



Attachment strength of the herbivorous rockweed isopod, *Idotea wosnesenskii* (Isopoda, Crustaceae, Arthropoda), depends on properties of its seaweed host

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ABSTRACT

Wave-induced forces can affect the distribution of intertidal organisms, changing the structure of communities along wave-swept shores. The risk of dislodgement for an intertidal animal depends on the forces experienced, relative to the force that animal is able to apply to resist dislodgement (hereby termed attachment strength). Isopods in the genus *Idotea* (Isopoda, Crustaceae, Arthropoda) are well adapted to wave-swept environments. They possess hooked claws on their walking appendages (peripods) that allow them to attach to seaweeds. In this study, we sought to compare the attachment strength of this isopod from various macroalgae. We used previously reported hydrodynamic data (drag coefficient) for *Idotea wosnesenskii* to predict the required velocity for dislodgement. Using this information, we were able to predict whether differences in attachment strength could limit substratum choice, and whether wave velocities could be mediating algal-invertebrate interactions. We found that attachment strength was dependent on substratum, and that seaweed breaking stress (MPa) and thickness (m) act as significant predictors of isopod attachment strength. Furthermore, we determined that differences between substrata were relevant to velocities commonly experienced in wave-swept environments. *I. wosnesenskii* are likely limited to stronger and thicker seaweeds in areas with greater wave intensity. Here, we identify a novel ecological implication of seaweed material properties that could be impacting organismal interactions along wave-exposed shores.

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1. Introduction

Forces imposed by high water velocities can limit the distribution of intertidal organisms (e.g. Denny et al., 1998; Koehl, 1982; Blanchette, 1997; Vogel, 2009) and reshape community structures by altering species interactions (e.g. Sousa, 1979; Menge, 1978a,b; Kilar and McLachlan, 1989; Burrows et al. 2008). The ability of an animal to remain attached depends on its ability to resist dislodgement with a force equal to that of the greatest combined vector of drag, lift, and acceleration reaction forces. Some studies have used this balance of attachment strength (also called tenacity or dislodgement force) and fluid forces to explain patterns exhibited in natural populations, such as distribution, maximum body size and invasion potential (e.g. Lau and Martinez, 2003; Martone and Denny, 2008; Clarke Murray et al., 2012). Efforts necessary to resist waves can result in decreased locomotion (Martinez, 2001). This may limit the distribution of mobile

invertebrates and hinder foraging abilities (e.g. Denny, 1994), imposing constraints on the ecological efficiency of animals living in wave-swept areas.

Species of isopods in the genus *Idotea* are important herbivores in intertidal ecosystems worldwide and are most commonly found on seaweeds from intertidal and shallow subtidal areas of both wave-exposed and wave-protected shores (Naylor, 1955; Gutow and Franke, 2003; Orav-Kotta and Kotta, 2004; Gunnarsson and Berglund, 2012). Species in this genus can have cascading effects on their communities by preferentially grazing some algal species over others (Orav-Kotta and Kotta, 2004; Leidenberger et al., 2012) and thus play important, regulatory roles in their respective ecosystems. Nevertheless, the physical and biological factors affecting their distribution are poorly understood.

Like many parasitic isopods (see Ravichandran and Rameshkumar, 2014), the walking legs of *Idotea* terminate with hooked claws (Fig. 1; Oliver, 1923) that play a role in attachment to seaweeds and various substrata. The ability of *Idotea* to attach to different substrata could limit its distribution on wave-swept shores; if isopods cannot attach to a seaweed with enough force to resist wave velocities, then that habitat (and food source) would be inaccessible. Yet, it remains open to

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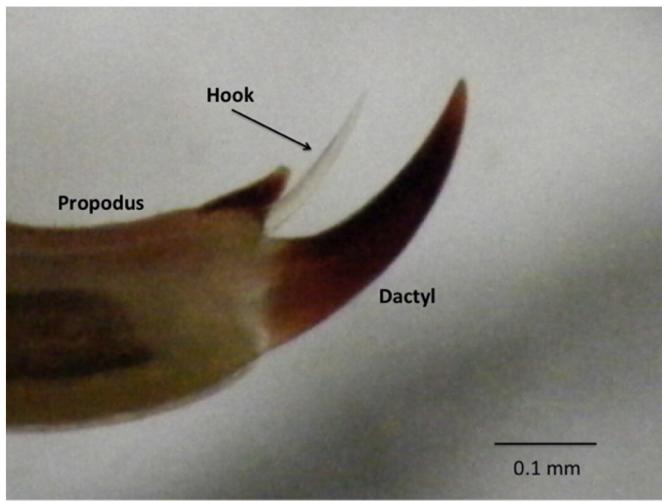


Fig 1. Hooked claws of *Idotea wosnesenskii* with propodus, dactyl and hook. Claws were excised by cutting mid-propodus.

question whether substratum can influence the attachment strength of *Idotea* spp.

