COSTS AND BENEFITS OF INTERTIDAL ALGAL EPIPHYTISM

by

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Abstract

Organisms in the intertidal zone are regularly exposed to wave action, emersion, and competition. Competition for space may have been a factor leading to the evolution of epiphytes which have circumvented this problem by growing on other algae. Epiphytism is generally considered deleterious to hosts but, is this always true? This study explored costs and benefits of interactions between the epiphyte, *Soranthera ulvoidea*, and its host, *Odonthalia floccosa*, involving biomechanics, light acquisition, desiccation, and herbivory.

Drag on epiphytized and unepiphytized hosts was measured in a recirculating water flume. Epiphytes increased drag on hosts by approximately 50% at each test velocity. Increased drag caused epiphytized hosts to be more likely to break from the substratum than hosts without epiphytes. Epiphytes experienced reduced drag when attached to hosts but sometimes broke before hosts. In fact, epiphytized hosts and epiphytes were equally likely to dislodge; this suggests that drag added by epiphytes may not be entirely harmful to hosts if epiphytes dislodge half the time, reducing overall drag on epiphytized hosts.

The effects of epiphytism on light acquisition, desiccation, and herbivory were also investigated. Photosynthesis versus irradiance curves were constructed for hosts and epiphytes; saturation irradiances for both were approximately $50\mu mol\ m^{-2}s^{-1}$, and were not significantly different from irradiances under submerged algal canopies in the field. Thus, it was inferred that these epiphytes do not likely affect host light acquisition. Also, these epiphytes may not have arisen in response to light limitation as they reached photosynthetic saturation when exposed to light levels under other algae. When hosts with and without epiphytes were exposed to air, epiphytes doubled the time required for hosts to lose 50% of the water originally associated with their thalli. By delaying desiccation, epiphytes likely reduce physiological damage of emergent hosts. Lastly, invertebrate herbivores common to this study's field site preferred grazing

epiphytes over hosts. This feeding preference could benefit hosts by diverting herbivores away from host tissue and toward epiphytes.

In sum, this study demonstrates that hosts and epiphytes often benefit by closely associating; these complex interactions could help explain the evolution and persistence of intertidal algal epiphytism.

Table of Contents

List of Tables

List of Figures

Acknowledgements

Introduction

Many organisms exist in direct contact with another organism; the effects of these interactions, or symbioses, on constituent organisms range from harmful (parasitic), to neutral or beneficial (commensalistic), to combinations of these outcomes. Epiphytes are symbiotic organisms that grow on plants (Harder, 2008) contrary to more typical substrata such as rock or soil commonly utilized by a majority of other organisms. Many epiphytes are photosynthetic and not parasitic; although hosts generally provide substrate only for epiphytes, existing in such close proximity has direct and complex impacts on both constituent organisms. It is unclear whether photosynthetic hosts and epiphytes generally experience costs or benefits from such close association, particularly in regards to biomechanics, light acquisition, desiccation, and herbivory.

Terrestrial epiphytes

Epiphytes occur worldwide in a variety of environments. Many epiphytic relationships exist on land, where species assemblages have been well described (e.g. McCune et al., 2000; Hietz and Hietz-Seifert, 1995; Callaway et al., 2002), but the effects of epiphytism on epiphytes and hosts in particular have not been extensively quantified. Epiphytes may negatively alter plant biomechanical interactions. Trees and other vascular plants must occasionally withstand heavy wind forces, and although the effects of these forces have been investigated (Vogel, 1989; Ennos, 1997; Niklas and Speck, 2001), the exacerbating effect of epiphytes plus these forces have not. Increased tree fall frequency in the tropics has been attributed to high epiphyte abundance and biomass (Strong, 1977), but this has yet to be empirically tested.

Other terrestrial epiphyte research has generally focused on the benefits achieved by epiphytes as a consequence of occupying an epiphytic habit. For example, epiphyte distribution is likely influenced by differences in light and water availability throughout tree canopies;

epiphytes that require extensive light gain access to this resource via peripheral positions on hosts (Sillet, 1994; Hietz and Briones, 1998, 2000). Epiphytes with poor desiccation resistance avoid water loss by growing in cool, shaded refugia provided by hosts (Sillet, 1994; Hietz and Briones, 1998, 2000).

Besides benefitting by growing on plants, some terrestrial epiphytes provide other species with advantageous nutrients and microhabitat (Stuntz et al., 2002; Ellyson and Sillet, 2003). For example, aside from providing water and nesting materials, some epiphytes are important sources of food such as nectar, fruits, and invertebrates for tropical bird species (Nadkarni and Matelson, 1989). In this way, terrestrial hosts essentially seem unaffected by epiphytes while epiphytes generally benefit from this association and sometimes provide resources to other non-host species.

Aquatic epiphytes

Many epiphytes are also aquatic, and within this category are myriad epiphytic marine species. Algal epiphytes often inhabit the intertidal zone of rocky coastlines. This environment consists of a narrow band of substratum characterized by dense populations of marine organisms that must tolerate stresses associated with exposure to terrestrial conditions at low tide. Because intertidal organisms are constrained to a small region, there is pronounced competition for space (Dayton, 1971). Marine algal epiphytes may have evolved to avoid or decrease space competition in the intertidal zone by growing on other algae instead of vying for space on bare rock (Seed, 1986; Wahl, 1989; Todd and Keough, 1994). The evolution of epiphytism may have also implicated epiphyte access to nutrients and light, as well as epiphyte herbivory (Harder,

2008). Interactions between intertidal epiphytic algae and hosts are complex, however, and have not been well assessed.

While terrestrial studies rarely take into account the impacts of epiphytes on their hosts, research on marine epiphytes generally focuses on these effects (Littler and Littler, 1999; Hay et al., 2004; Harder, 2008). This could be because marine epiphytes are often large relative to their hosts; for example, algal epiphytes growing on certain types of seagrasses have been shown to comprise up to 95% of above ground biomass in these systems (Mukai and Ishijima, 1995). This is unlike terrestrial epiphytes that are usually much smaller than their hosts which often tend to be large trees. Large aquatic epiphytes may have large negative impacts on their small hosts. This aquatic host-epiphyte size discrepancy may be especially important in regards to epiphytic biomechanical and photosynthetic relationships, host desiccation, and interactions involving herbivory.

Intertidal organisms are heavily affected by hydrodynamic forces (Denny, 1988); drag forces in the intertidal zone have been estimated to reach orders of magnitude larger than similar drag forces experienced by land plants (Denny and Gaylord, 2002). The extent to which drag affects objects in flow is partly dependent on size (Denny, 1988), and aquatic epiphytes often add substantial surface area to hosts. Light acquisition interactions between terrestrial hosts and epiphytes differ from those of marine epiphytic systems; terrestrial epiphytes benefit by varying their vertical position within canopies to acquire necessary amounts of light (Sillet, 1994; Hietz and Briones, 1998, 2000), whereas marine epiphytes often harm hosts by reducing light availability (Sand-Jensen, 1977; Sand-Jensen and Borum, 1984). Marine studies on desiccation have demonstrated that epiphytes decrease dehydration of seagrass hosts during low tide (Penhale and Smith, 1977; Richardson, 1980), but epiphytic terrestrial studies on this same topic

focus on epiphytes only and how their position on hosts mediates epiphytic desiccation. This is likely because vascular hosts attain the majority of their water requirements through underground root systems (Taiz and Zeiger, 2002), and their relatively small epiphytes are unlikely capable of affecting host water retention. Lastly, reductions in epiphyte cover via herbivore grazing have mostly been regarded as indirect benefits to aquatic hosts (Brönmark, 1989); on the other hand, direct herbivory of terrestrial epiphytes seems less common (but see Nadkarni and Matelson, 1989).

In sum, marine algal epiphytes exist in an environment distinct from terrestrial equivalents in that they must contend with submersion. Terrestrial hosts, such as trees, generally seem unaffected by epiphytes while aquatic hosts likely experience costs due to epiphyte cover (Figure 1). Just as it is injurious for parasites to overly affect the hosts upon which they depend (Anderson and May, 1978), so it would seem maladaptive for epiphytes to inflict excessive harm to hosts, thereby causing mortality and possibly evolutionary selection against epiphytic settlement on hosts. Epiphytes in both terrestrial and aquatic ecosystems have generally been assumed to benefit by living epiphytically (Harder, 2008) (Figure 1); although positive interactive effects are not necessary for evolutionary progression, beneficial responses could expedite and help explain the evolution and continued persistence of epiphytic relationships. An increased understanding of aquatic epiphytic interactions could help inform our knowledge of terrestrial systems and vice versa. Epiphytic relationships may be more complex than supposed; hosts and epiphytes likely experience a continuum of associational effects that result in beneficial or negative outcomes.

	Hosts	Epiphytes
Terrestrial	Neutral	**Benefit**
Aquatic	**Costs**	**Benefit**

Figure 1: General paradigm of costs and benefits experienced by terrestrial versus aquatic hosts and epiphytes.

Costs to aquatic hosts

Aquatic epiphytism has generally been regarded as deleterious to host species (Littler and Littler, 1999; Hay et al., 2004; Harder, 2008). The biomechanical effects of epiphytes on hosts could coincide with this common concept of epiphytes harming hosts. Epiphytic algal systems often occur in challenging hydrodynamic environments. Although little has been done on the biomechanics of host-epiphyte interactions, it has been shown that fouling organisms increase drag on intertidal red algal hosts (Ruesink, 1998). Increases in drag could in turn increase the likelihood of algal host dislodgement and mortality.

Epiphytes are also thought to hinder the acquisition of light by hosts; algal epiphytes often shade host tissue which reduces photosynthesis and subsequent growth of hosts (Sand-Jensen, 1977; Sand-Jensen and Borum, 1984). A majority of studies demonstrating light attenuation caused by epiphytes have focused on seagrass host species (Brush and Nixon, 2002; Drake et al., 2003; Williams and Ruckelshaus, 1993; Tomasko and Lapointe, 1991), and not fleshy algal host-epiphyte interactions. Findings from studies on seagrasses cannot necessarily be generalized; these organisms often inhabit calm and protected environments (excluding species in the genus *Phyllospadix*) that are characterized by physical factors much different from those

5

experienced by organisms on most rocky outer-coasts. For example, in sheltered aquatic areas, the effects of drag are often negligible, but light acquisition can be challenging (Larkum et al., 2010). Conversely, the wave-swept intertidal zone experiences frequent water motion that increases the effects of drag, but simultaneously repositions algal thalli resulting in decreased difficulty with which algae intercept light due to reductions in self-shading (Koehl and Alberte, 1988; Norton, 1991).

Epiphytes may also hinder the exchange of gases and nutrients at the surface of hosts (Jagels, 1973; Sand-Jensen et al., 1985). Marine seaweeds do not have specialized structures for uptake of nutrients and exchange of gases; instead, these substances are diffused across cell membranes throughout algal thalli (Wheeler, 1980). Thus, anything interfering with exchange processes likely has negative effects on host algae. Epiphytes compete for nutrients with their hosts; when nutrient levels are high, epiphyte growth often increases at the expense of host growth (Worm, 2000; Tomasko and Lapointe, 1991). This decrease in host growth could be simultaneously due to an increase in indirect competition for light between hosts and epiphytes (Sand-Jensen 1977, Sand-Jensen and Borum 1984). Epiphytic photosynthesis also causes a build-up of oxygen around host surfaces that increases the difficulty of transporting dissolved substances across these surfaces (Jagels, 1973; Sand-Jensen et al., 1985). Negative impacts such as these may ultimately result in decreased reproductive output of host algae (D'Antonio, 1985).

Another possible cost experienced by hosts is increased herbivory. Certain epiphytes may attract herbivores that would otherwise avoid grazing particular host species (Dixon et al., 1981). Although many studies have described deleterious effects of epiphytism on hosts, there is a paucity of studies investigating how epiphytes benefit from associating with hosts.

Benefits to aquatic epiphytes

Epiphytic species are nested within clades of species that grow on rock in all major seaweed groups (Abbott and Hollenberg, 1976); thus, epiphytism appears to be a derived life-history trait that has arisen several times, perhaps from a common selective pressure. The continued existence of epiphytism suggests epiphytes benefit, or at least are not harmed, by growing on hosts. For example, epiphytes often grow in elevated positions on hosts. This elevation could increase epiphytic access to nutrients (Keough, 1986); because seaweeds uptake nutrients via diffusion (Wheeler, 1980), the farther they are from the substratum, the more flow they experience and the more nutrients are delivered (Falkowski and Raven, 2007). Being elevated above the substratum also exposes epiphytes to greater light levels, manifesting in higher rates of photosynthesis (Brouns and Heijs, 1986). This elevated position could help epiphytes escape herbivory by benthic grazers as well (Brönmark, 1989). Herbivores may avoid epiphytes that successfully settle on hosts with chemical defenses; i.e. if predators avoid specific defended hosts, associated epiphytes may also be spared (Hay, 1986).

Costs to aquatic epiphytes

Although there are few studies demonstrating benefits incurred by epiphytes, there are even fewer that address epiphytes experiencing associational costs. This may be because it is assumed there is some sort of fitness benefit that led to the evolution of epiphytism. Epiphytes may experience costs by comprising the outer layer of hosts, however; occupying this position may place them in more direct contact with herbivore mouthparts which might be especially problematic if certain hosts are particularly attractive to predators. In this case, associated epiphytes, that would otherwise be avoided, might be eaten during predators' attempts at grazing

hosts (Wahl and Hay, 1995). Hosts may also provide unstable/breakable settlement surfaces for epiphytes, leading to dislodgment and subsequent mortality of epiphytes (Harder, 2008). Similarly, some algae are obligate epiphytes that must grow on specific hosts to survive (Lobban and Harrison, 1994); when this is the case, the absence of specific hosts would preclude obligate epiphytes from settling and persisting in specific habitats.

