

RESEARCH ARTICLE

Biomechanical consequences of epiphytism in intertidal macroalgae

Laura M. Anderson* and Patrick T. Martone

ABSTRACT

Epiphytic algae grow on other algae rather than hard substrata, perhaps circumventing competition for space in marine ecosystems. Aquatic epiphytes are widely thought to negatively affect host fitness; it is also possible that epiphytes benefit from associating with hosts. This study explored the biomechanical costs and benefits of the epiphytic association between the intertidal brown algal epiphyte *Soranothera ulvoidea* and its red algal host *Odonthalia floccosa*. Drag on epiphytized and unepiphytized hosts was measured in a recirculating water flume. A typical epiphyte load increased drag on hosts by ~50%, increasing dislodgment risk of epiphytized hosts compared with hosts that did not have epiphytes. However, epiphytes were more likely to dislodge from hosts than hosts were to dislodge from the substratum, suggesting that drag added by epiphytes may not be mechanically harmful to hosts if epiphytes break first. Concomitantly, epiphytes experienced reduced flow when attached to hosts, perhaps allowing them to grow larger or live in more wave-exposed areas. Biomechanical interactions between algal epiphytes and hosts are complex and not necessarily negative, which may partially explain the evolution and persistence of epiphytic relationships.

KEY WORDS: Epiphyte, Host, *Soranothera ulvoidea*, *Odonthalia floccosa*, Biomechanics, Drag, Seaweed, Algae, Intertidal

INTRODUCTION

The rocky intertidal zone is one of the most hydrodynamically stressful environments on Earth. Organisms in this habitat must resist wave forces greater than comparable forces applied by hurricane winds in terrestrial systems (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). Consequently, hydrodynamic forces can affect overarching patterns of zonation (Harley and Helmuth, 2003; Harley and Paine, 2009) and community structure (Connell, 1972) in the intertidal zone.

Wave-induced 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). While motile organisms are capable of relocating to spaces less affected by hydrodynamic stress, 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 to survive in environments characterized by

frequent hydrodynamic disturbance (Puijalon et al., 2008). 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; Wolcott, 2007); reconfiguration is more readily achieved by algae composed of flexible tissue (Boller and Carrington, 2006a; Demes et al., 2011; Harder et al., 2004).

In the intertidal zone, where competition for space is intense (Dayton, 1971), some algae have evolved to grow on other algae rather than hard substrata. The ecological consequences of these epiphytic relationships are not fully understood. Aquatic epiphytism is generally regarded as deleterious to host species (D'Antonio, 1985; Littler and Littler, 1999; Hay et al., 2004; Harder, 2008). Aquatic epiphytes are often large relative to their hosts; for example, algal epiphytes growing on certain types of seagrasses have been shown to compose up to 95% of above-ground biomass in these environments (Mukai and Ishijima, 1995). Large aquatic epiphytes may have large negative impacts on smaller hosts by intercepting sunlight (Sand-Jensen, 1977; Sand-Jensen and Borum, 1984), interfering with nutrient acquisition (Lobban and Harrison, 1994), and increasing drag and dislodgement of hosts (Ruesink, 1998).

Aquatic epiphytes increase drag on intertidal seaweeds (Ruesink, 1998) and invertebrates (Witman and Suchanek, 1984; Wahl, 1996), perhaps by adding surface area to hosts, changing the overall shape of their hosts, and affecting the ability of hosts to reconfigure in flow. For example, mussels with algae growing on their shells experience increased dislodgement in the field following heavy wave action and storm events (Witman and Suchanek, 1984; O'Connor et al., 2006). However, such biomechanical consequences are not well studied. Because dislodgement often leads to death and generally prevents intertidal organisms from completing their life cycle, it is advantageous for these organisms to resist dislodgement. This situation is a double-edged sword for epiphytes, however: they must hold on tight to their hosts, but are not guaranteed survival as their hosts may fail beneath them.

This study aimed to address four specific biomechanical questions regarding intertidal host–epiphyte interactions: (1) do algal epiphytes increase drag on algal hosts; (2) if so, do epiphytes always increase the dislodgement risk of hosts; (3) do epiphytes receive a hydrodynamic benefit by growing on hosts; and (4) what is the likelihood of epiphytes dislodging before hosts? These questions were addressed using the brown algal epiphyte *Soranothera ulvoidea* Postels and Ruprecht 1840 and its host, the perennial red alga *Odonthalia floccosa* (Esper) Falkenberg.

RESULTS

Host drag and dislodgement

Drag increased on both epiphytized hosts (Fig. 1) and unepiphytized hosts as water velocity increased in a high-speed recirculating water flume (Fig. 2). At each test velocity, however, epiphytized hosts experienced significantly more drag than unepiphytized hosts

Department of Botany and Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

*Author for correspondence (lmanders@ucsc.edu)

Received 28 March 2013; Accepted 25 November 2013

List of symbols and abbreviations

A	planform area
C_d	drag coefficient
D_{epi}	drag on detached epiphytes
D_{host}	drag on hosts without epiphytes
D_{together}	drag on epiphytized hosts
F	force
K_1	slope constant
K_2	intercept constant
L	characteristic length (\sqrt{A})
Re	Reynolds number
Re_{crit}	critical Reynolds number
U	water velocity
U_{crit}	critical velocity
ρ	density of seawater
ν	kinematic viscosity of seawater

(paired t -tests, $P < 0.001$ for all velocities). On average, epiphytes added $50.6 \pm 4.5\%$ (mean \pm s.e.m.) more drag to hosts at each test velocity within the flume.

The 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), of hosts with and without epiphytes declined with increasing Reynolds number (Re) (Fig. 3), a parameter that takes into account both algal size and test velocity in the flume. Epiphytes did not seem to affect the drag coefficient of their hosts (and therefore functional shape), as slopes of lines fitted to C_d versus Re for each fond with ($n=14$) and without epiphytes ($n=14$) were not significantly different (paired t -test, $t=1.086$, d.f.=13, $P > 0.3$). Nor were the intercepts of these same lines significantly different (paired t -test, $t=-0.643$, d.f.=13, $P > 0.5$).

