

Research Article

Limpets and Their Algal Epibionts: Costs and Benefits of *Acrosiphonia* spp and *Ulva lactuca* Growth

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Epibiont and basibiont relationships can have positive and negative effects on both organisms involved, ranging in intensity from minor to major effects. Limpets of species *Lottia pelta* are commonly found with two algal species growing on their backs, *Ulva lactuca* and *Acrosiphonia* spp. Previous research has shown that basibionts (substrate organism) and epibionts (organism growing on the surface) have complex interactions that can be positive, negative, or neutral. A force transducer and flume were used to measure the drag forces experienced by a limpet at various water velocities. Presence of either epiphyte significantly increased limpet drag. *Acrosiphonia* produced a greater drag effect than *U. lactuca*, increasing the force substantially. When dropped in a tank, limpets with algal growth landed foot-down significantly more often than limpets without algal growth. *Acrosiphonia* spp. had a greater effect than *Ulva lactuca*. Lastly, limpets in a wind tunnel with algal growth (especially *Acrosiphonia*) had cooler body temperatures than limpets without algal growth. In conclusion, the effects on the basibiont of this relationship were found to be both positive and negative.

1. Introduction

In the rocky intertidal environment, primary space is often a limiting resource. Because of this, many organisms have developed a life-history strategy of growing on the surface of another organism. The basibiont (substrate organism) and the epibiont (organism growing on the surface) often have complex direct and indirect interspecific associations [1]. The effects of epibionts on the basibiont may show positive, neutral, or negative consequences [1–4].

The mechanical effects of epizoic growth are of particular concern for the basibiont in a marine system. Hydrodynamic effects of epibionts have been well studied in a number of epibiont-basibiont systems. Epibionts may increase drag and lift in environments with high water flow, such as wave-swept intertidal zones [5]. *Mytilus* byssus receives a 2- to 6.7-fold increase in stress induced by drag forces from epibiotic kelp [6]. Epibiotic algae on *Mytilus* mussels increased dislodgement during storms, regardless of the size of the algae [4]. Indeed, mussel dislodgement due to algae may be more important than predation in certain systems [6, 7].

Hydrodynamic effects on the basibiont are not the only possible negative impacts of epizoic organisms. In *Littorina littorea*, for instance, the presence of barnacles growing on the shell causes an increase in the snail's volume and weight and a decrease in the locomotion speed and reproductive output [3]. The increase in shell volume is of particular hydrodynamic importance; increasing shell volume by epibiont presence in another mollusk, *Mytilus* mussels, can result in an increased chance of dislodgement [8].

One system that has not been directly studied is the relationship between intertidal limpets of the species *Lottia pelta* (Rathke, 1833) found in the rocky intertidal zone and epizoic green algal growth, in particular growth of *Acrosiphonia* spp (J. Agardh, 1846) and *Ulva lactuca* (Linnaeus, 1753). On San Juan Island, even in regions where space is not a limiting resource, growth on limpets is common in locations such as Cattle Point and Dead Man's Bay (personal observation). Possible costs related to hydrodynamics are of particular interest because research on epizoic growth has shown negative effects such as dislodgement and increased

drag forces. Three experiments were run to analyze the costs and benefits of these relationships.

It was hypothesized that epizoic growth would lead to a significant increase in drag forces on a limpet shell, resulting in a negative impact on the limpet, but that there are also possible benefits to the limpet. When limpets are dislodged, the algal epibiont may serve as a parachute (a drag-based mechanism), righting the animal as it falls through the water column towards the sea floor. Because foot reattachment is a critical step in the survival of a detached limpet, parachuting has the potential for alleviating the negative impact by increasing the hydrodynamic forces on the limpet [9]. Another possible benefit is that epizoic algal growth could reduce internal body temperature increases of limpets when they are exposed to light and wind. This is important because the heat induced stress on a limpet can lead to desiccation and death. All three of these possible effects were tested by laboratory experiments. Although two of the three aspects investigated here are static, the importance of thermal stress in wake of climate change should be noted.