Benefits to aquatic hosts

Aquatic epiphytism is generally considered detrimental to hosts, yet epiphytism remains a common interaction throughout aquatic ecosystems; this suggests that hosts may actually benefit in some capacity by being epiphytized. Sometimes herbivores prefer grazing epiphytes over hosts. Brönmark (1989, 1985) found herbivorous snails decreased the amount of epiphytes on the freshwater macrophyte, *Ceratophyllum demersum*, which ultimately facilitated host growth – likely because shading caused by epiphytes was decreased. Karez et al. (2000) found that the presence of epiphytic *Ulva lactuca* and *Elachista fucicola* on the brown alga, *Fucus vesiculosus*, shielded the host from herbivory by gammarid amphipods; only when epiphytes were absent did these herbivores eat *F. vesiculosus*. Algae that grow on some invertebrates, such as decorator crabs, have also been shown to protect their hosts from predation by serving as chemical deterrents or camouflage (Stachowicz and Hay, 1999).

Epiphytes may protect hosts against desiccation and deleterious effects of excess light as well. Desiccation impacts intertidal seaweeds during emersion at low tide by causing cellular damage, decreases in photosynthesis, and potential mortality (Davison and Pearson, 1996; Lobban and Harrison, 1997). Thus, adaptations that reduce desiccation in the intertidal zone are beneficial for seaweed survival. Algal epiphytes have been shown to reduce desiccation of

seagrasses in shallow estuarine areas during low tide, when the sun is out and the weather is warm, by trapping seawater between blades (Penhale and Smith 1977; Richardson, 1980). During low tide, intertidal algae are sometimes exposed to detrimental light levels as well; it is possible that epiphytes help shade hosts and protect against damaging irradiances.

Study system

Soranthera ulvoidea Postels *et* Ruprecht (*Soranthera*) is a conspicuous brown algal epiphyte in the family Chordariaceae (Cho et al., 2005). The sporophyte stage of this alga is a summer annual that grows as obligate saclike epiphytes on particular species of branched red algae in the mid to low intertidal zone from the Bering Sea to California (Abbott and Hollenberg, 1976). The perennial red alga, *Odonthalia floccosa* (Esper) Falkenberg (*Odonthalia*), grows on rocks throughout this same range, and often hosts the epiphyte, *Soranthera* (Abbott and Hollenberg, 1976) (Figure 2).

Figure 2: Line drawing of *Soranthera ulvoidea* growing epiphytically on *Odonthalia floccosa*.

Chapter 1 of this thesis investigates biomechanical interactions between the host, *Odonthalia*, and the epiphyte, *Soranthera*. Dislodgement forces of hosts were measured in the field, and drag forces were measured on hosts with and without epiphytes in a recirculating water flume. Predictions were then made about the effects of epiphyte cover on host drag and dislodgement. Epiphytes were found to increase drag on hosts, which also increased the risk of hosts being dislodged from the substratum. The biomechanical benefits of growing epiphytically were also explored, and it was shown that epiphytes experience reduced flow when attached to hosts. Lastly, the likelihood of which constituent breaks first in periods of hydrodynamic stress was compared – hosts and epiphytes were equally likely to break when exposed to high water velocities.

Chapter 2 examines the effects of epiphytism on light acquisition, host desiccation, and herbivory. Photosynthesis was measured under varying levels of irradiance for both *Odonthalia*, and *Soranthera*; epiphytes appeared to have a neutral effect on host light acquisition. Concomitantly, epiphytes were capable of reaching photosynthetic saturation when exposed to low light levels experienced beneath other algae, suggesting that they need not grow above hosts to gain access to light. Desiccation of emergent epiphytized and non-epiphytized hosts was monitored and epiphytes were found to delay host desiccation during periods of aerial exposure. Finally, the feeding preferences of three types of intertidal grazers were tested. All three herbivores preferred eating epiphytes over hosts, suggesting that hosts may benefit from being epiphytized.

Chapter 1

Biomechanical consequences of intertidal algal epiphytism

1.1 Introduction

The rocky intertidal zone is one of the most hydrodynamically stressful environments on Earth. Organisms in this habitat must persist when routinely exposed to forces well in excess of similar forces applied by wind in hurricanes (Denny and Gaylord, 2002). Intense wave action has been shown to affect mortality of individuals (Vadas et al., 1990; Shaughnessy et al., 1996), species distributions (Paine, 1979; Nielsen et al., 2006), as well as inter- and intra-specific interactions (Blanchette, 1997; Jonsson et al., 2006); all of which consequently affect overarching patterns of zonation (Harley and Helmuth, 2003; Harley and Paine, 2009) and community structure (Connell, 1972) in the intertidal zone.

1.1.1 Drag and dislodgement

Drag is one of the primary hydrodynamic forces experienced by intertidal organisms; it is encountered by objects in moving fluids, and acts in the same direction as flow (Carrington, 1990). Drag forces on intertidal organisms are proportional to water density, water velocity squared, organismal surface area perpendicular to flow, and drag coefficient – a parameter that varies with organismal shape (Denny, 1988). Whereas motile organisms are capable of relocating to spaces less affected by hydrodynamic stresses, sessile organisms such as seaweeds cannot (Bradshaw, 1972; Huey et al., 2002). Instead, macrophytes must either resist or reduce the amount of drag experienced in flow (Puijalon et al., 2008) to survive in environments characterized by frequent hydrodynamic disturbance. As seaweeds are important constituents of the intertidal zone that provide both food and habitat for other organisms, reductions in algal

abundance [due to hydrodynamic forces] could have cascading effects on intertidal ecosystems (Wahl, 2008).

By dislodging seaweeds before reproduction has occurred, wave forces are capable of exerting selective pressures on seaweed properties such as mechanical design; this results in the evolution of mechanisms by which algae resist or limit the amount of drag they experience. Algae either withstand drag by increasing tenacity and tissue strength (Koehl, 1984; Martone, 2007; Kawamata, 2001), or reduce drag by altering their size and shape in flowing water (Martone et al., 2012). Large sizes and certain algal shapes that are not streamlined increase drag and dislodgement of seaweeds (Denny et al., 1985; Gaylord et al., 1994). Many macroalgae consist of flexible tissue, however, which enables them to reduce drag by reconfiguring in flow (Boller and Carrington, 2006a; Demes et al., 2011; Harder et al. 2004); this in turn facilitates beneficial changes in shape and reductions in size (Martone et al., 2012). Sometimes, however, events still transpire that manage to rip seaweeds from the substratum and cast them ashore.

1.1.2 Epiphytes

Despite hydrodynamic stresses in the intertidal zone, rocky coastlines are highly populated by a diverse array of organisms; this often leads to a scarcity of bare space for colonization (Dayton, 1971). Intertidal epiphytism may have evolved as a solution to space competition, and epiphytic seaweeds have fundamentally circumvented this pressure by settling and growing on other organisms (Seed, 1986; Wahl, 1989; Todd and Keough, 1994). Because epiphytes add surface area to hosts, change the overall shape of their hosts, and potentially affect the ability of hosts to reconfigure in flow, fouling organisms increase drag on both intertidal seaweeds (Ruesink, 1998) and invertebrates (Witman and Suchanek, 1984; Wahl, 1996). For example, mussels with algae growing on their shells have been shown to experience increased

dislodgement in the field following heavy wave action and storm events (Witman and Suchanek, 1984; O'Connor et al., 2006). Because dislodgement often leads to death, and adhering to substrata is generally required for most intertidal organisms to successfully complete their life history, it behooves these organisms to resist dislodgement in this environment. This situation is a double edged sword for epiphytes – they must hold on tight to their hosts but are not guaranteed survival as their hosts may fail beneath them. How do epiphytes affect drag experienced by hosts? Does an increase in drag due to epiphytism always translate to increased host (and thereby epiphyte) dislodgement? If so, why hasn't intertidal epiphytism been selected against?

1.1.3 Chapter objectives

This study aimed to address four specific biomechanical questions regarding host-epiphyte interactions: (1) do epiphytes increase drag on hosts? (2) If so, is host dislodgement risk always increased? (3) Do epiphytes receive a hydrodynamic benefit by growing on hosts? (4) Which constituent of this system experiences mechanical failure more frequently: hosts or epiphytes?

1.2 Methods

1.2.1 Specimen collection

Epiphytized *Odonthalia* were haphazardly collected from the mid to low intertidal zone northwest of Fulford Harbour on Salt Spring Island, British Columbia, Canada (48°45'23.98"N 123°25'16.06"W) between May 20th and June 16th, 2011. Algae were placed in plastic Ziploc® bags, transported in a cooler with an ice pack, and deposited into a recirculating chilled seawater table at the University of British Columbia (UBC) within 5 hours of collection. Water table

13

conditions were kept between 8 and 10˚ C with 14 hours of fluorescent light per day (~115µmol

$m^{-2}s^{-1}$). All algae were tested within 18 days of collection.

Unepiphytized *Odonthalia* used for the second set of methods in section 1.2.3 were

haphazardly collected from the mid to low intertidal zone in Ruckle Provincial Park on Salt

Spring Island, British Columbia, Canada (48°46'30.23"N 123°22'3.89"W) on February 18th,

2012. Algae were placed in plastic bags and kept in a refrigerator overnight, until transported in a

cooler with an ice pack to the recirculating chilled seawater table at UBC the next day. Water

table conditions were the same as above; all algae were experimented upon within 30 days of

collection, at which point they visually appeared in the same condition as they did upon

collection.

1.2.2   Host drag and dislodgement

Forces to dislodge epiphytized *Odonthalia* fronds (n = 15) from the substratum in the

field were measured using a recording spring scale (Ohaus Corp., Pine Brook, NJ, USA). Size

and number of epiphytes varied among these differently sized host fronds. All epiphytes less

than 10 mm in length were removed from host fronds due to difficulty attaching these to

equipment for subsequent related experiments (section 1.2.3). Drag was measured on *Odonthalia*

fronds in a custom high-speed recirculating water flume (Ecological Mechanics, Rochester, NY,

USA) (Figure 3; modified from Boller and Carrington, 2006a). Each host was tied with thread to

a metal wire attached to a calibrated force transducer (World Precision Instruments, Inc.,

Sarasota, FL, USA), suspended in the flume, and subjected to 7 different water velocities (0,

0.25, 0.5, 0.75, 1, 1.5, 2 ms^{-1}). Maximum water velocities at this study's field site ranged from

4.2 to 9.4 ms^{-1}, but the flume could not produce velocities exceeding 2 ms^{-1}. Drag forces

experienced by fronds at these velocities were recorded with LabVIEW (National Instruments,

14

Austin, TX, USA). All remaining epiphytes were then detached and drag was measured a second time on these hosts without epiphytes at the same speeds. To determine whether epiphytes significantly affect drag on hosts, paired *t*-tests were conducted on drag forces experienced by epiphytized and unepiphytized hosts at each velocity using SYSTAT 13 (SYSTAT Software Inc., San Jose, CA, USA), $\alpha = 0.05$.

Figure 3: Custom high-speed recirculating water flume with which measurements of drag were taken on hosts and epiphytes (modified from Boller and Carrington, 2006a).

To test how epiphytes affect the drag coefficient of their hosts, the equation (1) for drag force (F):

$$F = \frac{1}{2}\rho U^2 A C_d \tag{1}$$

was rearranged to solve for drag coefficient (C_d), a dimensionless parameter that varies with algal shape (Carrington, 1990; Gaylord et al., 1994; Bell, 1999; Martone and Denny, 2008; Martone et al., 2012):

$$C_d = \frac{2F}{\rho U^2 A} \qquad (2)$$

where ρ is the density of seawater (approximately 1000 kgm^{-3}), U is water velocity, and A is planform area of hosts. Areas of all algae in this study were determined digitally from photographs (Olympus Stylus Tough 6020) using ImageJ (National Institutes of Health, Bethesda, MD, USA). C_d was calculated for each unepiphytized host at each velocity in the flume (n = 14). Drag coefficients were then plotted against Reynolds number (Re), a parameter that takes into account both algal size and the test velocity experienced by each host frond:

$$Re = \frac{L\,U}{\upsilon} = \frac{\sqrt{A}\,U}{\upsilon} \qquad (3)$$

where L is characteristic length (here assumed to be $\sqrt{A}$), υ is the kinematic viscosity of seawater (1×10^{-6} m^{2}s^{-1}), and A is planform area of hosts. Data were log transformed and lines were fitted to log C_d versus log Re for each frond. C_d and Re were then calculated for hosts with epiphytes (n = 14) using equations 2 and 3; (area$_{host}$ + total area$_{epiphytes\ per\ host}$) was substituted for A in both equations. These data were also log transformed and lines were fitted to these log C_d values versus values of log Re for each host frond. To determine whether algal epiphytes significantly affect the drag coefficient of their hosts as Re increases, a paired t-test was carried out on the slopes of C_d versus Re for each frond with and without epiphytes using SYSTAT 13.

Drag force experienced by epiphytized hosts (n = 14) was plotted against water velocity, and, because drag increases with velocity squared (Denny, 1988), quadratic curves ($F=kU^2$, where k is a constant and represents ($\frac{1}{2}\rho A C_d$) in equation 1) were fitted to these data using Table

Curve 2D v 5.01 (SYSTAT Software Inc., San Jose, CA, USA). Because k is a constant, Cd was

assumed to be constant, stabilizing at a point where reconfiguration was maximized (Bell, 1999),

values of which were generally less than Cd values calculated at 2 ms^{-1}. Quadratic curves were

extrapolated to the dislodgement forces measured in the field for each frond, and water velocities

required to break these fronds were estimated. Predicted breakage velocities were also

determined by fitting the same quadratic curves to force-velocity data for hosts without epiphytes

(n = 14). To determine whether the presence of epiphytes significantly affects the dislodgement

risk of hosts, a paired *t*-test was carried out to compare predicted breakage velocities for hosts

with and without epiphytes using SYSTAT 13.