Velocities predicted to dislodge hosts with epiphytes and hosts alone were significantly different ($t=-5.211$, d.f.=13, $P < 0.0001$; Fig. 4). On average, epiphytized hosts were predicted to resist only $10.2 \pm 0.9 \text{ m s}^{-1}$ water velocity before dislodging from the substratum, whereas hosts alone were predicted to break at $16.0 \pm 1.8 \text{ m s}^{-1}$ (means \pm s.e.m.).

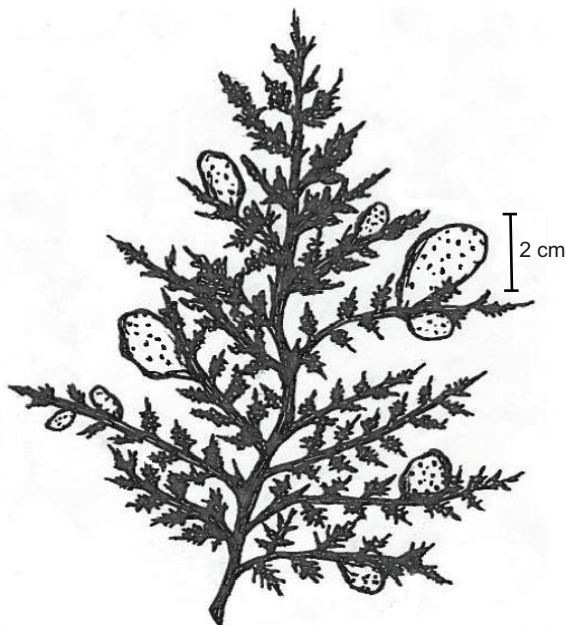


Fig. 1. Line drawing of *Soranthera ulvoidea* growing epiphytically on *Odonthalia floccosa*.

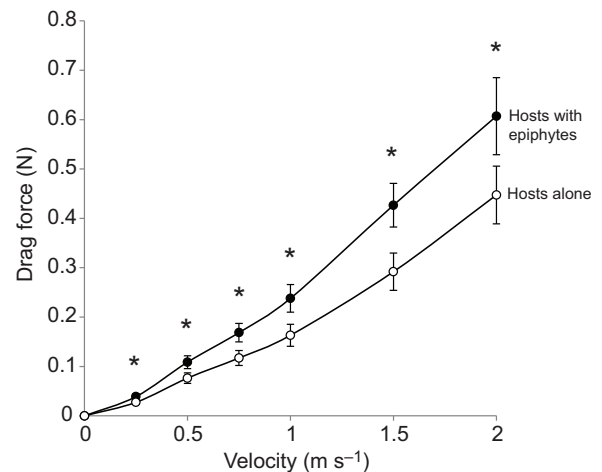


Fig. 2. Mean drag force experienced by hosts with epiphytes (closed circles) and hosts alone (open circles) at different test velocities in a recirculating water flume. $n=14$ for 0, 0.25, 0.5, 0.75, 1 and 1.5 m s^{-1} and $n=11$ for 2 m s^{-1} . Error bars are \pm s.e.m. Asterisks denote significant paired t -test results ($P < 0.05$).

Epiphyte drag and dislodgement

Total drag on detached epiphytes summed for all epiphytes per host (D_{epi}) was often greater than drag on epiphytized hosts (D_{together}) minus drag on hosts alone (D_{host}), especially when forces were above 0.15 N (Fig. 5). The linear trendline of total D_{epi} plotted against $D_{\text{together}} - D_{\text{host}}$ had a slope that was significantly greater than 1 ($t=3.471$, d.f.=76, $P < 0.001$), signifying that epiphytes experience more drag alone than when attached to hosts. Similarly, Lifesavers® used to simulate epiphytes, lost significantly less mass and thus experienced slower water velocities when attached to hosts in the flume than when not attached to hosts (ANOVAs, $P < 0.03$ at all velocities; Table 1, Fig. 6).

The weakest epiphytes of all but one host were predicted to break before their hosts were predicted to dislodge from the substratum (Table 2). Velocities predicted to dislodge epiphytized hosts were significantly different from velocities predicted to dislodge their weakest epiphytes ($t=5.615$, d.f.=13, $P > 0.0001$). In fact, seven out of 15 hosts had an epiphyte actually dislodge while being tested in the flume.

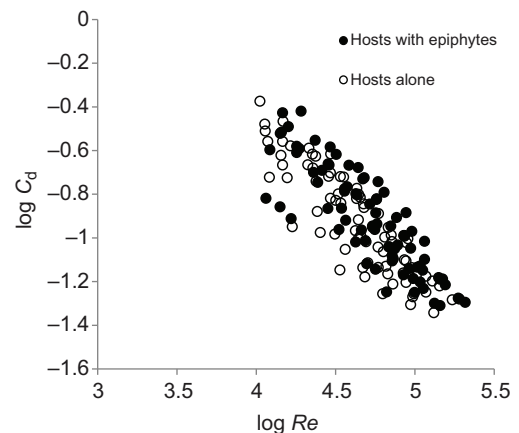


Fig. 3. \log_{10} drag coefficient versus \log_{10} Reynolds number (Re) of hosts with epiphytes (closed circles) and hosts alone (open circles). $n=14$ for Re incorporating velocities between 0 and 1.5 m s^{-1} and $n=11$ for 2 m s^{-1} .

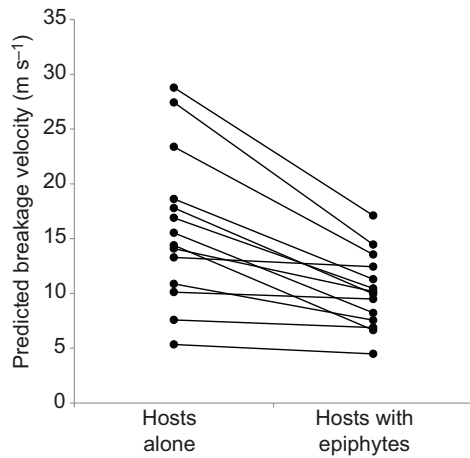


Fig. 4. Predicted dislodgement velocities for hosts without epiphytes versus predicted breakage velocities for the same hosts with epiphytes. $n=14$.