2. Materials and Methods

2.1. Parachute Hypothesis. 24 limpets were collected from Cattle Point, San Juan Island, WA, twelve with *Acrosiphonia* spp. and twelve with *U. lactuca* growing epizoically on their shells. Each limpet's length, width, height, and wet mass were measured. Wet algal mass was measured after removal from the limpet shell. The approximate length range of the algae used was 3 to 10 cm. Size of attached algae was not controlled for; it remained with the same amounts as what was collected in the field. Algae mass between the two species was measured after the experiment to test for significant differences between species. Mass measurements were made with a 1/100 gram scale.

A circular, 0.5 m deep with 0.5 m radius tank was used at Friday Harbor Labs for dropping limpets. Limpets were maintained in flowing seawater tanks for three days before being used in the experiment. Each limpet was held just below the surface of the water and then dropped in one of three positions: foot-down, foot-up, or sideways. Five drops were made by each position and the number of foot-down landings was recorded to give average landing position of each limpet with each drop orientation which was the proportion of foot-down landings to total number of drops. All limpets were then scraped clean of all epizoic growth and the dropping procedure was repeated for each cleaned limpet.

Contingency tests were run on all parachute data because the data did not conform to the assumptions of ANOVA testing. The data were nonnormal, consisting mostly of 0s and 100s. One-Way ANOVA was used to look at the effect of starting orientation for limpets with *U. lactuca*, which produced data that were normal enough to meet the assumptions of the test (unlike the *Acrosiphonia* bearing limpets). All ANOVA tests were conducted using JMP (SAS, 2007). 2-tailed Student's *t*-test was done to compare the mass of the algae by species to determine if average mass was related to species. Student's *t*-test was done as only two species

of algae were found growing epizoically on shells in the field at the two collection sites.

2.2. Drag Forces. 20 additional limpets were collected from Cattle Point, San Juan Island, WA, ten with *Acrosiphonia* and ten with *U. lactuca* growing epizoically on their shells. Limpet shells were cleaned of body tissue and filled with epoxy with a perpendicular mounting bolt. The bolt was used to attach the limpet to a force transducer mounted flush with the wall of a recirculating flume (0–3 m/s; working section of 0.15 m × 0.15 m × 0.30 m); see Boller and Carrington 2006 for a detailed description. Drag (in Newtons) was recorded using LabVIEW 8.6 software (Austin, TX) for each of the eight water velocities (0.2, 0.7, 1.2, 1.7, 2.2, and 2.7 m/s). Data were collected and the mean of the measurements was calculated for each speed. Algae were subsequently removed from the limpet shells and the drag measurements were repeated on the cleaned shell.

To calculate force in Newtons per cm², estimates were done for the area of the limpet facing the water flow. Area was an estimated value determined by measuring the height and width of the shell and then using the formula for the area of a triangle to give the forward facing surface of the shell. Then, the recorded force was divided by this number. This was done to normalize increased drag forces occurring due to differences in the size of limpet shells used. 3-Way Repeated Measures ANOVA was conducted to test for the effects of the presence of an epibiont, species of algae, and water velocity. Linear regression analysis was used to compare algal mass to drag force at the given water velocity of 1.71 m/s, the maximum speed at which data were collected for all limpets with all of their starting algae (some *U. lactuca* was ripped off in the flume). Drag data from the flume were analyzed using a fully factorial 3-Way ANCOVA with algal species (*Acrosiphonia*, *U. lactuca*), epibiont presence (with epibiont or removed), and water velocity as main effects and limpet cross sectional area as a covariate. Nonlinear regression was performed to create a model to estimate drag forces beyond the capabilities of the flume. Minimum and maximum forces to remove a limpet, 2 N and 25 N, were calculated to determine the required water velocity to dislodge a limpet only by drag forces. These force values come from research on *Cellana tramoserica* (Holten, 1802), a different limpet due to no specific force work being done on *L. pelta* [10]. 2-tailed Student's *t*-test was done to compare the mass of the algae to determine if average algal mass varied by species.