1.2.3 Epiphyte drag and dislodgement

Two methods were used to determine whether epiphytes receive a hydrodynamic benefit

by being attached to hosts. First, drag was measured on epiphytized hosts ($DRAG_{together}$, n = 14),

and then on these same hosts with epiphytes removed ($DRAG_{hosts}$) at 7 test velocities (0, 0.25,

0.5, 0.75, 1, 1.5, 2 ms^{-1}). Drag experienced by epiphytes was then estimated by subtracting

$DRAG_{hosts}$ from $DRAG_{together}$, assuming the difference represented the amount of drag added by

epiphytes alone. Drag was then measured on detached epiphytes, and summed for all epiphytes

per host (Total $DRAG_{epi}$). Total $DRAG_{epi}$ was plotted against ($DRAG_{together}$- $DRAG_{hosts}$) to

determine whether drag experienced by detached epiphytes was different from drag experienced

by epiphytes attached to hosts. Departures from the 1:1 line of unity were evaluated using a least

squares regression model with the null slope set to 1 in SYSTAT 13. A negative departure from

this line of unity indicates epiphytes on hosts experience greater drag then epiphytes alone,

whereas, a positive departure from the 1:1 line would signify Total $DRAG_{epi}$ is greater than

($DRAG_{together}$- $DRAG_{hosts}$).

Second, hydrodynamic benefits of epiphytism were examined directly by measuring "Pep-o-mint" Lifesaver® dissolution on and off hosts in the flume; dissolution is a proxy for water movement (Koehl and Alberte, 1988). Individual Lifesavers (n = 10) were tied to the wire on the force transducer and put in the flume for 1 minute at each of the following velocities: 0, 0.5, 1, 1.5, 2 ms^{-1}. Then, a Lifesaver was tied to a branch near the middle of a randomly selected host frond without epiphytes (n = 10) and put in the flume for 1 minute at each of the above velocities. Lifesavers were attached to branches in the middle of hosts because these are larger and presumably stronger; thus it was less likely the thread would cause these branches to break in flow. After being removed from the flume, Lifesavers were dried in an oven at 60˚C for 48 hours. Dried mass of experimental Lifesavers was subtracted from original mass to determine mass lost in the flume; mass loss was used as a proxy for water flow from which drag force was calculated (see below). To test whether mass lost by Lifesavers on and off hosts at different velocities was significantly different, an analysis of covariance (ANCOVA) was run on the average mass loss of Lifesavers on and off hosts at each velocity using SPSS Statistics 17.0 (SPSS, Inc., Chicago, IL, USA). The interaction term was examined to determine whether the slopes of the lines fitted to the average mass lost by Lifesavers on and off hosts versus flume test speeds were different.

Mass loss was plotted against water velocity for Lifesavers on and off hosts. To obtain velocities actually experienced by Lifesavers on hosts, i.e. "effective velocities," a line was fitted to average mass loss of Lifesavers not on hosts versus flume test velocities and the slope of this line was applied to mass loss measurements for Lifesavers on hosts. These "effective velocities" experienced by Lifesavers on hosts were plotted against velocities controlled by the flume ("true velocities"). A power curve was fitted to these data, and the equation for this curve was applied

to flume velocities run on actual epiphytes to determine "effective velocities" experienced by each epiphyte. Quadratic curves (F = kU^2) were fitted to force readings experienced by epiphytes versus "effective velocities" experienced by epiphytes. Cd (inherently connected with the constant k) was assumed constant and stable as described in 1.2.2. The constants (k) for these curves were used to correct the original drag force readings at these velocities for each individual epiphyte. These corrected force values for epiphytes were plotted against actual flume velocities and extrapolated to individual epiphyte removal forces. Removal forces were measured with a recording spring scale when epiphytes were dislodged from hosts in section 1.2.2. In this way, predicted breakage velocities for individual epiphytes were determined.

Occasionally, epiphytes dislodged from their hosts when drag on epiphytized hosts was being measured in the flume; actual removal forces were not able to be obtained for these individual epiphytes. In these instances, removal forces were estimated by fitting a line to epiphyte size by removal force data collected for 64 random epiphytes. Epiphyte size was then used to predict removal force using this regression. A paired *t*-test was carried out to determine whether velocities predicted to dislodge epiphytes from hosts were significantly different from those predicted to dislodge hosts from the substratum using SYSTAT 13.

To explore where epiphytes are commonly attached, primary, secondary, and tertiary host branches (Figure 4) were examined on 20 algal pressings from the UBC herbarium. Forces to break these branch types were subsequently measured on fresh specimens (N = 56) using a recording spring scale. To determine whether epiphytes are more likely to dislodge at their point of attachment, or to break with a piece of host branchlet attached, epiphyte removal forces were compared to branchlet breakage forces using a two sample *t*-test in SYSTAT 13. Most epiphytes

were attached to tertiary branchlets, and the maximum breakage force of a tertiary branchlet was 1N; thus, this value was used to estimate dislodgement of epiphytes in the field (see below).

Figure 4: Host branch types of which removal forces were measured.

To estimate the maximum size and water velocity that causes epiphytes to dislodge from hosts, drag force measurements for individual epiphytes (that were corrected using Lifesaver data) were plotted against Re (Equation 3). Lines were fitted to these log transformed data, and after being back-transformed out of log form, extrapolated to the maximum removal force for a tertiary host branch (1N); this allowed critical Re (Re_{crit}) to be obtained (Martone and Denny, 2008). Re_{crit} represents the critical combination of epiphyte size and water velocity that would dislodge epiphytes from their hosts. For comparison, drag force measurements on epiphytes that were not corrected using Lifesaver data were utilized in the same manner as above, and Re_{crit} values for these were also obtained.

Once Re_{crit} was estimated for both corrected and uncorrected drag force measurements on individual epiphytes, Equation 3 was rearranged as follows:

20

$$U_{\text{crit}} = \frac{\text{Re}_{\text{crit}}}{\sqrt{A} * \upsilon} \tag{4}$$

Theoretical values for epiphyte area (A) were substituted into this equation (4) to determine

critical water velocities (U_{crit}) that would dislodge epiphytes of given sizes from hosts. The same

was done using Re_{crit} for epiphytes not attached to hosts, i.e. theoretically growing on rock.

1.2.4   Field measurements

Maximum water velocity was measured monthly between May and August, and once

between September and November, in 2011 at the algal collection site on Salt Spring Island

using 10 calibrated dynamometers (Bell and Denny, 1994). Dynamometers were set up

approximately 10 meters from one another along the mid intertidal zone where *Odonthalia* was

common. Two holes were drilled in the rock, parallel to shore, into which wall anchors and

screws were inserted; a dynamometer was secured to these screws using zip ties so the affiliated

whiffle ball would be pulled perpendicular to shore by wave action. To observe the state of hosts

and epiphytes after becoming dislodged from along the collection site, drift *Soranthera* and

Odonthalia were collected from this area and photographed on June 16th, 2011.

1.3   Results

1.3.1   Host drag and dislodgement

Drag increased on both epiphytized hosts and unepiphytized hosts as water velocity

increased in the flume (Figure 5). At each test velocity, however, epiphytized hosts experienced

significantly more drag than unepiphytized hosts (Table 1). On average, epiphytes added 50.6 ±

4.5 % (mean ± SE) more drag to hosts at each test velocity (Figure 5).

Table 1: Drag forces (± SE) experienced by hosts with epiphytes and hosts alone in the flume at different velocities along with paired *t*-test results.

Velocity (ms^{-1})	Drag$_{epiphytized host}$ ± SE (N)	Drag$_{host alone}$ ± SE (N)	t	df	p-value
0.25	0.04±0.01	0.03±0.004	4.124	13	0.001
0.50	0.11±0.01	0.08±0.01	7.323	13	0.0001
0.75	0.17±0.02	0.12±0.02	6.796	13	0.0001
1.00	0.24±0.03	0.16±0.02	6.573	13	0.0001
1.50	0.43±0.04	0.29±0.04	7.710	13	0.0001
2.0	0.61±0.08	0.45±0.06	7.285	10	0.0001

Figure 5: Average drag force experienced by hosts with epiphytes (closed circles) and hosts alone (open circles) at different test velocities in a recirculating water flume. n = 14 for 0 - 1.5 ms^{-1} and n = 11 for 2 ms^{-1}. Error bars are SE. * denotes paired *t*-test results < 0.05.

Drag coefficient for both hosts with and without epiphytes declined with increasing Re (Figure 6). Epiphytes did not affect the drag coefficient of their hosts, as slopes of lines fitted to C_d versus Re for each fond with (n = 14) and without epiphytes (n = 14), and compared using a paired t-test, were not significantly different (t = - 0.354, df = 13, p > 0.7).

Figure 6: Log drag coefficient versus log Reynolds number of hosts with epiphytes (closed circles) and hosts alone (open circles). n = 14 for 0 - 1.5 ms^{-1} and n = 11 for 2 ms^{-1}.

Velocities predicted to dislodge hosts with epiphytes and hosts alone were significantly different ($t = 5.094$, df = 13, $p < 0.01$, Figure 7). On average, epiphytized hosts were predicted to resist only 5.7 ± 0.5 ms^{-1} water velocity before dislodging from the substratum, whereas hosts alone were predicted to break at 7.2 ± 0.7 ms^{-1} (means $\pm$ SE).

Figure 7: Predicted breakage velocities for hosts without epiphytes versus predicted breakage velocities for the same hosts with epiphytes. n = 14.

1.3.2 Epiphyte drag and dislodgement

Total DRAG$_{epi}$ was often greater than Drag$_{together}$ - Drag$_{host}$, especially when forces were above 0.15 N (Figure 8). The linear trendline of Total DRAG$_{epi}$ plotted against DRAG$_{together}$ - DRAG$_{host}$ fell above, and was significantly different from, the 1:1 line of unity ($t = 3.471$, df = 76, p < 0.001); this suggests epiphytes attached to hosts experience less drag than epiphytes not attached to hosts.

Figure 8: Total drag on epiphyte loads not attached to hosts versus epiphyte loads attached to hosts. Solid line is least squares trendline. Dotted line is the 1:1 hypothetical line of unity.

On average at all velocities, Lifesavers lost significantly more mass in the flume when not attached to hosts (Table 2, Figure 9). Original Lifesaver mass was 3.67 ± 0.09 g (mean ± sd). At 0.5 ms^{-1}, Lifesavers attached to hosts lost 0.62 ± 0.02 g while Lifesavers alone lost 0.73 ± 0.03 g. At 1 ms^{-1}, Lifesavers on hosts lost 0.96 ± 0.05 g, and Lifesavers alone lost 1.27 ± 0.12 g. Also, at 1.5 ms^{-1}, Lifesavers on hosts lost 1.27 ± 0.12 g while Lifesavers alone lost 1.70 ± 0.08 g. And, lastly, at 2 ms^{-1}, Lifesavers on hosts lost 1.55 ± 0.09 g, whereas Lifesavers alone lost 2.28 ± 0.10 g. Reported values are means ± SE.

Table 2: ANCOVA results for average mass lost by Lifesavers alone in the flume and Lifesavers attached to hosts in the flume at different velocities. Treatment is Lifesavers on or off hosts.

Source	Type III Sum of Squares	df	Mean Square	F	p-value
velocity	4.318	1	4.318	391.068	0.0001
treatment	0.001	1	0.001	0.122	0.739
velocity*treatment	**0.158**	**1**	**0.158**	**14.267**	**0.001**
error	0.066	6	0.011		

Figure 9: Average mass loss of Lifesavers alone (open circles) and Lifesavers on hosts (closed circles) at different velocities in a flume. Lines are linear trendlines for Lifesavers alone (dashed) and Lifesavers on hosts (solid). n = 10. Error bars are SE.

Ten out of 15 epiphytized hosts were predicted to break before any of their epiphytes, whereas, the remaining 5 hosts were predicted to lose epiphytes before being dislodged from the substratum (Table 3). However, velocities predicted to dislodge epiphytized hosts were not significantly different from velocities predicted to dislodge epiphytes ($t = -1.472$, df = 14, p > 0.2); this suggests that both hosts and epiphytes are equally likely to dislodge. In fact, 7 out of 15 (47%) hosts had an epiphyte actually dislodge while being tested in the flume.

Table 3: Predicted breakage velocities for hosts with epiphytes and velocities predicted to break the weakest epiphyte on each host. Bold values* denote epiphytes predicted to dislodge before corresponding hosts.

	Predicted Breakage Velocities (ms^{-1})	
Sample	Hosts with Epiphytes	Weakest Epiphyte
A	9.8	**8.4***
B	8.3	8.9
C	8.1	**6.0***
D	7.0	**5.2***
E	6.7	**6.4***
F	6.5	12.1
G	6.0	10.0
H	5.9	**4.2***
I	4.9	6.5
J	4.9	5.3
K	4.8	5.2
L	4.6	5.5
M	4.1	6.2
N	3.8	4.2
O	2.9	8.3

Re$_{crit}$ was higher for epiphytes on hosts (4.4x10^5) than for epiphytes alone (3.0x10^5) (Figure 10). When Re$_{crit}$ values were used in conjunction with theoretical epiphyte sizes, a model was generated to predict breakage velocities (Figure 11). According to the model, larger epiphytes require less velocity to be dislodged than smaller epiphytes, and epiphytes on hosts can resist faster flow and grow over twice the size of epiphytes theoretically growing on rock. For instance, at 9.4 ms^{-1} (the maximum velocity experienced at this study's field site), an epiphyte attached to a host should be able to grow up to 21 cm^2, whereas, a theoretical epiphyte exposed to the same velocity but not attached to a host, can only grow up to 9 cm^2 – less than half the area.

Figure 10: Force experienced by epiphytes not attached to hosts (open circles; dotted curve fit extrapolation) and force experienced by epiphytes on hosts (closed circles; solid curve fit extrapolation) plotted against Reynolds numbers. Dashed line represents the force at which tertiary branchlets break along with attached epiphytes. Dotted arrow depicts Re_{crit} for epiphytes not attached to hosts; solid arrow is Re_{crit} for epiphytes on hosts.