Re_{crit} , the critical combination of size and water velocity needed to cause dislodgement (see Martone and Denny, 2008), was 1.49×10^5 for epiphytes not attached to hosts (Fig. 7). Given this Re_{crit} , larger epiphytes are expected to dislodge at slower water velocities than smaller epiphytes both on and off hosts (Fig. 8). Theoretically, epiphytes growing on hosts should be able to grow over three times the size of epiphytes attached to rock. For instance, at 9.4 m s^{-1} (the maximum velocity experienced at this study's field site), an epiphyte attached to a host was predicted to be able to grow up to 7.8 cm^2 , whereas a theoretical epiphyte exposed to the same velocity, but not attached to a host, was predicted to grow up to 2.5 cm^2 . The largest epiphyte observed on a host throughout this study was 6.0 cm^2 , similar to our model's prediction (Fig. 8).

Out of 400 epiphytes observed on herbarium voucher specimens, the majority of *S. ulvoidea* epiphytes were attached to tertiary branchlets (Table 3). On average, primary host branches resisted the most force, and tertiary branchlets resisted the least (Table 3). The mean (\pm s.e.m.) force required to break a tertiary branchlet was

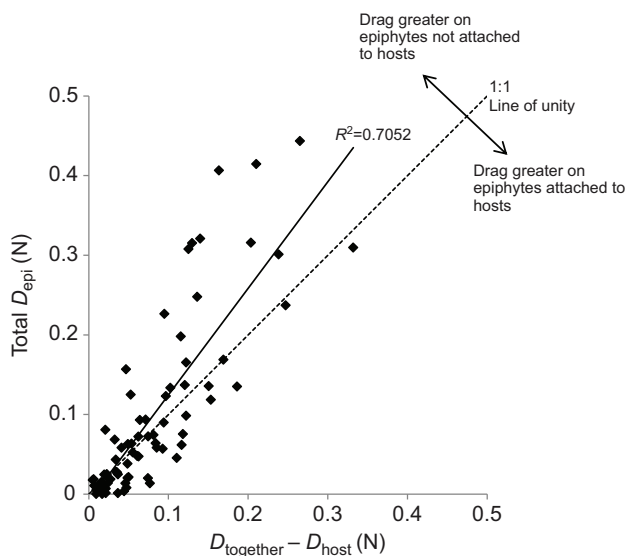


Fig. 5. Total drag on epiphyte loads not attached to hosts (D_{epi}) versus epiphyte loads attached to hosts ($D_{together} - D_{host}$). Solid line is least squares trendline. Dotted line is the 1:1 hypothetical line of unity.

Table 1. One-way ANOVA results for Lifesavers on and off hosts at different velocities

Velocity (m s^{-1})	d.f.	<i>F</i>	<i>P</i>
0	1,18	14.29	0.001
0.5	1,18	11.37	0.003
1.0	1,18	5.76	0.03
1.5	1,17	24.12	0.0001
2.0	1,18	27.48	0.0001

$0.37 \pm 0.07 \text{ N}$ and the mean (\pm s.e.m.) force required to break an epiphyte at its point of attachment was $0.45 \pm 0.03 \text{ N}$.

Field measurements

The highest maximum water velocity recorded by a dynamometer at the algal collection site on Salt Spring Island between May and November 2011 was 9.4 m s^{-1} (Table 4).

DISCUSSION

The intertidal zone is hydrodynamically stressful for seaweeds, and algae are often at risk of dislodgement and mortality (Denny et al., 1985; Gaylord et al., 1994). Epiphytic algae may affect both size and shape of host algae, which in turn could negatively affect the survival of hosts. The effects of epiphytes on hosts are complex, and host–epiphyte interactions are widespread in the intertidal zone; however, little biomechanical research has been performed on marine algal epiphytism.

Biomechanical costs of epiphytism

This study shows that a typical load of *S. ulvoidea* epiphytes increases drag on hosts by $\sim 50\%$ at speeds tested within a flume. This increase in drag is likely due to increased surface area caused by the addition of epiphytes, and not by a change in shape. Even though epiphyte morphology appears different from that of hosts, because the drag coefficient of hosts is not significantly affected by the addition of epiphytes (Fig. 3), the epiphytes in this study do not seem to change the 'functional shape' of their hosts in flow. This manifestation of added drag is in accordance with literature (Ruesink, 1998), that found *O. floccosa* fouled with diatoms

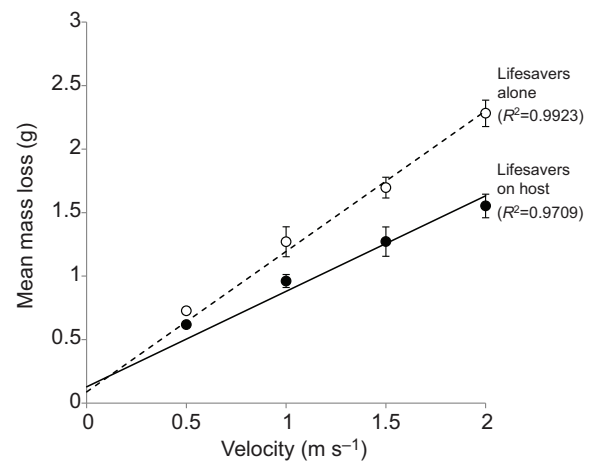


Fig. 6. Mean mass loss of Lifesavers alone (open circles) and Lifesavers on hosts (closed circles) at different velocities in a flume. Lines are linear trendlines for Lifesavers alone (dashed) and Lifesavers on hosts (solid). $n=10$ (except 1.5 m s^{-1} for Lifesavers on hosts: $n=9$). Error bars are \pm s.e.m. Asterisks denote significant ANOVA results ($P < 0.05$).

Table 2. Predicted velocities required to dislodge epiphytized hosts and to break the weakest epiphyte on each host

Sample	Predicted breakage velocity (m s ⁻¹)	
	Epiphytized host	Weakest epiphyte
A	10	2.7
B	7.6	4.6
C	6.9	5.4
D	12.4	4.8
E	14.5	4.9
F	17.1	4.0
G	13.6	2.7
H	10.2	5.2
I	11.3	6.7
J	10.5	4.9
K	6.6	3.4
L	9.5	5.2
M	4.5	5.4
N	8.2	4.0

Epiphytes were predicted to break before epiphytized hosts except for sample M (highlighted in gray).

experiences twice as much drag in the field as this same species without fouling epiphytes. The increase in drag in the aforementioned study (Ruesink, 1998) is attributed to increased algal cross-sectional area due to epiphytic diatom cover.