2.3. Temperature Experiment. Ten limpets were collected from Dead Man's Bay, San Juan Island, WA, five with *Acrosiphonia* and five limpets with *U. lactuca*. Limpets were spooned from their shells. Shells were filled with Z-Spar epoxy with thermocouples inserted and placed in a wind tunnel. Z-Spar-filled limpets match actual limpet internal body temperatures with an average correlation of 0.99 ± 0.01 [11]. Temperature was measured every 20 seconds by a datalogger (CSI 21X, Logan, UT) for 5 hours. Wind tunnel

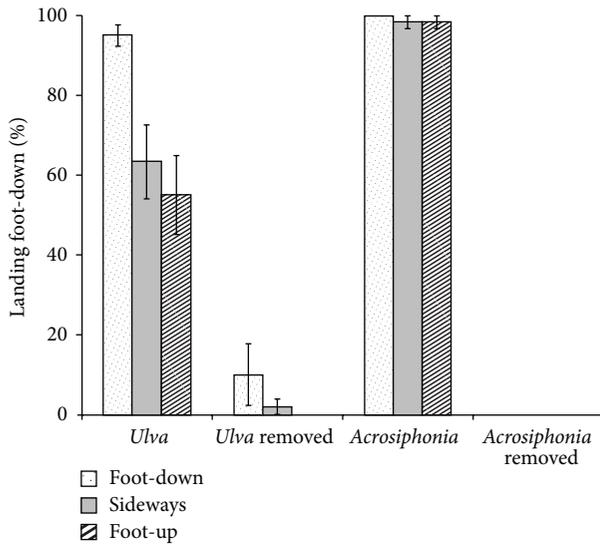


FIGURE 1: Percentage of trials in which limpet landed foot-down on the tank bottom when dropped from the three starting orientations. Data are means \pm standard deviation.

speed was 0.3 m/s and light intensity was in the range of 700–800 watts/m² across the tunnel. Limpet shells and algae were submerged in flowing seawater for 12 hours prior to being placed in the wind tunnel. Substrate was granite placed at an angle of 40 degrees relative to level table.

Air temperature within the wind tunnel was recorded during the course of the experiment with an exposed datalogger because air temperature was not directly controlled for. Each limpet went through the wind tunnel experiment twice. For the first run, limpet shells were placed with their algae still attached as collect in the field in the wind tunnel. At the end of the first experiment run, limpet shells were cleaned of all algae material and then placed in the same wind tunnel with the same speed and light settings. Over the course of both of the five-hour trials, the air temperature for the controls and the experiments started near 18°C and ended near 26°C. This occurred during both trials creating identical conditions for both runs regardless of temperature not being controlled for in the lab. Temperature data from the wind tunnel were analyzed using a fully factorial 3-Way ANOVA with algal species (*Acrosiphonia*, *U. lactuca*), epibiont presence (with epibiont or removed), and time as main effects. 2-tailed Student's *t*-test was done to compare the mass of the algae by species to determine if average mass was related to species.

3. Results

3.1. Parachute Hypothesis. The presence of either *Acrosiphonia* or *U. lactuca* had a highly significant effect on landing orientation of limpets (Figure 1, $G_1 = 881,072$, $P < 0.0001$). Although both algal species facilitated limpets landing upright, there were differences between them in the strength of this effect ($G_1 = 1487$, $P < 0.0001$). Average mass of algae was not significantly different ($P = 0.18$). Specifically,

limpets with *Acrosiphonia* landed foot-down >98% of the time, regardless of the starting orientation of the sinking limpet (Figure 1). The presence of *U. lactuca* also had an effect on landing orientation ($G_1 = 217$, $P < 0.0001$), but it was less consistent (Figure 1). Unlike *Acrosiphonia*, starting orientation for limpets with *U. lactuca* did make a difference ($\chi^2 = 10.488$, $P = 0.0053$, Figure 1). For the ANOVA tests done on the *U. lactuca* data, significant differences were seen between foot-down compared to sideways drops ($P = 0.0079$) and foot-down compared to foot-up drops ($P = 0.0011$). Drops starting foot-down were more likely (95% of the time) to land foot-down than in the other orientations (63% for sideways and 55% for foot-up). Comparison of starting sideways and foot-up starting orientation showed that they were not different in the frequency with which they landed foot-down ($P = 0.4624$). Starting orientation did not have an effect in the *Acrosiphonia* group (Figure 1). They almost always landed foot-down, regardless of the starting orientation. Without epizoic growth, limpets rarely landed foot-down. It should be noted that the distance and time to reach foot-down orientation were minimal; from release, a limpet starting in the foot-up orientation would spin to foot-down in a matter of a few centimeters.