Some studies have presented evidence that maximum attachment strength of an animal can depend on its substratum (e.g. Lau and Martinez, 2003; Santos and Flammang, 2007). For example, Lau and Martinez (2003) demonstrated that the shore crab, *Pachygrapsus crassipes* was able to resist greater forces when removed from a rugose rocky substratum than from either smooth rock or mud substrata. Additionally, studies conducted on wave-swept macroalgae have demonstrated increased attachment strength to rocks when compared to barnacles or mud substrata (e.g. Milligan and DeWreede, 2000; Malm et al., 2003), suggesting that a soft or brittle substratum may sometimes break, or give way before mechanical failure of the organism occurs (see Garden and Smith, 2015). Together, previous literature suggests that attachment to the substratum may not only be influenced by properties of the organism attaching, but also the substratum itself. In this way, the substratum properties could impose constraints on the range of habitats that mobile animals could occupy on wave-swept coastlines. This would be of particular interest, if intrinsic properties of macroalgal host species could limit the ability of *Idotea wosnesenskii* to use them for food and shelter, since this would differentially affect isopods living in wave-exposed and -sheltered areas. This could drive differences in community structure along natural gradients of wave-exposure.

The purpose of this study was to evaluate the factors affecting attachment strength in the rockweed isopod, *I. wosnesenskii*, and to assess whether drag forces could limit the host use of this species. We sought to determine the extent to which *I. wosnesenskii* depend on their hooks for attachment to seaweeds, and whether the attachment strength of an isopod is dependent on its substratum, which could be relevant in limiting distribution patterns along wave-swept shores. Finally, we tested the hypothesis that material properties of macroalgae can influence the attachment strength of *I. wosnesenskii*.

2. Methods

2.1. Specimen collection and study sites

We chose to conduct this study on individuals from multiple sites ($N = 3$) in order to determine the universality of any trends observed. Two of these sites were located along bedrock with few to no loose boulders or cobble: a northeast-facing shelf on Wizard Islet (hereby referred to as "Wizard Exposed"; W 48.858233, N 125.160116), and a north-facing bench located at Eagle/Scott's Bay near Bamfield, British Columbia (hereby "Scott's Exposed"; W 48.833747, N 125.148639).

From these sites, isopod specimens were collected from phaeophycean algae (e.g. *Fucus distichus* and *Egregia menziesii*). From all of our collections at these sites, *Idotea* were never found on red or green algae, and only one individual was found on rock. Our third site was a southeast-facing cobble beach on Wizard Islet (hereby "Wizard Cobble"; W 48.858148, N 125.159086). At this site, *I. wosnesenskii* were collected from underneath boulders. Isopods living here are likely to experience lower wave velocities, due to both the site's position on the island, and because of the presence of boulders that may allow refuge from waves. All specimens were collected between one and two meters above lowest astronomical tide (LAT). We collected the seaweeds *Ulva lactuca*, *E. menziesii*, *Mazzaella splendens*, *Chondracanthus exasperatus*, and *Macrocystis pyrifera* from Wizard Islet, and we collected *F. distichus*, and *Pyropia* sp. from the Bamfield Marine Science Centre foreshore.

2.2. Attachment strength measurements

We measured isopod attachment strength by tying a nylon string (approximately 15–20 cm in length) mid-thorax to each individual and pulling on the string with a tensiometer (spring scale). The method of applying force to a loop that is tied or glued to the animal has been previously used to quantify the attachment strength of many intertidal invertebrates including snails, bivalves, tunicates and crabs (e.g. Thayer, 1975; Denny et al., 1985; Lau and Martinez, 2003; Clarke Murray et al., 2012; O'Dwyer et al., 2014). After the loops were tied, isopods were allowed at least 4 h for acclimation prior to experimentation. We then placed individuals in bins filled with seawater, and to their assigned substrate and allowed up to 10 min for attachment. Due to the morphology of *Idotea*, we could not measure attachment strength in shear without directly hindering attachment by some appendages, instead we measured attachment strength in tension (as in Thayer, 1975; Denny et al., 1985; Lau and Martinez, 2003) by pulling on the lead perpendicular to the substratum with a Pesiola spring scale (100 g, or 1000 g). Seawater was changed between each trial and new substrata were used for each individual.