Hosts in the present study experience more drag when epiphytes are present, decreasing predicted dislodgement velocities and increasing host dislodgment risk. However, epiphytes are more likely to dislodge from hosts than epiphytized hosts are to dislodge from the substratum. Thus, as water velocity increases, epiphytes are expected to dislodge before their underlying host. Therefore, *S. ulvoidea* may have less of a negative biomechanical effect on its host, *O. floccosa*, than previously assumed.

Biomechanical benefits of epiphytism

Data presented here suggest that epiphytes receive a hydrodynamic benefit by growing on hosts. Algae growing epiphytically experience decreased flow, corresponding to decreased drag and reduced dislodgement risk. This reduction in flow, and subsequent decrease in drag, could be due to the majority of *S. ulvoidea* epiphytes growing attached to the tips of hosts (Table 3). This

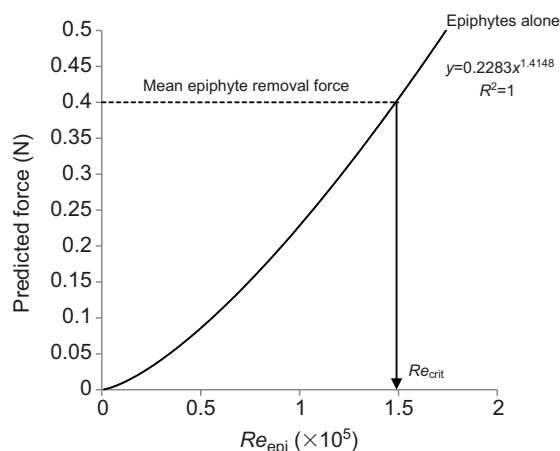


Fig. 7. Predicted force calculated for epiphytes not attached to hosts at potential Reynolds number values. Dashed line at 0.4 N represents the mean force at which tertiary branchlets break along with attached epiphytes. Arrow points to Re_{crit} (critical combination of velocity and epiphyte size required to dislodge epiphytes not attached to hosts).

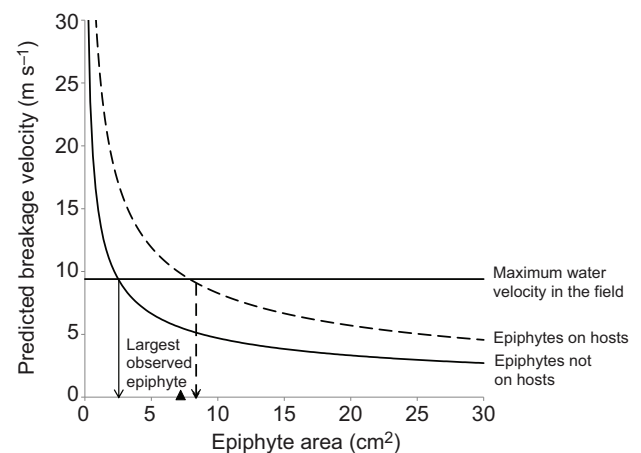


Fig. 8. Water velocities predicted to dislodge epiphytes on hosts (dashed line) and epiphytes theoretically attached to rocks (solid line). Arrows depict the maximum attainable sizes of epiphytes not attached to hosts (solid) and epiphytes attached to hosts (dashed) at this study's maximum water velocity (horizontal line). Triangle depicts the epiphyte with the largest area measured throughout the course of this study.

arrangement likely places epiphytes in the wake formed downstream of host branches. Although the wake of flexible objects can be chaotic, wakes are generally areas of slowed water movement (Johnson, 2001), which could allow epiphytes to 'draft' behind hosts, and thereby experience less drag force (Boller and Carrington, 2006b). Concomitantly, the flexible nature of these hosts may also play a role in the reduction of drag experienced by epiphytes. Flexibility enables algae to reconfigure in flowing water, becoming more streamlined (Boller and Carrington, 2006a; Demes et al., 2011; Harder et al., 2004; Martone et al., 2012). By growing epiphytically, *S. ulvoidea* is able to take advantage of the drag-ameliorating strategies of its flexible host. Moreover, although *S. ulvoidea* is an obligate epiphyte, our data show that *S. ulvoidea* growing on rock would theoretically experience increased drag.

Host-induced flow reduction may allow epiphytes to grow in areas of higher water velocities. As shown in Fig. 8, epiphytes on hosts should theoretically be able to grow to surface areas three times as large as epiphytes growing on rock before becoming dislodged. Increased growth capacity for epiphytic algae likely has important fitness implications: *S. ulvoidea*'s reproductive sori are distributed across the entire thallus, so larger individuals are likely capable of greater reproductive output (Chapman, 1986). Thus, epiphytic growth may be a strategy for increasing reproduction and maintaining high population densities.

The maximum observed epiphyte size (6.0 cm²) at our field site was approximately predicted by our biomechanical model (7.8 cm²; Fig. 8), suggesting that water velocities may indeed limit the maximum size of epiphytes in the field. This conclusion supports

Table 3. Mean and maximum forces required to dislodge epiphytes (N=56) from hosts, and percentages of epiphytes on University of British Columbia herbarium voucher specimens attached to primary, secondary and tertiary host branchlets (N=400 epiphytes)

Host branch	Mean breakage force (N)	Maximum breakage force (N)
Primary	2.0±1.3 (15)	6.3
Secondary	1.0±0.7 (17)	2.4
Tertiary	0.4±0.3 (24)	1.0

Mean values are presented ±s.d. (n).

Table 4. Maximum water velocities measured by dynamometers at the algal collection site between May and November 2011

Month	Maximum water velocity (m s^{-1})
May	9.4
June	4.2
July	8.1
August	4.2
September–November	5.2

previous work on the biomechanical constraints of organismal size in the wave-swept intertidal zone (Denny et al., 1985; Blanchette, 1997; Wolcott, 2007; Martone and Denny, 2008). Our work further suggests that, theoretically, epiphytes should be able to grow larger when living in areas of reduced flow. However, epiphytes are ultimately dependent on the presence of hosts, which may be spatially constrained by light, nutrient delivery, herbivory or some other ecological factor.