3.2. Drag Forces. Epibiont presence significantly increased drag (Table 1, Figure 2). The strength of this effect differed between algal species; *Acrosiphonia* caused a greater drag increase than *U. lactuca*. Algal mass also had a significant effect on drag ($P < 0.001$). Average mass of algae was not significantly different between species ($P = 0.10$). A positive, linear relationship between algae mass and drag at water velocity of 1.71 m/s was recorded ($R^2 = 0.93$, $P < 0.001$). However, when the largest limpet (which also had the most algal biomass) was excluded, the relationship was weakened ($R^2 = 0.13$, $P < 0.001$). Water velocity by epiphyte presence showed a significant interaction (Table 1); indicating that drag increasing with current velocity was affected by the presence, mass, and species of epibiotic algae (Figure 2). The 3-way interaction of water velocity with species of algae with epiphyte presence was also significant (Table 1); *Acrosiphonia* had a proportionally larger effect at higher velocities when comparing the limpet drag forces before and after algae removal compared to the effect seen with *U. lactuca* (Figure 3).

Nonlinear regression models predict an average decrease of 68% in the water velocity required to dislodge a relaxed limpet with *Acrosiphonia* by only drag forces alone while a clamped limpet showed a 28% decrease in the water velocity required to dislodge the limpet (Table 2). Dislodgment of clamped bare limpets and limpets with *U. lactuca* would only occur at wave forces of greater than 30 m/s. Drag forces from maximum theoretical water velocities of 20 m/s were also predicted to have more substantial increases with *Acrosiphonia* algal growth than *U. lactuca* (Table 3). Maximum theoretical water velocities are predicted velocities experienced in situ allowing for the determination of maximum drag force values. Two limpets with *U. lactuca* growing on them lost all of their algae prior to reaching the highest test velocity,

TABLE 1: RM-ANCOVA analysis of limpet drag forces per cm² of shell.

Source of variation	df	MS	F	P
Species	1	0.36	11.80	0.0016
Epiphyte	1	0.50	16.60	0.0003
Velocity	6	1.60	4.45	<0.0001
Species × epiphyte	1	0.16	5.26	0.0280
Velocity × species	6	0.70	3.28	0.0140
Velocity × epiphyte	6	0.70	3.26	0.0148
Velocity × species × epiphyte	6	0.53	2.48	0.0480

TABLE 2: Water velocities (m/s) required to generate sufficient drag to dislodge a clamped (25 N to remove) and relaxed limpet (2 N to remove). Values are predicted based on extrapolation of a nonlinear regression model.

	With <i>Acrosiphonia</i>	<i>Acrosiphonia</i> removed	With <i>Ulva</i>	<i>Ulva</i> removed
Clamped limpet	28.9	37.0	51.4	39.4
Relaxed limpet	4.7	7.9	9.3	9.6

TABLE 3: Predicted maximum drag forces experienced by limpets with and without epibionts at a water velocity of 20 m/s (theoretical maximum water velocity). Forces are in Newtons.

	With <i>Acrosiphonia</i>	<i>Acrosiphonia</i> removed	With <i>Ulva</i>	<i>Ulva</i> removed
Maximum drag forces	20.46	13.16	8.61	11.09

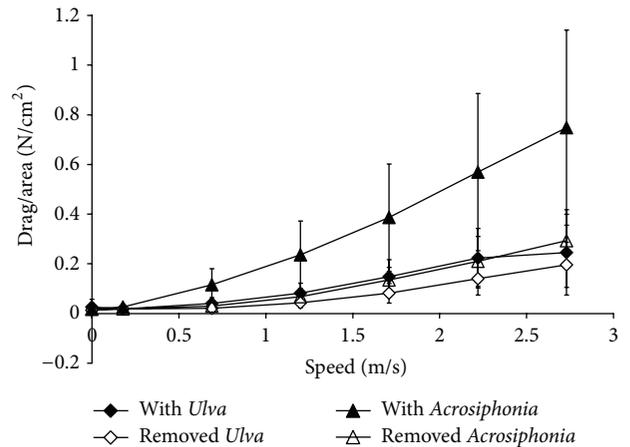
which may indicate a more temporary occurrence of this algal species.