Figure 11: Water velocities predicted to dislodge epiphytes on hosts (solid line) and epiphytes theoretically attached to rocks (dotted line). Arrows depict the maximum attainable sizes of epiphytes not attached to a host (dotted) and epiphytes attached to hosts (solid) at the collection site. The triangle depicts the epiphyte with the largest area observed during the course of this study.

29

Out of 400 epiphytes observed on 20 pressings from the UBC herbarium, the majority of

Soranthera epiphytes were attached to tertiary branchlets (Table 4). On average, primary

branches of hosts resisted the most force, and tertiary branchlets resisted the least (Table 4). The

maximum force required to break a tertiary host branchlet was 1 N, and the maximum force

observed to break an epiphyte at its point of attachment was 1.2 N.

Table 4: Average removal forces (N = 56), maximum removal forces, and percentages of epiphytes on 20 UBC herbarium pressings attached to primary, secondary, and tertiary host branchlets (N = 400 epiphytes).

Host Branch	Avg. Break Force ± sd (N)	Max. Break Force (N)	% Attachment Location in Herbarium
Primary	2.0±1.3 (n = 15)	6.3	0.3 (n = 1)
Secondary	1.0±0.7 (n = 17)	2.4	17.0 (n = 68)
Tertiary	0.4±0.3 (n = 24)	1.0	82.8 (n = 331)

1.3.3 Field measurements

The highest maximum water velocity recorded by a dynamometer at the algal collection site on Salt Spring Island between May and November was 9.4 ms^{-1} (Table 5). Both epiphytes alone and entire epiphytized hosts (Figure 12) were found as drift algae along the beach near the algal collection site on Salt Spring Island.

Table 5: Maximum water velocities measured by dynamometers at the algal collection site between May and November, 2011.

Month	Max Water Velocity (ms^{-1})
May	9.4
June	4.2
July	8.1
Aug	4.2
Sept-Nov	5.2

Figure 12: Image of *Soranthera* individuals and pieces of host with attached *Soranthera* individuals that dislodged from hosts (a), and entire epiphytized hosts that broke from substratum in the field (b).

1.4   Discussion

The intertidal zone is hydrodynamically stressful for seaweeds. Algae that are large and shaped in such a way that makes them not streamlined are often at risk of dislodgement and mortality (Denny et al., 1985; Gaylord et al., 1994). Epiphytic algae may negatively affect both size and shape of host algae, which could in turn affect the survival of hosts. *Soranthera* is one such epiphyte that likely complicates interactions involving drag forces imposed by moving water and intertidal host algae. These complex interactions are widespread in the intertidal zone; however, little biomechanical research has been done on marine algal epiphytism.

1.4.1   Biomechanical costs of epiphytism

This study showed that a typical load of *Soranthera* epiphytes increased drag on their hosts by approximately 50% at all speeds tested within a flume. This increase in drag is likely due to increased surface area caused by the addition of epiphytes, and not to a change in drag coefficient. Drag coefficient of hosts was not significantly affected by the addition of epiphytes; this likely means, although epiphyte morphology appears different from hosts, epiphytes do not change the "functional shape" of these hosts in flow (Figure 6). This is in accordance with findings from the field; *Odonthalia* fouled with diatoms experienced twice as much drag as this same species without fouling epiphytes (Ruesink, 1998). This increase in drag was attributed to increased algal cross-sectional area due to epiphyte cover. Increased size in the form of additional surface area due to epiphytes in the current study was more responsible for increases in drag experienced by hosts than changes in drag coefficient (i.e. functional shape).

Hosts in this study experienced more drag when epiphytes were present; this decreased the water velocity predicted to dislodge epiphytized hosts from the substratum compared to hosts without epiphytes. Decreased velocity required to break epiphytized hosts translates to an

increased dislodgement risk of hosts with epiphytes. Although this implies hosts experience costs due to epiphytism, epiphytes were found to be just as likely to dislodge from hosts as epiphytized hosts were to dislodge from the substratum. Hosts likely experience decreases in overall drag with the loss of each epiphyte. Thus, the epiphytes in this study that detach before hosts may have less of a negative biomechanical effect on hosts than previously assumed.

1.4.2   Biomechanical benefits of epiphytism

Despite the slight apparent biomechanical cost of epiphytism incurred by hosts, data presented here suggest epiphytes receive a hydrodynamic benefit by growing on hosts. Algae growing epiphytically experienced decreased flow which corresponded to decreased drag forces and increased water velocities required to dislodge epiphytes from hosts. This reduction in flow, and subsequent decrease in drag experienced by epiphytes, may be explained by the flexible nature of the hosts upon which these epiphytes grow. Flexibility enables algae to reconfigure in flowing water (Boller and Carrington, 2006a; Demes et al., 2011; Harder et al. 2004). Flexible hosts may also be more capable of bending close to the substratum and into the boundary layer in which flow velocities are reduced (Koehl, 1984). If *Soranthera* epiphytes were capable of growing on rock, they would likely experience difficulties reconfiguring in flow due to their saccate morphology; these epiphytes are filled with water, which is nearly incompressible. Thus, growing on hosts that have the ability to reconfigure in flow, may allow these epiphytes to reorient in such a way that they become more streamlined. Moreover, since most *Soranthera* epiphytes grow attached to the tips of hosts (Table 4), this might place them in the wake formed downstream of hosts. Although the wake of flexible objects can be chaotic, wakes are generally areas of slowed water movement (Johnson, 2001), which might allow epiphytes to "draft" behind hosts and experience less drag force.

Experiencing reduced flow on hosts may also allow epiphytes to grow in areas of relatively high water velocities. As shown by Figure 11, epiphytes on hosts were predicted to be able to grow to surface areas twice as large as theoretical epiphytes growing on rock before being dislodged. Although epiphytes in the flume were positioned parallel to flow, theoretical epiphytes growing on rock would be perpendicular to water movement in the field, and therefore would likely experience more drag. The model (Figure 11) would then predict epiphytes on hosts in the field to have even larger surface areas than the small areas already predicted for epiphytes growing on rock; this would increase the discrepancy between how large epiphytes on hosts are able to grow versus smaller epiphytes on rock. Increased growth capacity for epiphytes on hosts likely has important fitness implications; *Soranthera*'s reproductive sori are distributed across the entire thallus, thus, individuals with great surface areas are likely capable of more reproductive output (Chapman, 1986).

Although epiphytes in this study experienced decreased exposure to flow, which could thicken the boundary layer and limit gas and nutrient exchange in these seaweeds (Falkowski and Raven, 2007), there is little time for a boundary layer to develop in the turbulent intertidal zone (Denny and Gaylord, 2002). Therefore, it was concluded that *Soranthera* epiphytes generally benefit by experiencing reduced flow when attached to flexible hosts; this positive effect of growing epiphytically does not preclude other negative effects but could help explain the evolution of epiphytes, and why they continue to persist in intertidal habitats.

Interestingly, given water velocities encountered at this study's collection site (Table 4), the model represented by Figure 11 predicted that individual epiphytes should be capable of growing up to 21 cm^2; yet, the largest epiphyte observed during this study was only 6 cm^2. If the reason epiphytes experience less flow when on hosts is due to "hiding" amongst hosts and host

wakes, then the larger the epiphyte, the more it would project out of these "hiding places," and experience more drag. Thus, it may not be biomechanically advantageous for these epiphytes to get this large. Although previous studies (Denny et al., 1985; Martone and Denny, 2008) suggest the size of intertidal organisms may be constrained by wave induced forces, the mismatch between size predictions and observations in this study suggests other factors may limit the growth of these epiphytes. For example, hosts may break before associated epiphytes reach their maximum possible size; this could be due to stress caused by heat, elevated light levels and desiccation during low tides (Davison and Pearson, 1996). Host *Odonthalia* at the study site tended to decay/disintegrate toward the end of summer, when the majority of low tides occur during midday and the weather is at its warmest (Haring, 2002; Helmuth et al., 2002). *Odonthalia* is perennial (Abbot and Hollenberg, 1976) like its close relative, *Neorhodomela larix*, which often gets reduced to small basal protuberances by the end of summer; these basal portions persist through winter and re-grow upon more ideal conditions in the spring (D'Antonio, 1982). Although sizes and annual seasonality (Abbott and Hollenberg, 1976) of *Soranthera* (which is present during periods of low wave action) could be phenological, partial breakage of host branches toward the end of summer might also explain these phenomena. In addition, this breakage pattern could reduce the overall drag experienced by individual host plants during an opportune time before fall and winter storms increase along with water velocities, drag forces, and dislodgement risk.

Removal of host branchlets due to drag imposed by associated epiphytes may benefit hosts by allowing them to lose a few terminal branches rather than being wholly ripped from the substratum. Drag reduction via "self-trimming/pruning" has been shown to occur in two brown algal genera: *Fucus* (Blanchette, 1997) and *Egregia* (Black, 1976; Demes et al., *in review*).

Different tiers of *Odonthalia* host branches required different breaking forces (Table 3), which is likely due to red algal apical growth (Abbott and Hollenberg, 1976); tissue at the tips of these fronds has had less time to develop and strengthen which may explain why host branches break, but individual plants persist over time. Although new algal growth (especially of species that exhibit apical growth) can be more heavily defended by antifouling compounds than older, tougher parts of thalli, algal chemical defenses are often seasonal (Hay and Fenical, 1988). *Odonthalia* completes the majority of its growth cycle between January and June which includes the onset of reproductive structures (Bracken, 2001). On the Gulf Islands of British Columbia, *Soranthera* begins to appear on the tips of these hosts between May and June (pers. obs.). The closely related red alga, *Neorhodomela larix*, is three times as chemically defended in the winter (November-February) as it is in the summer (Phillips and Towers, 1982). If *Odonthalia* follows this same chemical pattern, individuals could be less defended in the summer when growth has essentially ceased. This may allow *Soranthera* epiphytes to settle on newly grown host extremities. Algal antifouling is also augmented by the presence of certain bacteria (Armstrong et al., 2000; Wahl, 2008). As it takes time for bacteria to become established (Rao et al., 2007), *Soranthera* might take advantage of this lag in bacterial presence and settle on the new growth of hosts. This would advantageously correspond to hosts being weaker/more likely to break at the tips of their branches when exposed to hydrodynamic stress; drag inducing epiphytes may detach with small pieces of host branches as opposed to entire hosts being dislodged. Since these hosts have already produced their reproductive structures by the time epiphytes are large enough to break host branchlets, this breakage of host extremities may not be entirely costly to host reproduction. In this way, intertidal hosts appear well adapted to mitigating the biomechanical effects of algal epiphytes.

As previously mentioned, entire epiphytized hosts were predicted to be just as likely to break from the substratum as individual epiphytes to break from hosts. This pattern may be consistent with Maxwell's Lemma (Parkes, 1965) which states: if all aspects of an object break at the same time (i.e. there are no weak points), then materials are used to maximum capacity with the least amount of investment required for construction (Denny, 1976). In other words, epiphytized *Odonthalia* and *Soranthera* individuals do not seem overdesigned. If hosts overinvested in tissue and/or attachment strength, resources would be wasted on preparing for catastrophic events involving extremely high water velocities analogous to rare and monstrous waves (in opposition to other important processes such as reproduction). And vice versa; it would be unreasonable for an epiphyte to invest large amounts of resources into attachment strength if the host branchlet to which it is attached breaks first. Interestingly, this study found that the maximum force required to break an epiphyte at its attachment point (1.2 N) was very similar to the force to break tertiary host branchlets (1 N) where epiphytes are often found attached.

Being dislodged from hosts may not be entirely costly to epiphytes, however. *Soranthera* individuals are often filled with water but, likely due to gas exchange processes, air bubbles can also accumulate in this saccate alga and cause some detached individuals to float. Floating and drifting algae have been shown to persist, and may aid in species dispersal (Macaya et al. 2005; Hernández-Carmona et al., 2006; McKenzie and Bellgrove, 2008). Thus, epiphyte reproduction may not be hindered by dislodgement. In fact, this possible epiphytic dispersal advantage could help explain why, even though these specific epiphytes have a 50% chance of being dislodged from their hosts, they continue to grow epiphytically and have not evolved to exhibit some other form of growth. Epiphytic relationships do not seem wholly detrimental nor have they

necessarily been selected against in hydrodynamically variable and stressful environments such as the intertidal zone.

1.4.4   Limitations and future directions

This study employed predictions extrapolated from flume data, which are sometimes unreliable (Bell, 1999; Martone et al., 2012), but necessary due to the difficulty of replicating high water velocities in controlled laboratory settings. Flume measurement extrapolations often underestimate drag forces experienced by flexible macroalgae (Martone et al., 2012), thus, predicted breakage velocities in this study may have been underestimated. *Soranthera* epiphytes and *Odonthalia* hosts in the UBC herbarium have been collected from areas that reportedly experience high water velocities, so the biomechanical interactions described in this study likely take place in areas receiving substantial wave action regardless of interpretations involving potential flume inaccuracies.

Additionally, flume experiments in this study were run on individual host fronds, but *Odonthalia* individuals in the field exist in dense clumps (pers. obs.). Clumping algae have been shown to gain hydrodynamic benefits by experiencing less drag due to a "drafting" phenomenon caused by neighboring individuals (Johnson, 2001; Boller and Carrington, 2006b). This study's measurements of drag may therefore be overestimated if *Odonthalia* individuals "draft" in the field. This would mean hosts likely experience less drag in the field than predicted which would reduce negative biomechanical effects of epiphytism, and thus lend support to epiphytism being less harmful than previously assumed. Concomitantly, if "drafting" does occur, and also applies to epiphytes in the field, the beneficial reduction in flow experienced by epiphytes on hosts may be even more pronounced than demonstrated because of surrounding algae; this would increase benefits experienced by epiphytes on hosts.