2.3. Effect of hooks on attachment strength

In order to determine the extent to which hooked claws (and thus tissue penetration) were responsible for attachment, we performed a claw removal experiment. We collected *I. wosnesenskii* ($N = 11$) from Wizard Islet and subsequently dislodged them, in the lab, from *F. distichus* plants with a 100 g Pesiola spring scale. Two individuals achieved attachment strengths greater than the range of the scale; 0.98 N (100 g) was recorded for these individuals. We removed the leads and placed individuals on ice for 10 min or until movement slowed. Individuals were randomly assigned to one of two treatment groups: (1) the hookless treatment ($N = 6$), in which individuals had their hooks removed; and (2) the injured treatment, in which seven incisions were made along the segments of the pereon above the peripods on each side without damaging the peripod claws. This treatment was used to account for the possible effect of injury on attachment strength ($N = 5$). We stored *I. wosnesenskii* individually in small cages with *U. lactuca* (as a food source) and allowed 28 h for recovery, reattaching leads at 24 h, which allowed for an additional 4 h of lead acclimation. After 28 h we dislodged the individuals a second time from *F. distichus*. A two-sample t-test was performed on the differences between the pre- and post-treatment attachment strengths in R (version 3.1.2).

2.4. Effect of substratum on attachment strength

We collected isopods from Wizard Cobble ($N = 16$), Wizard Exposed ($N = 8$), and Scott's Exposed ($N = 15$). We generated a series of random numbers for each individual to create an order of dislodgement on each substrate: *F. distichus*, *U. lactuca*, *M. pyrifera*, *Pyropia* sp.,

or rock. Selected rocks, while not quantified, were of similar observed properties and rugosity. We placed each individual in a separate bin with their assigned substratum, and allowed 10 min for attachment. Once attached, we dislodged *I. wosnesenskii* from the substrate with a 100 g (0.98 N) Pesiola spring scale attached to the nylon lead. A few individuals achieved forces greater than 0.98 N when dislodged from *Fucus* or *Macrocystis*; these were included in the analysis as 0.98 N. We dislodged each *I. wosnesenskii* from all 5 substrata, using a new alga or rock each trial. The effect of substratum on attachment strength was evaluated by performing a repeated measures two-way ANOVA in R.

2.5. Predicting dislodgement

Drag was estimated as follows:

$$\text{Drag} = \frac{1}{2} \rho U^2 A C_D \quad (1)$$

where ρ is the fluid density of seawater, U is the water velocity, S_A is a wetted surface area and C_D is the dimensionless parameter drag coefficient. Dislodgement velocity was then defined as the predicted velocity at which drag would equal attachment strength, such that:

$$U_D = \sqrt{\frac{2S_A}{\rho A C_D}} \quad (2)$$

where dislodgement velocity (U_D) is expressed as a function of wetted area (A) and attachment strength (S_A). We used a previously published drag coefficient ($C_D = 0.084$; Alexander, 1990) for *I. wosnesenskii*, based on wetted area, to estimate dislodgement velocity. Wetted area was estimated as twice the area of an ellipse, using measurements taken from the isopods. By estimating dislodgement velocity, we are able to determine whether differences in isopod attachment strength from dissimilar substrata could influence dislodgement at fluid velocities relevant to the wave-swept intertidal zone. To analyze this, we conducted a repeated measures ANOVA on dislodgement velocity using the “lme4” package in R (Bates et al., 2014), followed by Tukey's post-hoc comparisons, performed in R, using the “lmposthoc” package (Kuznetsova et al., 2014) to compare means.

2.6. Effect of macroalgal material properties on attachment strength

We collected *I. wosnesenskii* ($N = 35$) that were between 18 and 29 mm in length. We assigned isopods ($N = 5$) randomly to seven groups, one for each of the seaweed species collected for this study. The thickness of each alga was measured with calipers, and individuals ($N = 5$) were dislodged from each seaweed.

Breaking stress for *M. splendens*, *Pyropia* sp., and *Chondracanthus exasperatus* were obtained from Demes et al. (2011) and breaking stress data for *E. menziesii*, *M. pyrifera*, *F. distichus*, and *U. lactuca* were obtained from Hale (2001). In order to determine which parameters were most important in determining isopod attachment strength, regression models were fit between attachment strength and seaweed thickness, as well as breaking stress.