3.3. Temperature Experiment. Epibiont presence caused a significant reduction in the internal temperature increase of limpets (Figure 4, Table 3). However, the strength of this reduction effect was species-dependent, *Acrosiphonia* kept limpets cooler than *U. lactuca* (Table 4). This may have occurred due to significantly more *Acrosiphonia* present on the limpets collected ($P = 0.01$). Average temperature differences between limpets with and without algae also showed that *Acrosiphonia* had a greater impact on limpet temperature, but this pattern did not appear until after one hour in the wind tunnel (Figure 5).

During the first 45 minutes there were minimal temperature differences between limpets with and without algae (Figure 4). As the time in the wind tunnel increased, so did the effect of having epizoic algal growth (Table 4, Figure 4). The 3-way interaction of time with species of algae with epiphyte presence was also significant (Table 4), indicating that a load of *Acrosiphonia* caused proportionally more cooling relative to cleaned limpets as time passed than did a load of *U. lactuca*. Presence of the epiphyte and type of species of epiphyte had a greater effect on net temperature as time passed.

TABLE 4: RM-ANOVA analyses of limpet internal body temperature.

Source of variation	df	MS	F	P
Species	1	0.60	9.59	0.0069
Epiphyte	1	22.10	353.40	<0.0001
Time	5	1237.00	2968.00	<0.0010
Species × epiphyte	1	0.77	12.40	0.0029
Time × species	5	14.00	33.60	<0.0001
Time × epiphyte	5	11.90	28.70	<0.0001
Time × species × epiphyte	5	12.00	28.80	<0.0001

FIGURE 2: Drag force per cm² of shell cross-sectional area felt by the limpet as water velocity was increased. Data are means ± standard deviations.

4. Discussion

4.1. Costs and Benefits of Epizoic Algae. Distinct costs and benefits of the association between limpets and epizoically growing *Acrosiphonia* and *U. lactuca* were found. Having a tuft of either *Acrosiphonia* or *U. lactuca* increased a limpet's chance of landing foot-down if dislodgement occurs. Landing foot-down is important because limpets are unable to right themselves if they land upside-down (personal observation). *Acrosiphonia* acted as a better "parachute" than *U. lactuca*; in only two of 180 trials they landed foot-up, regardless of starting orientation. It should be noted that a single shell collected with *U. lactuca* landed foot-down after algae removal on rare occasions and almost solely when starting in a foot-down position. It appears that some natural variation in limpet shell shape may be beneficial, but this was not seen enough in this study to conclude more speculations. This result supports the hypothesis that there may be a benefit to having epizoic algal growth. However, actual dislodgment by limpets in the field is probably rare, at least due to hydrodynamic causes. Limpet movement during times of high tide and increased [12] wave action is minimal, reducing their risk of hydrodynamically induced dislodgment. Predators can also cause dislodgment. Crabs most often prey on limpets by trying to pry the margin of the limpet's shell away from the substrate, and other attempts to prey on limpets come from birds [13]. When predators are not successful the limpet may be left

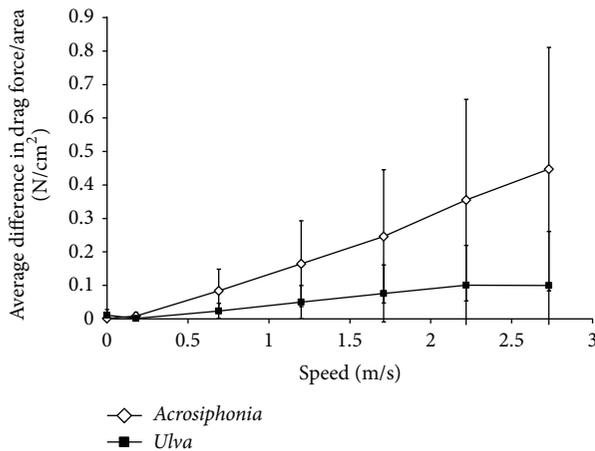


FIGURE 3: Average difference between an individual limpet's drag force before and after removal of algal growth. Data are means \pm standard deviation.