It is likely that all marine algal epiphytes increase drag on their hosts, but the extent of this effect may be species specific. Much like the brown alga, *Turbinaria ornata*, that has a particular morphology not conducive to shape change, nor reorienting in flow (Stewart, 2004), *Soranthera* epiphytes may experience considerable biomechanical effects as they are filled with water and seem unlikely capable of reconfiguring in flow without the aid of hosts. It would be interesting to determine whether epiphytes with different morphologies that are more flexible than *Soranthera*, experience less drag, and do not benefit as much as *Soranthera* by experiencing reduced flow when attached to hosts; this might suggest factors besides biomechanics, such as light acquisition or herbivory avoidance (see Chapter 2), could have been driving forces behind the evolution of epiphytism. Consequently, it would also be interesting to determine whether more flexible epiphytes are often non-obligate, meaning they are capable of growing on rock as well as other seaweeds; this would negate the above hypothesis and suggest biomechanical interactions involving algal morphology have been strong selective pressures, potentially explaining why the saccate alga, *Soranthera*, has evolved to grow epiphytically and not on rocks as well. *Microcladia coulteri* would be an excellent study specimen with which to investigate the above hypotheses; it grows epiphytically and on rock, and it is highly branched and flexible, which would likely aid in reconfiguration, allowing drag reduction by changing shape or size in flow. Examining the frequency with which epiphytes in general occur in intertidal areas of high wave exposure versus sheltered areas would also lend insight into whether biomechanical interactions between hosts, epiphytes, and water velocity have played an important role in the evolution of epiphytism. It would be useful, overall, to repeat these experiments on a wide variety of other marine algal epiphyte species and their hosts, to improve our knowledge of how appropriate it is to generalize/extrapolate this study's findings.

1.4.5 Conclusion

This study found that *Soranthera* epiphytes increase drag on their host, *Odonthalia*. This increase in drag increases dislodgement risk of the host. However, these epiphytes are just as likely to dislodge from their hosts as hosts are to dislodge from the substratum. This pattern of equal dislodgement between hosts and epiphytes could cause hosts to experience a slight decrease in overall drag with the loss of each epiphyte. Thus, epiphytes may have less of a biomechanical effect on these hosts than previously thought, which sheds doubt on the common perception that epiphytes exclusively impact hosts in a negative manner. It was also demonstrated that these epiphytes benefit from growing attached to their hosts by experiencing reduced flow and are likely able to grow to higher surface areas, as well as resist faster flow conditions when attached to hosts.

Algal epiphytes often either exacerbate or buffer challenges experienced by hosts in the intertidal zone; these interactions are complex, however, and may depend on particular species. Thus, further study of specific host-epiphyte systems is warranted. Regardless of generalizability, this study demonstrated that biomechanical interactions between intertidal algal hosts and epiphytes may lead to dislodgement and potential mortality of either, or both constituents. Patterns of mortality may ultimately affect the process of evolutionary selection (Reznik et al., 1996; Martone et al., 2012). Loss of epiphytic algal components attributable to intertidal wave action may have cascading impacts, affecting organisms that interact with, or depend upon, dislodged seaweeds. Thus, examining the biomechanics of intertidal algal epiphytism is important, and may shine light on patterns of algal survivorship, and thereby seaweed evolution, seasonality, and intertidal community dynamics.

Chapter 2

Photosynthesis, desiccation, and herbivory: do intertidal algal epiphytes always negatively affect host fitness?

2.1   Introduction

Intertidal organisms experience myriad stresses on a daily basis. When the tide is low, marine organisms inhabiting this zone must persist when exposed to terrestrial conditions. During emersion, intertidal organisms encounter nutrient and gas exchange limitations along with thermal, light, and desiccation stress (Davison and Pearson, 1996). Negative biotic interactions, such as competition and predation, can additionally take place (Lubchenco and Menge, 1978). Organisms in this zone are constrained to a narrow strip of substratum which intensifies competition, and may increase the chance of being preyed upon (Dayton, 1971). These stressors often have negative impacts on intertidal organisms (Davison and Pearson, 1996; Lubchenco and Gaines, 1981), yet this environment is characterized by high organismal abundance and diversity. Seaweeds are one such group of diverse and abundant organisms that are commonly capable of occupying a majority of space within zones in the intertidal environment (Lobban and Harrison, 1994).

Intertidal space competition is one factor that may have led to the evolution of marine algal epiphytes (Seed, 1986; Wahl, 1989; Todd and Keough, 1994). Biomechanical interactions (see Chapter 1), as well as light access, desiccation, and herbivory (see below), are all factors that may also have interacted throughout the evolution of intertidal epiphytism. Algal epiphytes exist within all major seaweed phyla (Abbot and Hollenberg, 1976); they are common in the intertidal zone (Lobban and Harrison, 1994), and are generally assumed to have negative effects on host algae (Littler and Littler, 1999; Hay et al., 2004; Harder, 2008). However, just as fatal damage to hosts by parasites would result in the disadvantageous death of said parasites

(Anderson and May, 1978), so it would seem unfavorable for epiphytes to have exclusively

negative impacts on hosts, causing mortality and thereby potential evolutionary selection against

epiphytism.

Interactions involving algal epiphytes, hosts, and their environment can result in both

negative and positive outcomes for constituent seaweeds. For example, when photosynthetic

organisms are shaded by other nearby organisms, they experience less net photosynthesis (Sand-

Jensen, 1977; Sand-Jensen and Borum, 1984), which can negatively affect biological processes

such as growth and reproduction (Carpenter, 1990; Reed 1990). Epiphytes on seagrasses have

been shown to decrease the growth of their hosts (Sand-Jensen, 1977; Sand-Jensen and Borum,

1984), but growing on the periphery of hosts increases epiphyte access to light (Brouns and

Heijs, 1986). Epiphytes on seagrasses have also been shown to protect hosts against deleterious

effects of desiccation during low tide by trapping seawater between blades which reduces

cellular damage of hosts (Penhale and Smith, 1977; Richardson, 1980). Herbivores may interact

with epiphytic systems as well. Either one, or both algal constituents can be harmed by direct

tissue damage via herbivory; sometimes hosts are concurrently grazed by herbivores originally

attracted to epiphytes only (Wahl and Hay, 1995). Hosts could simultaneously benefit, however,

by experiencing increased light access due to decreased epiphyte cover attributable to selective

grazing of epiphytes by herbivores (Brönmark, 1989). Epiphytes that are elevated above hosts

could also potentially benefit by being less accessible to benthic grazers (Brönmark, 1989).

2.1.1   Host-epiphyte photosynthetic interactions

Many epiphytes grow over the top of hosts, blocking light that would otherwise be

received by hosts (Sand-Jensen, 1977; Sand-Jensen and Borum, 1984). Concomitantly, growing

elevated above hosts increases epiphyte exposure to light (Harder, 2008). As epiphytism may

have evolved in response to intertidal space competition (Seed, 1986; Wahl, 1989; Todd and Keough, 1994), epiphyte light requirements may have been a driving factor in this process. Thus, this study aimed to address two questions regarding intertidal algal host-epiphyte light harvesting interactions: (1) Do epiphytes decrease light availability to hosts via shading and, (2) do hosts increase light availability to epiphytes by elevating them above other organisms in the intertidal zone?

Characteristics of photosynthetic organisms are often quantified by examining photosynthesis versus irradiance curves (Taiz and Zeiger, 2002) (Figure 13). Curves are made by measuring oxygen consumption (respiration) and oxygen evolution (photosynthesis) of photosynthetic tissue at increasing light levels. When photosynthetic tissue is without light, plants exclusively respire. When light levels increase, photosynthesis increases until photosynthetic saturation is reached and additional light no longer results in increased photosynthetic rates (Taiz and Zeiger, 2002). The irradiance at which light is no longer limiting is termed saturation irradiance (I_k), values of which are generally unique for different species and the same species inhabiting different environments (Taiz and Zeiger, 2002). When light is not limiting, photosynthetic rates are instead restricted by other reactions such as electron transport rate and/or the activity of RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase). A plant that saturates at a low irradiance is generally efficient at using all available light, and is not adapted to high irradiances; vice versa, plants with high saturation irradiances are often exposed to high light levels, and therefore do not need to make use of abundant sunlight as efficiently (Taiz and Zeiger, 2002). In this study, I hypothesized that net photosynthesis of hosts is inhibited by epiphytes and that epiphytes achieve a photosynthetic benefit by growing on top of hosts.

This was quantified by comparing saturation irradiances of hosts and epiphytes to light levels measured in the field under algal canopies.

Figure 13: A hypothetical photosynthesis versus irradiance curve. The curve begins to plateau near the saturation irradiance (I_k) at which point photosynthetic rate no longer increases with increased light levels.

2.1.2 Desiccation resistance

Desiccation is another stressor commonly experienced by intertidal algae. Gasses and nutrients diffuse through algal tissue via seawater (Wheeler, 1980). When exposed during low tide, intertidal seaweeds are separated from their source of nutrients, and often experience limited gas exchange abilities; this is usually preceded by a slight increase in photosynthesis due to increased diffusivity of carbon dioxide in air, but the deleterious effects of desiccation quickly reverse this initial spike (Davison and Pearson, 1996). When emergent, algae may also be exposed to damaging light levels, wind, and high temperatures that induce water loss from algal tissue (Lobban and Harrison, 1994). Dehydration increases the salinity of algal surroundings (Lobban and Harrison, 1994), and reduces net photosynthesis (Ji and Tanaka, 2002) by interrupting electron transport (Bewley, 1979); the less an alga photosynthesizes, the fewer resources are available for growth and reproduction (Carpenter, 1990; Reed, 1990). Desiccation

44

has been shown to damage photosynthetic pigments as well (Sampath-Wiley et al., 2008; Martone et al., 2010). Another stress associated with desiccation is the release of reactive oxygen species, which can cause DNA, protein, and lipid damage within algal cells (Collén and Davison, 1999). Given these negative effects of water loss, anything delaying desiccation likely benefits algae. Desiccation amelioration is especially important for seaweeds on the southern Gulf Islands of British Columbia, Canada, where this study took place, as summertime low tides generally occur during midday, when local weather is at its warmest (Haring et al., 2002; Helmuth et al., 2002).

Epiphyte cover may delay host desiccation. For example, although epiphytes are generally considered to impose negative effects on hosts (Littler and Littler, 1999; Hay et al., 2004; Harder, 2008), epiphytes on seagrasses have been shown to trap seawater between blades, thus reducing host desiccation during low tide (Penhale and Smith, 1977; Richardson, 1980), and potentially reducing resultant physiological damage. Water filled seaweeds have also been shown to experience less desiccation (Oates, 1985; Matta and Chapman, 1995) than algae lacking morphologies conducive to water retention. Surface area to volume characteristics are important in determining the effects of desiccation on seaweeds (Dromgoole, 1980), with small (Lobban and Harrison, 1994), and highly branched algae (Schonbeck and Norton, 1979) being especially susceptible to dehydration. Thus, part of this study tested whether the saccate, water-filled epiphyte, *Soranthera*, delays desiccation of its branched algal host, *Odonthalia*. It was hypothesized that *Soranthera* benefits its host by reducing host water loss during periods of emersion.

2.1.3 Protection against herbivory

Through tissue damage and mortality, herbivory affects algal abundance (Black, 1976; Duggins, 1980; Paine and Vadas, 1969), morphology (Black, 1976; Hay, 1981), distribution (Dayton, 1971; Lubchenco, 1980; Lubchenco and Menge, 1978; Pearse and Hines, 1979; Underwood, 1980), succession (Dayton, 1971; Duggins, 1980; Foster, 1975; Lubchenco and Menge, 1978; Sousa, 1979), and diversity (Dayton, 1971; Foster, 1975; Lubchenco, 1978). The effects of herbivory are complex, however, and depend not only on the specific seaweeds and herbivores involved, but also indirectly on surrounding predators and environmental factors such as wave action and temperature (Lubchenco and Gaines, 1981).

Although epiphytism is thought to have evolved in response to extreme space competition in the intertidal zone (Seed, 1986; Wahl, 1989; Todd and Keough, 1994), herbivory may also have come into play and likely influences host-epiphyte interactions. For example, epiphytes may avoid benthic herbivores by growing on hosts that elevate them above the substratum and out of reach of some grazers (Brönmark, 1989). Epiphytes that are able to settle and grow on other seaweeds, regardless of antifouling compounds often present in hosts (Hay and Fenical, 1988; Wahl, 2008), may benefit from associating with these chemical defenses; if predators are not attracted to hosts due to specific host chemical compositions, associated epiphytes may be spared predation (Hay, 1986; Wahl and Hay, 1995). On the other hand, hosts might benefit if herbivores prefer grazing epiphytes rather than hosts; conversely, hosts may be grazed more intensely if palatable epiphytes attract herbivores to poorly defended hosts (Wahl and Hay, 1995). As there are many possible outcomes, this study explored the effects of epiphytism on herbivore feeding preference and grazing impacts of gammarid amphipods, littorine snails, and isopods in the genus *Idotea*. These invertebrates were chosen as they are

known to ingest the host alga, *Odonthalia* (Ruesink, 1998), and commonly inhabit this study's field site (pers. obs.).

By exploring the way epiphytism mediates net photosynthesis, desiccation, and herbivory, this study aimed to expand the current paradigm of host-epiphyte interactions. These data may therefore lend insight into the evolution and maintenance of epiphytic relationships.

2.2   Methods

2.2.1   Photosynthesis

Odonthalia and *Soranthera* were haphazardly collected from the mid to low intertidal zone near the west end of North Beach, Calvert Island, British Columbia, Canada (51°40'3.23"N 128° 8'47.85"W) on August 15th, 2011. Algae were placed in plastic Ziploc® bags and stored in a refrigerator for 15 hours until they were put in a cooler along with ice packs, and returned to a recirculating chilled sea water table at the University of British Columbia (UBC) within 8 hours of being removed from the refrigerator. Water table conditions were kept between 8 and 10˚ C with 14 hours of fluorescent light (~115 μmol m^{-2}s^{-1}) per day. Algae were allowed to acclimatize to these conditions for 2 to 6 days.