Epiphytes in this study were commonly situated on the distal branchlets of hosts, which require slightly less force to break than epiphytes at their attachment points. Epiphytized hosts may avoid being wholly ripped from the substratum when these epiphytized terminal branches break. Such 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., 2013). *Soranthera ulvoidea* seems to appear on the tips of *O. floccosa* between May and June, when this host’s annual growth cycle has essentially come to an end (Bracken, 2004). Thus, *O. floccosa* hosts have likely reproduced by the time epiphytes are large enough to break host branchlets. In this way, breakage of host extremities may not affect host reproduction. Host growth and reproduction thusly appear well synchronized to mitigating the biomechanical impact of algal epiphytes in the intertidal zone; despite host breakage, the impact of epiphytes on hosts may be negligible.

Dislodgement of epiphytes may not be entirely costly to epiphytes either. *Soranthera ulvoidea* individuals are often filled with water, but air bubbles produced by photosynthesis also accumulate in this saccate alga, allowing some detached individuals to float. Floating and drifting algae have been shown to persist unattached, which may aid dispersal (Macaya et al., 2005; Hernández-Carmona et al., 2006; McKenzie and Bellgrove, 2008). Thus, reproduction of buoyant epiphyte species may not be hindered by dislodgement and may instead aid in the dispersal of *S. ulvoidea*.

It should be mentioned that the present study used extrapolations from flume data, which are sometimes inaccurate (Bell, 1999; Martone et al., 2012) but necessary because of the difficulty replicating high water velocities in controlled laboratory settings. However, flume measurement extrapolations often underestimate drag forces experienced by flexible macroalgae (Martone et al., 2012); thus, estimates here may be conservative. Regardless of these possible caveats, it is likely that intertidal epiphytes universally increase drag on their hosts, but that the overall impact of epiphytism may not be as negative to hosts as previously assumed.

The hydrodynamic benefits of epiphytism described in this study may clarify patterns of other epiphytic plants and animals. For example, many sessile animals, such as hydroids, bryozoans, sponges and tunicates, also grow epiphytically. These organisms may benefit from epiphytic habitat, circumventing competition for space on hard substrata and living in areas of reduced flow and dislodgement risk. In particular, epiphytic suspension feeders may especially benefit from localized flow reduction, allowing them to feed in areas of more

intense water velocities where they otherwise would be unable to do so (Harvell and LaBarbera, 1985; Miller, 2007). In sum, this study helps resolve the complex interactions between epiphytes and their hosts, and lends insight into the maintenance of these close ecological associations over evolutionary time.

Conclusions

This study found that *S. ulvoidea* epiphytes increase drag on their host, *O. floccosa*. This increase in drag ostensibly increases the risk of hosts becoming dislodged. However, epiphytes are more likely to dislodge from hosts than hosts are to dislodge from the substratum. Thus, epiphytes may have less of a biomechanical effect on these hosts than previously thought. Epiphytes benefit from growing attached to their hosts by experiencing reduced flow, and are likely able to grow larger and resist faster flow conditions when attached. This is the first study to demonstrate and quantify mechanical benefits experienced by epiphytic algae. Further examination of the biomechanics of intertidal algal epiphytism may shine light on patterns of algal survivorship, and thereby seaweed evolution, seasonality and intertidal community dynamics.

MATERIALS AND METHODS

Study species and specimen collection

Soranthera ulvoidea 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 sac-like epiphytes on certain 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* grows on rocks throughout this same range, and often hosts the epiphyte *S. ulvoidea* (Abbott and Hollenberg, 1976) (see Fig. 1).

Epiphytized *O. floccosa* were haphazardly collected from the mid to low intertidal zone northwest of Fulford Harbour on Salt Spring Island, British Columbia, Canada ($48^{\circ}45'23.98''\text{N}$, $123^{\circ}25'16.06''\text{W}$), between May and June 2011. Algae were placed in 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 h of collection. Water table conditions were kept between 8 and 10°C with 14 h of fluorescent light per day ($\sim 115 \mu\text{mol m}^{-2} \text{s}^{-1}$). All algae were tested within 18 days of collection.

Unepiphytized *O. floccosa* used for the second set of experiments (see Epiphyte drag and dislodgement, below) were haphazardly collected from the mid to low intertidal zone in Ruckle Provincial Park on Salt Spring Island, British Columbia, Canada ($48^{\circ}46'30.23''\text{N}$, $123^{\circ}22'3.89''\text{W}$), in February 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 upon collection.

Host drag and dislodgement

Forces to dislodge epiphytized *O. floccosa* fronds ($n=14$) from the substratum in the field were measured using a 10 N recording spring scale (Ohaus Corp., Pine Brook, NJ, USA). Size and number of epiphytes varied among these differently sized host fronds. Epiphytes less than 10 mm in length were removed from host fronds because of the difficulty in attaching these to equipment for subsequent related experiments (see Epiphyte drag and dislodgement, below); more than 10 small epiphytes were never observed on hosts tested in the flume. Drag on hosts was measured in a custom high-speed recirculating water flume (Ecological Mechanics, Rochester, NY, USA) (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 seven different water velocities (0, 0.25, 0.5, 0.75, 1, 1.5, 2 m s^{-1} ; the flume could not produce velocities exceeding 2 m s^{-1}). Drag forces were recorded with LabVIEW software (National Instruments,

Austin, TX, USA). Epiphytes were then detached, and drag was measured a second time on these hosts without epiphytes at the same speeds. Drag on the wire alone was also measured at all velocities, and drag force measurements on algae were corrected accordingly. 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. All statistical analyses in this study were performed using SYSTAT 13 (SYSTAT Software Inc., San Jose, CA, USA), $\alpha=0.05$.

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

$$F = \frac{1}{2} \rho U^2 A C_d, \quad (1)$$

was rearranged to solve for the 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):

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

where ρ is the density of seawater (approximately 1000 kg m^{-3}), U is water velocity and A is the planform area of hosts, defined as the area within the outline of an object when viewed from above. Planform 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) for the same hosts without epiphytes, a parameter that takes into account both algal planform area and the test velocity experienced by each host frond:

$$Re = \frac{LU}{\nu} = \frac{\sqrt{A}U}{\nu}, \quad (3)$$

where L is characteristic length (here assumed to be \sqrt{A}), ν is the kinematic viscosity of seawater ($1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$). C_d versus Re data were \log_{10} transformed and regression lines were fitted for each frond without epiphytes. C_d and Re were then calculated for hosts with epiphytes ($n=14$) using Eqns 2 and 3, and by substituting ($A_{\text{host}} + A_{\text{all epiphytes}}$) for A in both equations. C_d versus Re data for these hosts with epiphytes were also \log_{10} transformed and regression lines were fitted for each frond with epiphytes. To determine whether algal epiphytes significantly affect the drag coefficient of hosts as Re increases, a paired *t*-test was carried out on the slopes and intercepts of $\log_{10} C_d$ versus $\log_{10} Re$ for each frond with ($n=14$) and without ($n=14$) epiphytes.