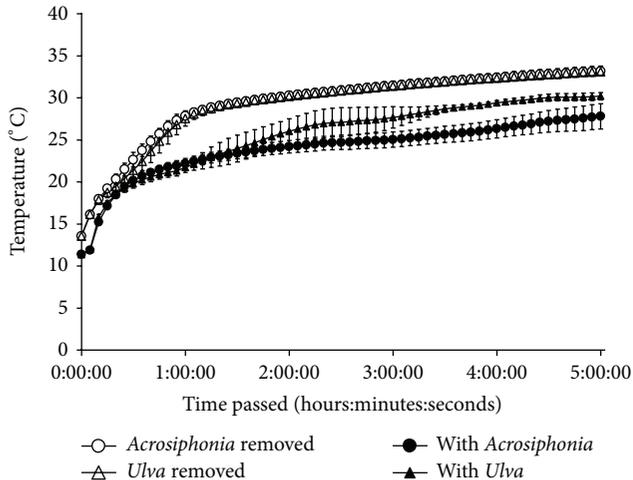


FIGURE 4: Internal limpet temperature as a function of time in the wind tunnel. Minimal differences were recorded until the one hour mark was approached. Data are \pm standard deviation.

not fully attached and susceptible to dislodgment or the foot may be damaged making it more difficult to hold on [13]. It should also be noted that predation attempts can also leave a permanent effect on shell morphology through scarring [14]. In terms of predation, however, epizoically growing algae may act as a form of crypsis. Crypsis is the ability of an organism to avoid detection by other organisms. It is possible, although it was not measured in this study, that the algae covering the shell make detection more difficult than open exposure along the rock face.

Acrosiphonia has a relatively large impact on the amount of drag forces that limpets experience, particularly at higher water velocities. In some instances, it caused a threefold increase in drag relative to limpets that were unadorned. Thus, in terms of drag, *U. lactuca* is the algal species with less cost to the limpet, with the increase of drag only averaging 0.1 N/cm^2 . In the field, drag forces can become critical to

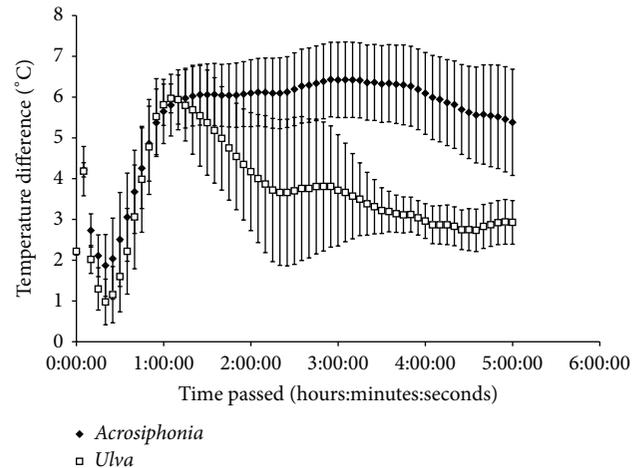


FIGURE 5: Average temperature difference (mean \pm standard deviation) between limpets before and after having epibionts removed. *Ulva* and *Acrosiphonia* appear to have a similar cooling effect until after one hour had passed.

limpets. They are subjected to wave forces in excess of 20 m/s , almost ten times the wave forces measured in this study [15]. Even in environments where dislodgment is not a major concern, higher drag forces could lead to substantially higher costs for limpet movement. Limpets clamp the substrate with an intensity proportional to the forces trying to remove the limpet [10]. A limpet with epizoic growth may therefore be consistently exerting more energy when holding onto the substrate. It should also be noted that dislodgment risks are not minimized by the limpet shell shape, as species and individuals vary greatly from the theoretically perfect shell in terms of hydrodynamics [15]. One limitation of this study and models should be acknowledged, which is that the drag measurements were done in a continuous current environment as opposed to a wave-swept system.