Photosynthetic characteristics of *Soranthera* and *Odonthalia* were examined by measuring oxygen flux within an experimental apparatus (Figure 14). *Soranthera* individuals were scrubbed with a soft brush to remove fouling organisms, and 12 circular subsamples were cut from different individuals using a hollow plastic soda straw. These 12 subsamples were put into a 10mL glass vial along with a magnetic stir bar and filtered chilled seawater. This vial was placed on a magnetic stir plate for 5 minutes to force air bubbles out of solution, which were displaced by adding more filtered seawater. Calibrated Neofox oxygen and temperature probes (Ocean Optics, Dunedin, FL, USA) were inserted through holes in a rubber stopper and secured

with plumber's putty. This combination was inserted into the vial with *Soranthera* and stir bar, making the setup airtight. Another vial was prepared the same way, and both were put into a water bath maintained at 9-11˚C by copper coils connected to a water chiller via tubing. This water bath was positioned on top of a magnetic stir plate to ensure water movement, via the stir bar, within each vial throughout experimentation. A slide projector (Kodak Ektagraphic) was positioned above the experimental setup. All of this was covered in black plastic, and samples were allowed to acclimatize in the dark for 1 hour. Respiration readings were then taken in the dark (0 μmol m^{-2}s^{-1}) for 5 minutes. This was followed by 5 minute readings at subsequent irradiance levels (7, 11, 24, 35, 46, 96, 144, 304, 486, 834, 1050 μmol m^{-2}s^{-1}). These light levels were achieved using different combinations of wire mesh screens placed in front of the light projector, and were measured underwater with a calibrated Li-Cor® spherical (4 π) light sensor LI-193 and a 250A Li-Cor® light meter (LI-COR Biosciences, Lincoln, NE, USA).

The above process was replicated 10 times with *Soranthera* subsamples, and 10 times with the same amount of *Odonthalia* branch tip subsamples. All subsamples were then dried in an oven at 60˚C for a minimum of 48 hours so that net oxygen flux could be expressed in μmol O_2 g Dry Weight^{-1} hr^{-1}.

Table Curve 2D v 5.01 (SYSTAT Software, Inc., San Jose, CA, USA) was used to fit a curve (Platt, 1980) to the average oxygen flux at each light level for each sample:

$$P_{net} = \left[\left((P_{max} - P_0) * \left(1 - e^{(-\alpha * I / P_{max})} \right) \right) + P_0 \right] \qquad (5)$$

Where: P_{net} = Total oxygen flux (μmol O_2 gDW^{-1} hr^{-1})
P_{max} = Maximum photosynthetic rate (μmol O_2 gDW^{-1} hr^{-1})
P_0 = Respiration (μmol O_2 gDW^{-1} hr^{-1})
α = Photosynthetic efficiency
I = Irradiance (μmol m-^{2}s^{-1})

This equation (5) does not take photo-inhibition into account, as this was not observed at any point during this experiment. Average α's and average P_{max}'s calculated by Table Curve were inserted into equation 5 to construct an average light response curve for each species. The saturation irradiances (I_k) were calculated for each species during each trial using the following equation (6):

$$I_k = \frac{(P_{max} + P_0)}{\alpha} \tag{6}$$

Light measurements were taken in the field below *Odonthalia* canopies using a calibrated Li-Cor® spherical light sensor LI-193 in association with a 250A Li-Cor® light meter. Measurements were taken on May 20th, 2011 in the mid/low intertidal zone northwest of Fulford Harbour on Salt Spring Island, British Columbia, Canada (48°45'23.98"N 123°25'16.06"W) during what was considered a sunny day. Although many algae mainly photosynthesize when submerged (Johnson et al., 1974; Quadir et al., 1979; Guenther and Martone, *in review*), it was necessary to measure sub-canopy light levels during low tide due to logistics. Light attenuates with depth (Jerlov, 1976), so the amount of light reaching these algae in the field during high tide is less than measured. To correct field irradiances for submersion, values were multiplied by 0.27, the percentage of irradiance that typically penetrates 2 m of relatively clear coastal water (representative of depths commonly covering algae in the mid to low intertidal zone during fairly high tides in this region), or 1 m in more turbid coastal water. This percentage of surface irradiance (27%) is representative of sunlight transmitted from a 45° solar altitude consisting of wavelengths between 300-2,500 nm in upwelling regions along the west coast of North America (Jerlov, 1976).

To determine whether saturation irradiances were different from irradiances under submerged algal canopies in the field, two sample *t*-tests were carried out between I_k values for

Soranthera and corrected field irradiances, and between values of I_k for *Odonthalia* and corrected field irradiances. These tests were done using SYSTAT 13 (SYSTAT Software Inc., San Jose, CA, USA).

Figure 14: Experimental apparatus used for measuring photosynthesis of host and epiphyte tissue.

2.2.2 Desiccation

Odonthalia specimens with *Soranthera* epiphytes were collected haphazardly from the mid to low intertidal zone northwest of Fulford Harbour on Salt Spring Island, British Columbia, Canada (48°45'23.98"N 123°25'16.06"W) in June, 2011. Algae were placed in plastic bags and transported in a cooler with an ice pack to a recirculating chilled seawater table at UBC within no more than 5 hours of being collected. Water table conditions were the same as above (Section 2.2.1), and algae were experimented upon within 6 days.

Odonthalia fronds (n = 10) were randomly removed from the seawater table, cleared of epiphytes, and weighed. More *Odonthalia* (n = 10) were taken from the seawater table, epiphytes were detached and weighed, hosts were weighed, and epiphytes were haphazardly scattered back on top of original host fronds. These saccate *Soranthera* epiphytes were in their natural state as found on corresponding hosts, meaning most were filled with water, but a few had been punctured (probably due to herbivory), and were therefore not completely full of water.

Odonthalia fronds with and without epiphytes were placed on the roof of the UBC Biological Sciences building and left exposed for 1 hour. Depending on the tidal cycle, algae in the mid to low intertidal zone growing at an elevation of approximately 1 m (where *Odonthalia* and *Soranthera* occur) can experience up to 4 hours of emersion during low tides. Mass loss of desiccating hosts and mass loss of epiphytes was monitored every 15 minutes. An average measurement of 5 irradiances was taken at the same frequency with the Li-Cor® spherical light sensor LI-193 in conjunction with the 250A Li-Cor light meter. Weather measurements (temperature, relative humidity, and wind speed) were also collected every 15 minutes by the UBC weather station on top of the Earth and Ocean Sciences building, which was approximately 250 meters from the Biological Sciences building. It was assumed that the weather was similar on top of both buildings. Average weather conditions ± SE throughout the experiment were as follows: temperature was $19.7 \pm 0.8°$ C, relative humidity was 58.9 ± 7.2 %, wind speed was 6.8 ± 1.9 km hr^{-1}, and irradiance was $2,447.9 \pm 167.6$ μmol m^{-2}s^{-1}. After exposure on the roof, dry weight was quantified by dehydrating host fronds in an oven at 60˚C for a minimum of 48 hours.

Desiccated host masses and epiphyte masses at each time point were divided by the oven dry weight of these samples. Levene's test detected heterogeneity of variance within resulting values; this was corrected by log transforming the data. A repeated measures analysis of variance

(RMANOVA) was run on transformed data. Mauchly's test of sphericity was not satisfied: $\chi^2(5)$ = 27.435, p < 0.05, so degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (ε = 0.66). All statistics were run using SPSS Statistics 17.0 (SPSS Inc., Chicago, IL, USA). Data were depicted in percent relative water content using the following equation (7):

$$\% \text{ Relative water content} = \left(\frac{\text{Deisccated weight} - \text{Oven dry weight}}{\text{Initial fresh weight} - \text{Oven dry weight}}\right) * 100 \qquad (7)$$

2.2.3 Herbivory

Odonthalia and *Soranthera* were haphazardly collected from the mid to low intertidal zone northwest of Fulford Harbour on Salt Spring Island, British Columbia, Canada (48°45'23.98"N 123°25'16.06"W) on July 30th, 2011, and put in plastic bags. Snails in the genus *Littorina* and gammarid amphipods were also collected from this area and put in small plastic screw top containers. Effort was extended to collect only *Littorina scutulata* but individuals of a different littorine species may have accidentally been included; amphipods were not keyed to species, thus, littorines and amphipods are referred to by genus only throughout this thesis. The above algae and invertebrates were transported in a cooler with an ice pack to the recirculating chilled seawater table at UBC within 5 hours of being collected. Water table conditions were the same as above (Section 2.2.1). Algae and invertebrates were allowed to acclimatize to these conditions for 2 days during which time invertebrates were starved of food.

Soranthera and *Odonthalia* were also collected from the west end of North Beach Calvert Island, British Columbia, Canada (51°40'3.23"N 128° 8'47.85"W) on August 15th, 2011. This location was selected as *Soranthera* and *Odonthalia* were becoming less abundant on Salt Spring Island at this time. These algae were stored in a refrigerator for 15 hours, and then placed in a cooler with ice packs. *Idotea* used in conjunction with these seaweeds were collected from the north side of West Beach Calvert Island (51°39'27.89"N 128° 8'48.48"W) on August 16th, 2011,

and put in the same cooler with the above algae. All *Idotea* individuals were most likely *Idotea wosnesenskii*, but these are referred to by genus only for consistency. Algae and invertebrates were returned to the water table at UBC within 8 hours of collection, and were kept at the same conditions as above.

Twenty *Soranthera* individuals were cut into pieces approximately 2cm x 2cm, and similarly sized apical fronds of *Odonthalia* were also detached from whole fronds. Each piece of *Soranthera* was weighed and accompanied by a piece of pre-weighed *Odonthalia* in individual Tupperware® tubs. These tubs were given mesh sides to allow water to flow through but algae and invertebrates not to escape. Five randomly selected *Littorina* were put in 10 of these tubs, and 10 were left without any herbivores to serve as controls. All tubs were monitored for 8 days, at the end of which algae were re-weighed. Algal mass loss was used as a proxy for herbivore feeding preference. To determine whether littorines eat more host tissue in the absence of epiphytes, remaining *Soranthera* was removed from all tubs, but host tissue and herbivores were left for another 8 days. At the end of this time, *Odonthalia* was weighed once more. The above process was also done with amphipods (using 3 individuals per treatment for 8 days) and *Idotea* (with 1 per treatment for 6 hours). Feeding rates of each herbivore in the presence of hosts and epiphytes were also calculated.

It was assumed that the change in mass of control algae and treatment algae (not due to herbivory) was similar, and that the starting mass of algae in the herbivore treatments averaged out between treatments. Raw mass measurements were thus converted to percent mass lost by the following equation (8):

$$\% \text{ mass loss} = \left(\frac{\text{final mass} - \text{initial mass}}{\text{initial mass}} \right) \text{x} 100 \qquad (8)$$

Differences in percent mass loss between hosts and epiphytes and control and treatment algae were tested with the *Littorina* data using a two way analysis of variance (ANOVA) in SYSTAT 13. The amphipod data was analyzed using a generalized linear model with a normal distribution and identity link function in SPSS Statistics 17.0; this was done on account of unequal variances (Levene's test). The *Idotea* data were not normal (Shapiro-Wilk test) and exhibited unequal variance, so the data were rank transformed and analyzed using a two way ANOVA in SYSTAT 13. Herbivore preference data were accompanied with 95% confidence intervals to depict approximate significance between treatments. The effect of herbivores on *Odonthalia* with and without *Soranthera* present was tested using paired *t*-tests in SYSTAT 13.

Herbivore abundance was quantified the following field season on May 8th and 9th, 2012 at the same site on Salt Spring Island, British Columbia, Canada (48°45'23.98"N 123°25'16.06"W). Sampling was done by laying out a meter tape along 40 meters of the mid to low intertidal zone. Half meter by half meter polyvinyl chloride (PVC) quadrats were set down on every meter mark from 0 m – 40 m, with a total of 31 meter marks being sampled (9 were bypassed on account of rising water level). Amphipod, littorine, and *Idotea* abundances were counted in each quadrat. Quadrats in which certain herbivores were especially abundant were subsampled using either a quarter, or a half of the quadrat. Herbivore abundance data was neither normal, nor did it exhibit equal variance, so a nonparametric Kruskal-Wallis test was carried out using SYSTAT 13. To estimate grazing pressure of different herbivores on algae in the field, previously calculated feeding rates were multiplied by the average number of herbivores per quadrat.

2.3 Results

2.3.1 Photosynthesis

The average irradiance (± sd) in the field under an *Odonthalia* canopy (and corrected for submergence) was 75.4 ± 18.8 µmol m^{-2}s^{-1} (Figure 15). Variance is likely due to some canopy-forming algae being sparse, whereas others are dense. The saturation irradiance for *Soranthera* was 56.8 ± 7.2 µmol m^{-2}s^{-1}, and *Odonthalia* was 50.2 ± 3.5 µmol m^{-2}s^{-1} (means ± SE). Values for both hosts and epiphytes were not significantly different from irradiances corrected for submergence under algal canopies (*Soranthera*: $t = 0.965$, df $= 17$, $p > 0.3$; *Odonthalia*: $t = 1.388$, df $= 17$, $p > 0.2$).

Figure 15: Average net photosynthesis of hosts and epiphytes measured as oxygen evolution by increasing irradiance level. Smoothed lines are a photosynthetic model (Platt, 1980) constructed using estimated parameters of P_{max} and α. Dotted line represents saturation irradiance (I_k). Solid line is the average irradiance under an algal canopy in the field surrounded on either side by sd (gray). Error bars are SE, n = 10.