Regression parameters from C_d versus Re lines were used to predict C_d and drag forces at hypothetical Re values (exceeding those measured). C_d values were calculated for each host alone and each epiphytized host using the equation:

$$\log_{10} C_d = K_1 \times \log_{10} Re + K_2, \quad (4)$$

where Re are theoretical values, K_1 is the slope of the $\log_{10} C_d$ versus $\log_{10} Re$ lines for each individual host with and without epiphytes and K_2 is the intercept of these same lines. For each Re , C_d values were calculated from Eqn 4, and drag forces were calculated by substituting C_d into Eqn 1 as a way of extrapolating from the data. Hypothetical drag forces were plotted against hypothetical Re values, and power curves were fitted to these data for each host with and without epiphytes. Dislodgement forces of each host were used in combination with fitted curves to calculate critical Reynolds numbers (Re_{crit}) of hosts with and without epiphytes using Eqn 3. Re_{crit} (see Martone and Denny, 2008) represents the critical combination of host size (with and without epiphytes) and water velocity that would dislodge each host from the substratum. Eqn 3 was then rearranged as:

$$U_{\text{crit}} = \frac{Re_{\text{crit}}}{\sqrt{A\nu}}, \quad (5)$$

and Re_{crit} values were used to calculate the critical velocity (U_{crit}) required to dislodge each host with and without epiphytes. To determine whether the presence of epiphytes significantly affects the dislodgement risk of hosts, a paired *t*-test was performed on predicted breakage velocities of hosts with and without epiphytes.

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 (D_{together} , $n=14$), and then on these same hosts with epiphytes removed (D_{hosts}) at seven test velocities (0, 0.25, 0.5, 0.75, 1, 1.5 and 2 m s^{-1}). Drag experienced by epiphytes was then estimated by subtracting D_{hosts} from D_{together} , assuming the difference represented the amount of drag added by epiphytes only. Drag was then measured on detached epiphytes, and summed for all epiphytes per host (total D_{epi}). Total D_{epi} was plotted against ($D_{\text{together}} - D_{\text{hosts}}$) 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. A positive departure from the 1:1 line would suggest that epiphytes experience more drag alone than when attached to hosts.

Second, hydrodynamic benefits of epiphytism were examined directly by measuring dissolution of 'Pep-o-mint' Lifesavers[®] on and off hosts in the flume. Individual Lifesavers ($n=10$) were tied to the wire on the force transducer and put in the flume for 1 min at each of the following velocities: 0, 0.5, 1, 1.5 and 2 m s^{-1} . Lifesavers were then tied with thread to branches of haphazardly selected host fronds without epiphytes ($n=10$, except 1.5 m s^{-1} , $n=9$) so that they dangled near terminal branchlets, where epiphytes are commonly found attached. These hosts with attached Lifesavers were put in the flume for 1 min at each of the above velocities. Experimental Lifesavers were then dried in an oven at 60°C for 48 h. Dried mass of experimental Lifesavers was subtracted from original mass to determine mass lost in the flume. Dissolution is a proxy for bulk water movement (Koehl and Alberte, 1988) and may be affected by both water velocity and turbulence (Denny, 1988). Fast experimental water velocities applied for 1 min likely create a fully turbulent boundary layer around the Lifesavers [see ch. 9 in Denny (Denny, 1988)]. While we acknowledge that the exact contribution of turbulence to dissolution requires further testing, in this study it was assumed that dissolution rate varies primarily as a function of water velocity. Thus, mass loss was used to estimate the reduction in water velocity experienced by Lifesavers attached to hosts (see below). One-way ANOVAs were used to detect differences in mass loss of Lifesavers on and off hosts at all test velocities in the flume.

To estimate velocities experienced by Lifesavers on hosts ('effective velocities'), mass loss measured on Lifesavers alone was used to create a linear function correlating mass loss and water velocity ('true velocity'). This function was then used to convert mass loss into water velocities experienced by Lifesavers on hosts. Effective velocities were plotted against true velocities, and a regression line was fitted to these data to estimate the reduction in water velocity experienced by epiphytes on hosts.

C_d and Re were calculated for all individual epiphytes in the flume at all test velocities using Eqns 2 and 3, respectively. A regression line was fitted to $\log_{10} C_d$ versus $\log_{10} Re$. Breakage velocities for solitary epiphytes were predicted the same way as for hosts (see Host drag and dislodgement, above). If epiphytes dislodged from their hosts during an experiment and actual removal forces were not obtained, removal forces were estimated from a linear regression of epiphyte size versus removal force data collected for 64 random epiphytes. Briefly, at each theoretical Re , C_d values were calculated using Eqn 4 and then drag forces were calculated using Eqn 1. A power curve was fitted to drag force versus Re , and Re_{crit} was determined for each epiphyte using individual epiphyte removal forces (determined when epiphytes were dislodged from hosts using a spring scale). Breakage velocities for solitary epiphytes were determined from Re_{crit} . The regression of effective velocity versus true velocity was then used to estimate the actual velocity required to break epiphytes on hosts. A paired *t*-test was used to detect differences between velocities predicted to dislodge epiphytes from hosts and velocities predicted to dislodge hosts from the substratum.

To explore where epiphytes are commonly attached, 400 *S. ulvoidea* individuals were examined on UBC herbarium voucher specimens, and the number of epiphytes attached to primary, secondary and tertiary host branches were quantified. Forces to break these branch types were subsequently measured on fresh specimens ($N=56$) using a spring scale. To determine whether epiphytes or host branchlets break first, epiphyte removal forces were compared with branchlet breakage forces using a two sample *t*-

test. The mean (\pm s.e.m.) force required to dislodge an epiphyte from its point of attachment was 0.45 ± 0.03 N, but most epiphytes were attached to tertiary branchlets, which broke on average (\pm s.e.m.) at 0.37 ± 0.07 N; thus, the value 0.4 N was used to model dislodgement of epiphytes from hosts in the field (see below).

