polysaccharides) on cell surfaces (Sharon and Lis, 1989).

In the marine environment, glycoconjugates are present in biological exudates (Decho, 1990). They contribute to the pool of components for the conditioning film that precedes settlement by microbes and biofilm development (Baier, 1973). These macromolecules have an activity similar to that of lectins; they enhance both adhesion of microalgae to glass and aggregation to each other (Iman *et al.*, 1984). Settlement and metamorphosis of some larvae is viewed as a lectin-mediated surface interaction (Kirchman *et al.*,

1982). Discrete distributions of glycoconjugates on cell surfaces have been demonstrated for select species in the algal divisions Cyanophyta, Pyrrophyta, Raphidophyta, Euglenophyta, Chromophyta and Chlorophyta (Iman *et al.*, 1984) that relate to cell-to-cell and/or cell-to-substrate interactions.

Attachment behavior, in some systems, has been demonstrated to involve lectins, or lectin-like molecules, and receptors at the cell surface (Iman *et al.*, 1984; Maki and Mitchell, 1986). The localization of lectins and glycoconjugates, as potential adhesives can contribute to our understanding of basic processes involved in the early stages of community development in the benthic marine environment. Michael and Smith (1995) compared the surface chemistry of newly emergent leaves of the endemic, Hawaiian seagrass, *Halophila hawaiiiana* Doty and Stone to that of an artificial substrate and found distinct glycosylated chemistry that was different from that of the non-living substrate. The uniqueness is not surprising in respect to the cell wall composition, chemistry of the surface cells and presumed exudates as a living substratum. Specific glycoconjugates were described at the cell walls and were associated with the secretory organelle-rich regions of the epidermal cells, as well as chloroplasts and mitochondria. Biofilms were not observed on the newly emergent leaf surfaces but were observed on glass slides exposed to seawater for the same time interval. The glycoconjugate chemistry of the older, epiphytized blades, and the presence of biofilms on the older blades has not been described.

Conclusions: As hosts, macrophytes differ from one another in morphology, anatomy, surface rugosity, and chemistry of both the photosynthetic surface and exuded products. How might information on surface interactions in the marine environment help explain patterns in benthic marine communities? Propagule pools are diverse and influenced by environmental factors. Bacteria, as part of the propagule pool are generally considered to be the first colonists on substrates in the ocean. Bacteria interact with diatoms, form microbial consortia in a biofilm, and change the micro-topography and chemistry of the surface microzone. Living surfaces exude and retain metabolic products that potentially promote adhesion and and/or retard colonizing propagules. Settlement and metamorphosis of some marine organisms may require specific biofilms. Each colonist may have specific requirements for adhesion, and following attachment alter the surface for subsequent colonists. Once colonists adhere and a film has formed, the surface properties change and remain changed after the initial colonists disappear. Colonization and community development on living substrates involve a plethora of cellular interactions that form the bases for observable patterns. Knowledge of the growth dynamics and ecology of the seagrass hosts set the stage for observing both patterns in epiphyte community development and understanding the mechanisms that contribute to the patterns. As seagrasses and epiphytes interface with the environment, both are involved with biotic and abiotic environmental interactions including recruitment from a propagule pool, settlement and species interactions

leading to community development. Interfacial forces have been described here including surface chemistry that could be involved in cell-to-cell and cell-to-substrate aspects of settlement. The multifaceted importance of seagrasses to near-shore ecosystems, the growth forms and replicate number lead us to focus on the interfacial dynamics that occur at the population and leaf levels.

We have described from the literature aspects of seagrasses as well as scientific concerns over seagrass decline. Epiphytes as part of seagrass ecosystems are reported to have diverse effects on the hosts and contributions to the systems which include enhancement of primary productivity and diversity. As they are generally sensitive to nutrients and other environmental perturbations, epiphytes and are being regarded as bioindicators for factors that could be causal in seagrass decline. We consider the process of colonization or biofouling of the seagrasses to be important in terms of species selection, species composition, as well as biomass. The stages involved in site selection and community development in this and in biofouling community development may be the most vulnerable targets to environmental perturbations from any source and so influence the epiphyte and biofouling communities. In concluding this review we propose a series of questions that need to be addressed in future research. What are structural and physiological aspects of the leaf and epiphyte interface? How is the host physiology affected by specific colonists? How do colonization of seagrasses and man-made structures relate to diverse propagule pools? How do biofilms form on seagrasses and are they involved in epiphyte settlement? How do epiphytes on seagrasses relate to grazers and how do grazers impact seagrass meadows? And what are the roles of varied environmental parameters including perturbations relative to seagrass meadow dynamics and declines? This is an exciting field of research that has applicability to understanding seagrass community and ecosystem structure and dynamics.

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