2.3.2 Desiccation

When out of water, *Odonthalia* with associated epiphytes, *Odonthalia* without epiphytes, and epiphytes alone all lost mass (water) over time (Figure 16). Hosts without epiphytes desiccated significantly more quickly than hosts with epiphytes (Table 6), and retained only 19.6 ± 5.7 % (mean + SE) of their original water content after just 30 minutes of exposure to air (Figure 16). Hosts with epiphytes desiccated more slowly, retaining 52.0 ± 5.4% of the water originally associated with their thalli after the same amount of time (Figure 16). In other words, hosts without epiphytes lost approximately 50% of their water content in just 15 minutes, whereas hosts with epiphytes required twice that amount of time to reach approximately 50% water loss (Figure 16). Epiphytes desiccated the least, and retained 60.9 ± 4.5% of their original mass after 30 min; it took 45 min for epiphytes to lose approximately 50% of their water content.

Table 6: Repeated measures ANOVA results for hosts with and without epiphytes exposed to air for 1 hour.

Source	Type III Sum of Squares	df	Mean Square	F	p-value
time	2.244	1.98	1.133	196.451	0.0001
log treatment	1.372	1	1.372	13.408	0.002
time*log treatment	0.095	1.98	0.048	8.277	0.001
error(time)	0.206	35.643	0.006		
error (log treatment)	1.842	18	0.102		

Figure 16: Change in average percent relative water content of *Odonthalia* fronds with epiphytes (closed circles), *Odonthalia* fronds without epiphytes (open circles), and epiphytes alone (triangles) during exposure to air for 60 mins. Dashed line illustrates points at which different algae reached 50% relative water content (RWC). n = 10. Error bars are SE.

2.3.3 Herbivory

Amphipods significantly preferred grazing the epiphyte *Soranthera* over its host *Odonthalia* (Table 7). *Soranthera* in containers with amphipods lost 63.4 ± 16.4 % (mean + 95% CI) original tissue mass over 8 days, whereas *Odonthalia* in the same containers lost only 11.0 ± 7.2 % (Figure 17). Control *Soranthera* associated with these amphipod treatments degraded slightly in the seawater table, losing 15.0 ± 6.5 % original mass over the same 8 days, whereas control *Odonthalia* grew slightly, and gained 5.6 ± 3.1 % of its original mass.

Littorina also preferred grazing the epiphyte *Soranthera* over its host *Odonthalia* (Table 8). Over 8 days, *Soranthera* lost 39.0 ± 9.4 % (mean + 95% CI) tissue mass to littorine herbivory, which was the least amount eaten by any of the herbivore species in this study (Figure 17). *Odonthalia* lost 0.5 ± 5.6 % of its original mass to littorines. *Soranthera* without herbivores lost 10.7 ± 8.6 % original mass whereas *Odonthalia* gained 7.9 ± 3.8 %.

Idotea showed a slight preference for *Soranthera* over *Odonthalia* (Table 9). Over 6 hours, *Idotea* consumed 56.2 ± 25.9 % (mean + 95% CI) of *Soranthera* tissue and 13.1 ± 6.7 % of *Odonthalia* in the same containers (Figure 17). Over the same 6 hours, *Soranthera* without herbivores lost 13.6 ± 4.0 % of its original mass, whereas *Odonthalia* gained 1.8 ± 2.1 %.

After removing the remaining epiphyte tissue from the above containers, amphipods were the only invertebrate to consume significantly more host tissue in the absence of epiphytes (Table 10; Figure 18).

When presented with both food options, *Idotea* ate the fastest (Figure 19); *Soranthera* was consumed at a rate of $6.6 \pm 3.1 \times 10^{-3}$ g herbivore^{-1} hr^{-1} and *Odonthalia* at $4.3 \pm 2.0 \times 10^{-3}$ g herbivore^{-1} hr^{-1} (mean + 95% CI). Amphipods ate *Soranthera* at a rate of $7.0 \pm 2.7 \times 10^{-5}$ g herbivore^{-1} hr^{-1} and *Odonthalia* at $1.8 \pm 1.3 \times 10^{-5}$ g herbivore^{-1} hr^{-1}. Lastly, *Littorina* ate

Soranthera at a rate of $2.1 \times 10^{-5} \pm 1.0 \times 10^{-5}$ g herbivore^{-1} hr^{-1} and, although *Odonthalia* was eaten overall by these invertebrates, it appeared to grow faster than it was eaten at $-7.3 \pm 2.1 \times 10^{-6}$ g herbivore^{-1} hr^{-1}.

Amphipods were the most abundant herbivores of interest at the collection site (H = 52.074, df = 2, p < 0.001), with 9.7 ± 3.4 amphipods 0.25m^{-2} in the mid-low intertidal zone along the transect line (Figure 20). There were 2.7 ± 1.1 *Littorina* 0.25m^{-2} and 0.2 ± 0.1 *Idotea* 0.25m^{-2} in the same zone where the transect line was placed. Values are means $\pm$ 95% confidence intervals.

Even though amphipods were the most abundant, when feeding rates and abundances were simultaneously taken into account, *Idotea* seemed most likely to have the largest grazing effect on *Soranthera* and *Odonthalia* in the field (Figure 21).

Table 7: Generalized linear model results for hosts and epiphytes with and without herbivorous amphipods for 8 days.

Source	Wald Chi-Square	df	F	p-value
treatment	48.449	1	24.789	0.001
algae	61.227	1	59.901	0.001
treatment*algae	11.640	1	7.265	0.001

Table 8: Two-way ANOVA results for hosts and epiphytes with and without *Littorina* herbivores for 8 days.

Source	Type III Sum of Squares	df	Mean Square	F	p-value
treatment	0.337	1	0.337	24.789	0.001
algae	0.813	1	0.813	59.901	0.001
treatment*algae	0.099	1	0.099	7.265	0.01
error	0.489	36	0.014		

Table 9: Two-way ANOVA results (rank transformed) for hosts and epiphytes with and without *Idotea* herbivores for 6 hours.

Source	Type III Sum of Squares	df	Mean Square	F	p-value
treatment	1416.1	1	1416.1	21.422	0.001
algae	1322.5	1	1322.5	20.006	0.001
treatment*algae	211.60	1	211.60	3.201	0.082
error	2379.8	36	66.106		

Figure 17: Average percent change in mass of the epiphyte, *Soranthera* (gray), and its host, *Odonthalia* (black), in the presence and absence of amphipods (3 over 8 days, n = 10), *Littorina* (5 over 8 days, n = 10), and *Idotea* (1 over 6 hours, n = 10). Error bars are 95% confidence intervals.

Table 10: Paired *t*-test results comparing mass loss of *Odonthalia* host fronds in the presence of 3 different (Amphipods, *Littorina*, and *Idotea*) herbivores before and after removal of the epiphyte, *Soranthera*.

Source (Herbivore)	Host mass loss with epi. (avg % ± SE)	Host mass loss without epi (avg % ± SE)	t	df	p-value
Amphipods	11.00±3.68	22.34±4.40	2.414	9	0.039
Littorina	0.52±2.87	1.89±2.58	0.448	9	0.665
Idotea	13.10±3.41	15.30±4.69	0.332	9	0.747

Figure 18: Average percent change in mass of the host, *Odonthalia*, in the presence of 3 different herbivores (Amphipods, *Littorina*, and *Idotea*) before (black) and after (hashed) removal of the epiphyte, *Soranthera*. n = 10 for each before and after trial in the presence of each different herbivore. * denotes significant difference. Error bars are SE.

Figure 19: Average feeding rate of amphipods, *Littorina*, and *Idotea* in the presence of epiphyte tissue (gray) and host tissue (black). n = 10. Bars are 95% confidence intervals.

Figure 20: Average number of herbivorous invertebrates per 0.25 m^2 along 40m of the mid-low intertidal zone at the algal collection site. n = 31. Error bars are 95% confidence intervals.

Figure 21: Average feeding pressure on epiphytes (gray) and hosts (black) by amphipods, *Littorina*, and *Idotea* per 0.25 m^2 along 40m of the mid-low intertidal zone at the algal collection site. Error bars are 95% confidence intervals. n = 10.

2.4   Discussion

The ecological effects of epiphytic interactions are poorly understood. It has been assumed that epiphytes benefit from this relationship at some expense to hosts (Littler and Littler, 1999; Hay et al., 2004; Harder, 2008), but this paradigm is not well tested, and epiphytic relationships persist in the intertidal zone. Besides exacerbating stresses experienced by hosts in intertidal habitats, epiphytes may also beneficially buffer some inherent challenges experienced by hosts in this environment. For example, algal hosts and epiphytes compete for space (Seed, 1986; Wahl, 1989; Todd and Keough, 1994) and light (Sand-Jensen 1977, Sand-Jensen and Borum 1984) in habitats that generally receive high levels of light, they desiccate when the tide recedes, and they experience varying degrees of herbivory in the intertidal zone. How do these seaweeds interact with one another in regards to the above processes and what role have these factors played in the evolution of intertidal algal epiphytism?

This study demonstrates that most of these ecological factors may have contributed to the evolution of the intertidal algal host-epiphyte relationship investigated here. Moreover, contrary to prevailing ideas, data presented here suggest hosts may benefit from epiphyte cover. Benefits experienced due to the association between hosts and epiphytes may in turn have helped perpetuate these interactions through evolutionary time. Light acquisition requirements likely have not played a role in the evolution of this study's epiphytic relationship as host algae were not shown to be negatively affected by shading caused by other algae; concomitantly, epiphytes were able to acquire sufficient amounts of light for photosynthesis when under algal canopies. Epiphytes decrease host desiccation during periods of aerial exposure, and herbivore feeding preferences may divert common herbivores away from hosts and toward epiphytes. There may

be little adaptive value in traits that reduce the probability of epiphytization if epiphytes provide a net benefit to hosts.

2.4.1 Host-epiphyte photosynthetic interactions

Contrary to what was hypothesized, this study found that the host alga, *Odonthalia*, is not likely negatively affected by shading due to algal epiphyte cover. Although host algal tissue reached photosynthetic saturation just below the lowest value of standard deviation for sub-canopy irradiances (Figure 15), averages between submerged field irradiances and saturation irradiances for *Odonthalia* were not statistically different. This indicates that the saturation irradiance for hosts and the average irradiance under submerged algal canopies were essentially the same; thus, hosts are capable of saturating when exposed to low light levels experienced under canopies in the field. Photosynthetic behavior of whole algal fronds can be different from photosynthesis by portions of algal fronds; extrapolating net photosynthesis of pieces of fronds to entire thalli often results in underestimation of saturation irradiances (Binzer and Middelboe, 2005). It was necessary to use pieces of algae, and not entire fronds for this study, due to the size of the available experimental apparatus and various related equipment. It would be interesting to repeat this study on entire host fronds to determine whether this makes a difference. A study by Mazzela and Alberte (1986) on seagrass epiphytes also found no effect of epiphytism on net photosynthesis of hosts. Most other studies investigating the effects of epiphytes on light attenuation have examined seagrasses as well, but generally have demonstrated negative effects (Brush and Nixon, 2002; Sand-Jensen, 1977; Sand-Jensen and Borum, 1984).

The effect of epiphytes on host light acquisition likely varies in the field. Field irradiances were measured during low tide and corrected to represent values experienced during submersion, but light attenuation depends on several parameters including both seawater depth

and sedimentation (Jerlov, 1976). Thus, when the tide is high and there are high levels of particulates in the water column, hosts with epiphytes likely experience light acquisition challenges. On the other hand, epiphytes may actually benefit hosts by providing photo-protection during periods of exposure; light levels above algal canopies often exceed 1,000 μmol $m^{-2}s^{-1}$ during low tides in the summer (Larkum and Barrett, 1983). Extreme levels of light can be deleterious to intertidal algae by causing photo-inhibition which decreases photosynthetic activity (Davison and Pearson, 1996) by diverting absorbed light energy towards photo-protective processes (Taiz and Zeiger, 2002; Fork et al., 1986). Photo-inhibition was not observed to occur in hosts without epiphytes in this study, potentially because the experimental apparatus was incapable of projecting irradiances greater than 1,000 μmol $m^{-2}s^{-1}$. If photo-inhibition does occur in these hosts at light levels greater than produced in the lab, epiphytes may ameliorate deleterious effects of exposure due to damaging light levels often experienced by [host] algae in the field during low tide.

Contrary to expectations, epiphytes growing under algal canopies seemed as photosynthetically productive as epiphytes on top of hosts. This study showed that epiphytes saturate almost exactly at the lowest value of standard deviation for values of irradiance experienced under submerged canopies in the field and, like hosts, the saturation irradiance for epiphytes was not significantly different from irradiances under submerged algal canopies (Figure 15). This means these epiphytes are capable of reaching photosynthetic saturation in low light levels, and likely do not absolutely need to grow above hosts to acquire sufficient amounts of sunlight for photosynthesis. These findings suggest that intertidal algal epiphytism may not have evolved in response to light limitation associated with intertidal space competition; it is

unlikely that light requirements were a strong selective pressure leading to the evolution of this specific epiphytic pair.