To estimate the maximum combination of size and water velocity that causes epiphytes to dislodge from hosts in the field, Re_{crit} was determined for epiphytes not attached to hosts (i.e. theoretically growing on rock) by substituting the mean removal force for an epiphyte (0.4 N) into the equation for the power curve fitted to drag force versus Re for epiphytes. Theoretical values for epiphyte area (A) were substituted into Eqn 5 to determine critical water velocities that would dislodge epiphytes of these given sizes. The regression of effective velocity versus true velocity (determined using Lifesavers) was then used to estimate the velocity predicted to break epiphytes of the same sizes attached to hosts for comparison with water velocities predicted to dislodge epiphytes not attached to hosts.

Field measurements

Maximum water velocities were measured monthly between May and August 2011, and once between September and November 2011, at the algal collection site on Salt Spring Island using 10 calibrated dynamometers (Bell and Denny, 1994). Dynamometers were installed ~ 10 m apart in the mid-intertidal zone (where *O. floccosa* was common) by zip-tying them to screws inserted in the rock that ensured drogues were pulled perpendicular to the shoreline by wave action.

Acknowledgements

We would like to thank Kyle Demes for his initial insight involving the formulation of this project and for his invaluable statistical advice in conjunction with editing help. We are grateful to Chris Harley and Brian Leander for also helping with the development of this project along with editing. This manuscript further benefitted from comments and edits made by Mark Denny, Paul Gabrielson, Rebecca Guenther, Kyra Janot and an anonymous reviewer. Thanks to Sam Starke for his help in the field, and to Becca Kordas for her expertise in all things involving Salt Spring Island. Lastly, this could not have been done without the continued encouragement and support of Pete Raimondi.

Competing interests

The authors declare no competing financial interests.

Author contributions

This study was done as part of a MSc thesis completed by L.M.A. at the University of British Columbia. L.M.A. conducted the experiments, analyzed the data, and wrote the manuscript. P.T.M. supervised the research, and helped design experiments, interpret the results, and revise the manuscript.

Funding

Funding for this research was provided by a Discovery Grant from the Natural Sciences and Engineering Research Council to P.T.M.

References

- Abbott, I. A. and Hollenberg, G. J. (1976). *Marine Algae of California*. Stanford, CA: Stanford University Press.
- Bell, E. C. (1999). Applying flow tank measurements to the surf zone: predicting dislodgement of the Gigartinales. *Phycol. Res.* **47**, 159-166.
- Bell, E. C. and Denny, M. W. (1994). Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. *J. Exp. Mar. Biol. Ecol.* **181**, 9-29.
- Black, R. (1976). The effects of grazing by the limpet, *Acmea innessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. *Ecology* **57**, 265-277.
- Blanchette, C. A. (1997). Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. *Ecology* **78**, 1563-1578.
- Boller, M. L. and Carrington, E. (2006a). The hydrodynamic effects of shape and size change during reconfiguration of a flexible macroalga. *J. Exp. Biol.* **209**, 1894-1903.
- Boller, M. L. and Carrington, E. (2006b). *In situ* measurements of hydrodynamic forces imposed by *Chondrus crispus* Stackhouse. *J. Exp. Mar. Biol. Ecol.* **337**, 159-170.
- Bracken, M. E. S. (2004). Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. *J. Phycol.* **40**, 1032-1041.
- Bradshaw, A. D. (1972). Some of the evolutionary consequences of being a plant. *Evol. Biol.* **5**, 25-47.
- Carrington, E. (1990). Drag and dislodgement of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützinger. *J. Exp. Mar. Biol. Ecol.* **139**, 185-200.
- Chapman, A. R. O. (1986). Age versus stage: an analysis of age- and size-specific mortality and reproduction in a population of *Laminaria longicruris* Pyl. *J. Exp. Mar. Biol. Ecol.* **97**, 113-122.
- Cho, G. Y., Kim, M. S. and Boo, S. M. (2005). Phylogenetic relationships of *Soranthera ulvoidea* (Chordariaceae, Phaeophyceae) on the basis of morphology and molecular data. *Algae* **20**, 91-97.
- Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* **3**, 169-192.
- D'Antonio, C. (1985). Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores? *J. Exp. Mar. Biol. Ecol.* **86**, 197-218.
- Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision of subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**, 351-389.
- Demes, K. W., Carrington, E., Gosline, J. and Martone, P. T. (2011). Variation in anatomical and material properties explains differences in hydrodynamic performances of foliose red macroalgae (Rhodophyta). *J. Phycol.* **47**, 1360-1367.
- Demes, K. W., Pruitt, J. N., Harley, C. D. G. and Carrington, E. (2013). Survival of the weakest: increased frond mechanical strength in a wave-swept kelp inhibits self-pruning and increases whole-plant mortality. *Functional Ecology* **27**, 439-445.
- Denny, M. W. (1988). *Biology and the Mechanics of the Wave-Swept Environment*. Princeton, NJ: Princeton University Press.
- Denny, M. and Gaylord, B. (2002). The mechanics of wave-swept algae. *J. Exp. Biol.* **205**, 1355-1362.
- Denny, M. W., Daniel, T. L. and Koehl, M. A. R. (1985). Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**, 69-102.
- Gaylord, B., Blanchette, C. A. and Denny, M. W. (1994). Mechanical consequences of size in wave-swept algae. *Ecol. Monogr.* **64**, 287-313.
- Harder, T. (2008). Marine epibiosis: concepts, ecological consequences and host defense. *Mar. Indust. Biofouling* **4**, 219-231.
- Harder, D. L., Speck, O., Hurd, C. L. and Speck, T. (2004). Reconfiguration as a prerequisite for survival in highly unstable flow-dominated habitats. *J. Plant Growth Regul.* **23**, 98-107.
- Harley, C. D. G. and Helmuth, B. S. T. (2003). Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol. Oceanogr.* **48**, 1498-1508.
- Harley, C. D. G. and Paine, R. T. (2009). Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. *Proc. Natl. Acad. Sci. USA* **106**, 11172-11176.
- Harvell, C. D. and LaBarbera, M. (1985). Flexibility: a mechanism for control of local velocities in hydroid colonies. *Biol. Bull.* **168**, 312-320.
- Hay, M. E., Parker, J. D., Burkepile, D. E., Caudill, C. C., Wilson, A. E., Hallinan, Z. P. and Chequer, A. D. (2004). Mutualisms and aquatic community structure: the enemy of my enemy is my friend. *Annu. Rev. Ecol. Syst.* **35**, 175-197.
- Hernández-Carmona, G., Hughes, B. and Graham, M. H. (2006). Reproductive longevity of drifting kelp *Macrocystis pyrifera* (Phaeophyceae) in Monterey Bay, USA. *J. Phycol.* **42**, 1199-1207.
- Huey, R. B., Carlson, M., Crozier, L., Frazier, M., Hamilton, H., Harley, C., Hoang, A. and Kingsolver, J. G. (2002). Plants versus animals: do they deal with stress in different ways? *Integr. Comp. Biol.* **42**, 415-423.
- Johnson, A. S. (2001). Drag, drafting, and mechanical interactions in canopies of the red alga *Chondrus crispus*. *Biol. Bull.* **201**, 126-135.
- Jonsson, P. R., Granthag, L., Moschella, P. S., Åberg, P., Hawkins, S. J. and Thompson, R. C. (2006). Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology* **87**, 1169-1178.
- Kawamata, S. (2001). Adaptive mechanical tolerance and dislodgement velocity of the kelp *Laminaria japonica* in wave-induced water motion. *Mar. Ecol. Prog. Ser.* **211**, 89-104.
- Koehl, M. A. R. (1984). How do benthic organisms withstand moving water? *Am. Zool.* **24**, 57-70.
- Koehl, M. A. R. and Alberte, R. S. (1988). Flow, flapping, and photosynthesis of *Nereocystis leutkeana*: a functional comparison of undulate and flat blade morphologies. *Mar. Biol.* **99**, 435-444.
- Littler, M. M. and Littler, D. S. (1999). Blade abandonment/proliferation: a novel mechanism for rapid epiphyte control in marine macrophytes. *Ecology* **80**, 1736-1746.
- Lobban, C. S. and Harrison, P. J. 1994. *Seaweed Ecology and Physiology*. Cambridge: University Press.
- Macaya, E. C., Boltaña, S., Hinojosa, I. A., Macchiavello, J. E., Valdivia, N. A., Vásquez, N. R., Buschmann, A. H., Vásquez, J. A., Vega, J. M. A. and Thiel, M. (2005). Presence of sporophylls in floating kelp rafts of *Macrocystis* spp. (Phaeophyceae) along the Chilean Pacific coast. *J. Phycol.* **41**, 913-922.
- Martone, P. T. (2007). Kelp versus coralline: cellular basis for mechanical strength in the wave-swept seaweed *Calliarthron* (Corallinales, Rhodophyta). *J. Phycol.* **43**, 882-891.
- Martone, P. T. and Denny, M. W. (2008). To break a coralline: mechanical constraints on the size and survival of a wave-swept seaweed. *J. Exp. Biol.* **211**, 3433-3441.
- Martone, P. T., Kost, L. and Boller, M. (2012). Drag reduction in wave-swept macroalgae: alternative strategies and new predictions. *Am. J. Bot.* **99**, 806-815.
- McKenzie, P. F. and Bellgrove, A. (2008). Dispersal of *Hormosira banksii* (Phaeophyceae) via detached fragments: reproductive viability and longevity. *J. Phycol.* **44**, 1108-1115.
- Miller, L. P. (2007). Feeding in extreme flows: behavior compensates for mechanical constraints in barnacle cirri. *Mar. Ecol. Prog. Ser.* **349**, 227-234.