Although both *U. lactuca* and *Acrosiphonia* reduced the total body temperature increase of limpets exposed to sun and wind forces, *Acrosiphonia* was much more effective. The epizoic *Acrosiphonia* maintained the limpets body temperature at a lower level (by 6°C) than would occur in the absence of algae after one hour had passed, and the algae itself retained water enough to allow this cooling effect to persist for at least five hours. *U. lactuca* had a similar short-term effect, but its cooling impact tapered off quickly because it desiccates more quickly than *Acrosiphonia*. It should be noted that, although water content was not measured, by the end of the exposure period, *U. lactuca* was completely dry while *Acrosiphonia* remained moist to the touch. Because of this the cooling effect may be directly affected by the frequency with which water saturation of the algae occurred, which would be dependent on the location of the limpet in regards to splash zones and general sun exposure. This may have been to higher algal mass amounts of *Acrosiphonia* than *U. lactuca*. Desiccation is of particular importance in terms of limpet foraging behavior and shell shape. Limpet foraging trips are behaviorally optimized to minimize time

away from their home scar, the location on the rock face often returned to prior to the tide receding, to prevent desiccation and predation [16]. Attempts to minimize thermal stresses can also be seen in the variations in shell shape ratios [17]. Heat budget models have also shown that limpets' body temperature can be predicted by external air temperature. Thus, future warmer air temperatures associated with future climate change may increase limpet mortality rates due to desiccation [18].

4.2. Environmental Variation Leads to Variation in Epibiont Detriment and Benefit. The species of algae that would provide the most benefit to the limpet probably varies with habitat. Limpets in areas of high wave exposure would have a high cost to living with the algal growth due to drag forces. In this habitat type epizoic *Acrosiphonia* growth may carry an especially high cost. The additional cost of epibiosis has been measured with *Littorina littorea*, where snails had a 35% decrease in growth rate [19]. However, if wave exposure or attempted predation causes dislodgement, the most advantageous algal species would be the one that allowed the limpet to land foot-down on the substrate. If the limpet is flipped upside down or knocked side-ways, *U. lactuca* is not going to function as a parachute in some circumstances, as seen by it averaging foot-down landing only half the time. Under these circumstances, *Acrosiphonia* may be a better epibiont. In terms of desiccation stress and body temperature, neither of algal species has an impact if exposure to the air is brief. However, as exposure time increases, the benefit of *Acrosiphonia* becomes more apparent. In the San Juan Island, WA Region, midday spring tides during summer make this desiccation effect important [20]. Because of these relationships, the balance of positive and negative effects of the epibiont is going to be dependent on the habitat of the limpet.

In conclusion, *U. lactuca* may be the most advantageous algal species as an epibiont if wave velocities are high, dislodgment is low, and sun and wind exposure is either low or of short duration. *Acrosiphonia* is likely better if wave velocities are low, chances of dislodgment are high, and exposure to the sun and wind is high or of long durations.

There are many other aspects of the limpet-alga relationship that still need to be evaluated. For instance, the extra mass of the alga may cause the crawling speed of the limpet to decrease or the chances of dislodgment to increase. If this was the case, foraging behavior may change because of the difficulty of moving. Less food would lead to less growth or reduced reproductive output, which has been shown in previous epibiont-basibiont research on snails [3]. Lift forces may also cause a significant physical stressor for the limpet along with drag forces [21]. Measuring lift could produce a more complete view of the energy costs of movement and avoidance of dislodgment. Another dynamic that is not explored here is the potential to increase or decrease predation. Past research on the crab *Emerita analoga* found that algal epibiont growth increased predation possibly due to negative effects on burrowing time and increased visualization by predators [22].

Epibiont-basibiont interactions are complex; the effects considered here are just part of a much larger picture. Taking these single organism effects and considering effects and implications on the population level of that organism, such as abundance and density numbers, are of particular interest. This scaling up would then allow research to shift foci from physiological effects of an individual to community wide effects. These potential community wide effects could then shed light on the importance of epibiosis to an ecosystem as a whole [23]. Ultimately the most desirable epibiont species is probably context-dependent for all organisms facing this interaction and additional research may help improve our understanding of the net cost/benefit of different epibiont species among different habitats.

Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

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