2.4.2 Desiccation resistance

This study demonstrated that algal epiphytes delay the desiccation of their algal hosts during low tide conditions. *Odonthalia* hosts without associated epiphytes desiccated significantly faster than hosts with epiphytes when exposed to air for one hour (Figure 16). Because this host alga and its epiphytes can experience up to four hours of emersion during low tides, and hosts without epiphytes in this study desiccated to 50% RWC after only 15 min, epiphytes benefit hosts by decreasing water loss and damage during aerial exposure. *Odonthalia* is a finely branched alga with a relatively high surface area to volume ratio. Although branching morphologies have been shown to effectively diffuse heat (Bell, 1995), they also increase susceptibility to dehydration (Schonbeck and Norton, 1979). Thus, *Odonthalia* may be especially vulnerable to the effects of desiccation. Other branching/turf seaweeds, such as *Dictyota bartayresii*, *Halimeda opuntia*, *Laurencia papillosa* (Hay, 1981), and *Endocladia muricata* (Hunt and Denny, 2008) also have high surface area to volume ratios but manage to survive in areas frequently exposed to air. Some of these seaweeds experience partial dieback of apical branches causing thicker subsequent growth; dense branching retains more water during successive periods of exposure (Hay, 1981). Some bladed algae, such as *Porphyra*, are extremely thin and also have high surface area to volume ratios. These algae are capable of employing strategies that allow the alteration of photosynthetic pigments in ways that afford protection during periods of emersion (Figueroa et al., 1997; Sampath-Wiley, 2008; Fork et al., 1986). These seaweeds are well adapted to recovery following stressful periods of desiccation as well (Lipkin et al., 1993). Thus, the possession of mechanisms aiding in the resistance of desiccation

during periods of exposure are essential and beneficial for seaweeds inhabiting intertidal environments.

Epiphytes may serve as a mechanism by which *Odonthalia* individuals resist desiccation. Seagrasses with epiphytes have been shown to experience less desiccation due to affiliated epiphytes trapping seawater between seagrass blades (Penhale and Smith, 1976; Richardson, 1980) which likely reduces cellular damage due to exposure. This same phenomenon likely occurred in this study, and the hollow, water-filled morphology of *Soranthera* may have further augmented the already beneficial effects of epiphytes on reduced desiccation experienced by hosts. The link between desiccation resistance and saccate morphologies has been demonstrated for other seaweed species (Oates, 1985; Mattas and Chapman, 1996). This study is the first to show that proximal algae may benefit from the ability of saccate seaweeds to retain water during periods of aerial exposure. Contrary to other research demonstrating costs experienced by hosts (Littler and Littler, 1999; Hay et al., 2004; Harder, 2008), this species of algal host benefits from being epiphytized, and experiences decreased water loss during emersion.

2.4.3   Protection against herbivory

All three invertebrate herbivores chosen for this study preferred eating the epiphyte, *Soranthera*, over its host, *Odonthalia* (Figure 17). Because algal morphology has been shown to play an important role in plant-herbivore interactions (Lubchenco and Gaines, 1981), it would have been preferable to present herbivores with entire, water-filled *Soranthera* thalli during feeding trials. However, it would not have been possible to accurately determine algal mass before and after exposure to herbivores, because grazers perforate these saccate epiphytes, and cause water loss. Presenting herbivores with host and epiphyte algae that were detached from one another, a scenario that does not occur in nature, was also necessary to accurately track algal

mass change due to herbivory of individual species. Regardless of these limitations, when amphipods, *Idotea*, and *Littorina* were presented with separated pieces of host and epiphyte tissue, all three herbivores grazed epiphytes more than hosts. Thus, herbivore preference may cause epiphytism to be advantageous for hosts; epiphytized hosts are likely spared grazing damage because herbivores prefer eating epiphytes. However, the effect of epiphytes on host vulnerability to herbivory depends on whether there is a numerical response in herbivore density. If consuming epiphytes leads to an increase in herbivore numbers, hosts could be negatively affected by comprising the only remaining food source for an increased herbivore population. Hosts in this study were also shown to benefit from the ability of epiphytes to decrease desiccation and/or possibly increase photo-protection during low tide; preferential removal of epiphytes by herbivores could therefore slightly disadvantage hosts in need of these ameliorating effects.

Impacts of herbivores on marine plants are highly dependent on algal traits; generally more so than grazer traits or environmental conditions (Poore et al., 2012). The mechanism behind this study's observed herbivore feeding preferences could be related to overall algal nutritional characteristics (Carefoot, 1967); in regards to lipid and protein content, green algae are generally more nutritious than browns which are generally more nutritious than reds (Montgomery and Gerking, 1980). Thus, *Soranthera*, a brown alga, may provide more nutrients to herbivores than the red alga, *Odonthalia*. Algal chemical defenses could also have come into play; species in the genus *Odonthalia* synthesize phenols which deter some, but not all herbivores (Kurata et al., 1997). Although many brown algae produce phlorotannins, which likely help defend against herbivores (Hay and Fenical, 1988), *Soranthera's* chemical composition has never been investigated so it cannot be said whether this alga employs

71

secondary metabolites against herbivory. All three herbivores have been shown to eat

Odonthalia (Ruesink, 1998) and, throughout this experiment, at least small amounts of host

tissue were eaten by all of the herbivore species (Figure 17). Thus, *Odonthalia's* secondary

metabolites are not lethal to these specific herbivores, which are capable of eating *Odonthalia*

but prefer grazing its epiphyte, *Soranthera*.

Amphipods were the only herbivores that ate significantly more host in the absence of

Soranthera (Figure 18). Amphipods were also the most abundant of all three herbivores

investigated at this study's field site (Figure 20). Therefore, by diverting amphipod grazing away

from hosts, epiphytes may have an especially beneficial effect on hosts in areas abundantly

populated by amphipods. Small grazers, such as amphipods, frequently live in chemically

defended algae that deter predators (Hay et al., 1988); simultaneously, these herbivores are

typically incapable of differentiating habitat choice from food preference (Poore and Steinberg,

1999), which may help explain the significant consumption of chemically defended host tissue

by amphipods in the absence of epiphytes.

Although amphipods were the most abundant herbivorous invertebrate at this study's

field site, and *Idotea* were the least (Figure 20), when feeding rates and abundances were

simultaneously taken into account, it could be seen that *Idotea* likely applies the greatest grazing

pressure (Figure 21). Because *Idotea* are less selective than the other herbivores, they may have

the largest effect on populations of both hosts and epiphytes in the field. The small amount of

algal tissue eaten at a slow rate by *Littorina* (Figure 21) seems relatively inconsequential in

contrast to the feeding patterns of amphipods and *Idotea*, but these snails may have a greater

effect on host-epiphyte interactions than suspected. *Littorina* were observed to preferentially

graze *Soranthera* reproductive structures (Figure 22). These animals feed with a specialized

mouth part, or radula (Voltolina and Sacchi, 1990); the raised nature of *Soranthera's* reproductive patches could place these structures in more direct contact with snail feeding parts. Regardless of the mechanism behind the selective grazing of sori by *Littorina*, this pattern could greatly reduce *Soranthera's* reproductive output and cause cascading effects capable of impacting the abundance of subsequent epiphyte generations.

Laboratory feeding assays can overestimate the impacts of herbivory on communities because variables such as natural densities, alternate food choices, and interactions involving conspecifics and predators are often ignored (Ruesink, 2000). Regardless of the magnitude with which the herbivores in this study affect hosts and epiphytes in the field, results here suggest they are capable of impacting epiphytic communities. Reductions in epiphyte abundance could in turn affect biomechanical (see Chapter 1), photosynthetic, and desiccation interactions (see above) between *Odonthalia* hosts and their epiphytes.

As in the example above, although grazing may not always necessarily cause algal mortality, it can still detrimentally affect the algae involved. For instance, grazing compromises the integrity of *Soranthera's* saccate thallus by creating holes which facilitate internal water loss. *Soranthera* is an organism in which water storage likely reduces the effects of desiccation; thus, herbivore induced damage decreases this epiphyte's ability to resist the effects of drying out. Hosts that benefit by experiencing less desiccation when covered with these epiphytes would also likely be negatively affected by herbivores puncturing saccate epiphytes. As mentioned in Chapter 1, dislodged and floating *Soranthera* individuals may experience increased dispersal opportunities; being perforated by herbivores before becoming dislodged would thereby disallow dispersal of propagules via floating epiphytes.

It would be interesting and advantageous to use more species of herbivores in feeding assays, such as kelp crabs that also eat *Odonthalia* (Ruesink, 2000), and were fairly abundant at this study's field site (pers. obs.), to more fully understand regional host-epiphyte-herbivore interactions between these two algae.

Figure 22: Photograph of a piece of *Soranthera* before (a) and after (b) exposure to littorine grazing.

2.4.4. Conclusions and future directions

In conclusion, this study found that avoiding space competition is not the only way in which epiphytes benefit from living on hosts, and that hosts are not necessarily always negatively impacted by epiphytes. Instead, epiphytes were shown to have a neutral impact on net photosynthesis of hosts, a positive effect on host desiccation, and a slightly beneficial effect on interactions involving hosts, epiphytes, and herbivores. These results could lend insight into how these epiphytic relationships have been sustained over time, and continue to persist in a stressful marine environment. As these interactions may be species specific, the extent to which these findings can be applied more generally is unclear. It would be advantageous to repeat some or all of the above experiments on other epiphyte systems involving different phyla, morphologies, and habitats. Subtidal environments, where epiphytes also occur (Abbot and Hollenberg, 1976),

would be especially interesting to examine as this habitat is characterized by different challenges; i.e., biomechanical pressures are reduced, light acquisition is further compromised via greater attenuation at depth, desiccation is nonexistent, and the threat of herbivory is likely greater compared to the intertidal zone (Graham et al., 2008). Algal host-epiphyte relationships are complex; understanding epiphytic interactions could elucidate patterns of intertidal evolution and stress resistance mechanisms applicable to a suite of important organisms inhabiting a unique and challenging marine environment.

Conclusion

Epiphytic associations occur worldwide, but the ecological effects of epiphytism are not well described. On land, photosynthetic epiphytes are commonly thought to benefit by achieving increased access to light while generally having little effect on hosts (Figure 1). Aquatic hosts are often assumed to experience costs from being epiphytized, whereas epiphytes usually benefit by occupying epiphytic habitats (Figure 1). But, does this pattern always hold true? Do photosynthetic epiphytic relationships in different habitats, such as aquatic and terrestrial ecosystems, result in different associational effects? Results presented in this study show aquatic epiphytism is much more complex than previously presumed (Figure 23).

Data presented in Chapter 1 demonstrate that the intertidal algal epiphyte, *Soranthera*, increases drag on its host alga, *Odonthalia*, and that this increase in drag translates to an increased dislodgement risk of this host. However, when dislodgement of these epiphytes was also taken into account, hosts and epiphytes were equally likely to dislodge when exposed to high water velocities. Thus, there may not be as large a biomechanical effect of these epiphytes on their intertidal hosts in the instances where epiphytes are dislodged from hosts before hosts are dislodged from the substratum. Interestingly, these epiphytic algae were shown to benefit by growing attached to hosts. The flexible nature of this study's host may increase these epiphytes' ability to resist drag; this pattern suggests a selective advantage to living on another alga.

Chapter 2 explored other ecological effects of epiphytism. Epiphytes in this study did not seem to negatively affect host light acquisition. Although these epiphytes could be capable of hindering net photosynthesis of hosts during high tide when the water column contains a large amount of sediments, they could also protect hosts against harmful effects of high light levels during low tide. Moreover, these epiphytes likely do not need to grow above hosts as they seem

capable of reaching photosynthetic saturation at light levels experienced under submerged algal canopies. These results suggest the aspect of intertidal space competition involving light limitation may not have played a role in the evolution of this study's epiphytic partnership.

Epiphytized hosts desiccated more slowly than hosts alone when exposed to air for an extended period of time. Epiphytes allow water to remain associated with hosts during low tide, the extent of which may be related to this epiphyte's saccate, water-filled morphology. Desiccation of hosts can cause physiological damage; epiphyte cover, therefore, may beneficially mitigate harmful effects of desiccation.

Three common invertebrate herbivores preferred eating the epiphyte, *Soranthera*, over its host, *Odonthalia*. Thus, epiphytism likely reduces the effects of grazing on these hosts by diverting herbivores toward epiphytes. In particular, amphipods may have a large effect on these hosts in the absence of epiphytes; amphipods were the most abundant herbivore of interest at this study's field site and ate significantly more host tissue when epiphytes were not an option. Even though *Idotea* were less abundant and less selective, they could still heavily impact populations of both hosts and epiphytes due to their extremely high feeding rates. In addition, littorine snails could have a large effect on epiphyte populations in particular, as they targeted epiphyte reproductive structures while grazing. Although the impact of epiphytes on host vulnerability to herbivory depends on whether there is a numerical response in herbivore density following consumption of epiphytes, all three invertebrate herbivores investigated in this study have the potential to affect both epiphyte and host populations.

Contrary to the prevailing paradigm (Figure 1), data presented here demonstrate marine algal epiphytes do not always negatively impact their hosts (Figure 22); the host in this study often benefits from closely associating with its epiphyte. Although the existence of parasites,

viruses, and diseases attest to the fact that interactive affects do not need to be beneficial for these entities to persist and evolve, if both symbiont organisms benefit, there could be a positive feedback that quickens and facilitates the evolution of these types of relationships. The potential benefits experienced by both host and epiphyte do not preclude concurrent negative impacts of epibiosis but may lend insight into the evolution of these associations. By combining their existence with another alga, both host and epiphyte often perform better than they would alone. Moreover, this study found few costs associated with epiphytism. Biomechanically, the increased dislodgement risk of hosts is likely decreased when epiphytes dislodge before hosts. And, although these epiphytes could hinder host light acquisition during extremely high tides, they may also protect hosts against physiological damage during low tide. Lastly, even though epiphytes are preferred by herbivores, this may not be dependent on epiphytic habit; i.e., mobile grazers would likely eat these epiphytes whether they were growing on hosts or rock. Given the few costs and multifaceted benefits of epiphytic association, data presented here may help explain the development and continued existence of intertidal algal epiphytism.

	Aquatic Hosts	Aquatic Epiphytes
Biomechanics	Cost-Neutral	**Benefit**
Photosynthesis	Cost-**Benefit**	Neutral
Desiccation	**Benefit**	Neutral
Herbivory	**Benefit***	Neutral

Figure 23: Summary of costs and benefits experienced by intertidal algal hosts and epiphytes. *Herbivory is only a benefit if consuming epiphytes does not increase herbivore density and cause remaining hosts to be grazed.

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