- Mukai, H. and Ishijima, A.** (1995). Grazing effects of a grammarian Amphipoda, *Amphithoe* sp., on the seagrass, *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. *Ecol. Res.* **10**, 243-257.
- Nielsen, K. J., Blanchette, C. A., Menge, B. A. and Lubchenco, J.** (2006). Physiological snapshots reflect ecological performance of the sea palm, *Postelsia palmaeformis* (Phaeophyceae) across intertidal elevation and exposure gradients. *J. Phycol.* **42**, 548-559.
- O'Connor, N. E., Crowe, T. P. and McGrath, D.** (2006). Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). *J. Exp. Mar. Biol. Ecol.* **328**, 265-276.
- Paine, R. T.** (1979). Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. *Science* **205**, 685-687.
- Puijalon, S., Léna, J. P., Rivière, N., Champagne, J. Y., Rostan, J. C. and Bornette, G.** (2008). Phenotypic plasticity in response to mechanical stress: hydrodynamic performance and fitness of four aquatic plant species. *New Phytol.* **177**, 907-917.
- Ruesink, J. L.** (1998). Diatom epiphytes on *Odonthalia floccosa*: the importance of extent and timing. *J. Phycol.* **34**, 29-38.
- Sand-Jensen, K.** (1977). Effects of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* **3**, 55-63.
- Sand-Jensen, K. and Borum, J.** (1984). Epiphyte shading and its effect on photosynthesis and diel metabolism of *Lobelia dortmanna* L. during the spring bloom in a Danish lake. *Aquat. Bot.* **20**, 109-119.
- Shaughnessy, F. J., DeWreede, R. E. and Bell, E. C.** (1996). Consequences of morphology and tissue strength to blade survivorship of two closely related Rhodophyta species. *Mar. Ecol. Prog. Ser.* **136**, 257-266.
- Vadas, R. L., Wright, W. A. and Miller, S. L.** (1990). Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Mar. Ecol. Prog. Ser.* **61**, 263-272.
- Wahl, M.** (1996). Fouled snails in flow: potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. *Mar. Ecol. Prog. Ser.* **138**, 157-168.
- Witman, J. D. and Suchanek, T. H.** (1984). Mussels in flow: drag and dislodgement by epizoans. *Mar. Ecol. Prog. Ser.* **16**, 259-268.
- Wolcott, B. D.** (2007). Mechanical size limitation and life-history strategy of an intertidal seaweed. *Mar. Ecol. Prog. Ser.* **338**, 1-10.