3. Results

3.1. Reliance on hooks

The attachment strength of hookless individuals decreased significantly when compared to that of individuals in the injured control group, (two-sample t-test: $P = 0.0148$, $t = 3.01$, $df = 9$; Fig 2). After application of the treatment, hookless individuals were virtually unable to attach to *F. distichus*. A maximum attachment strength of 0.01 N was observed in two individuals that successfully wrapped their peripods

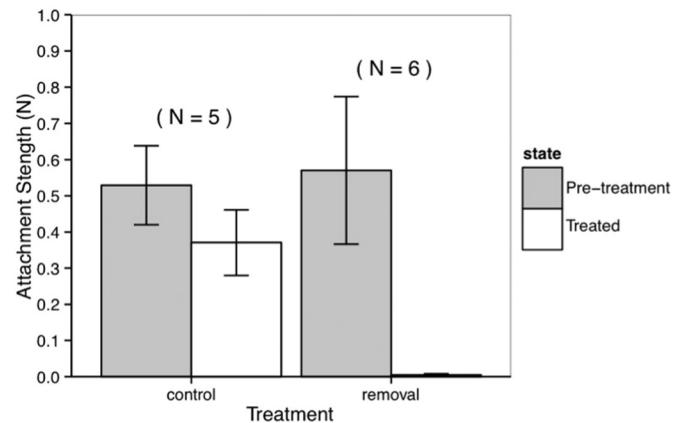


Fig 2. Average attachment strength (N) from *Fucus distichus* for each treatment in the hook removal experiment. Gray bars represent baseline measurements taken on all individuals before application of the treatment, and white bars represent treated individuals. Error bars represent 95% confidence intervals.

around the branches of the thallus. These individuals had previously been able to achieve forces between 0.7 and 0.9 N. All hooks were observed to grow back within six weeks of being excised, during the next molt.

3.2. Substrate affects attachment strength

There was a significant effect of substratum on attachment strength for isopods from all three sites (Wizard Exposed: repeated measures ANOVA: $F = 14.355$; $df = 28$; $P < 0.001$; Wizard Cobble: repeated measures ANOVA: $F = 19.342$; $df = 75$; $P < 0.001$; Eagle Exposed: repeated measures ANOVA: $F = 16.639$; $df = 56$; $P < 0.001$). On average, individuals were more strongly attached to *F. distichus* than to other macroalgae and generally had the lowest attachment strengths when attached to rocks (see Tukey post-hoc results in Fig. 3). During attachment strength measurements, isopod detachment was sometimes associated with small tears in the macroalgae from which it had been dislodged.

3.3. Dislodgement velocity

Given that trends were consistent between sites, dislodgement velocity analyses were performed on a pooled sample of individuals from all sites. There was a significant effect of substratum on dislodgement velocity (repeated measures ANOVA: $F = 67.453$; $df = 152$; $P < 0.001$). *Idotea* were predicted to dislodge from rock, *Pyropia* and *Ulva* at velocities significantly lower than *Egregia* and *Fucus* (Fig. 4).

3.4. Attachment strength is influenced by macroalgal material properties

There was a significant, positive linear relationship between attachment strength and both thickness (linear regression: $F = 56.9492$; $df = 34$; $P < 0.001$; $R^2 = 0.622$) and breaking stress (linear regression: $F = 35.9473$; $df = 34$; $P < 0.001$; $R^2 = 0.521$) (Fig. 5). However, the product of breaking stress and thickness was found to be the best predictor of isopod attachment strength (linear regression: $F = 61.9911$; $df = 34$; $P < 0.001$; $R^2 = 0.653$; $\text{Log}[\text{Attachment Strength}] = 0.3331 * \text{Log}[\text{Breaking Stress} \times \text{Thickness}] + 0.6634$).

4. Discussion

4.1. Attachment strength depends largely on substratum properties

Hooked claws are the main mechanism by which *I. wosnesenskii* attach to their algal hosts (Fig. 2). Hooked claws anchor isopods to

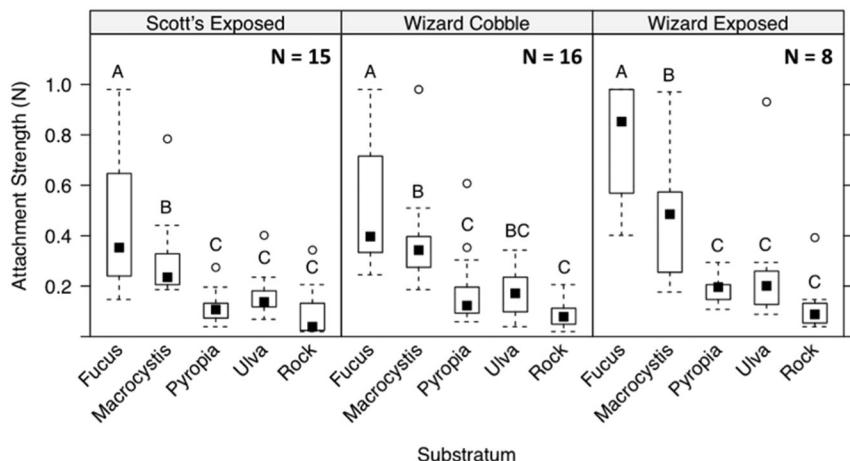


Fig 3. Boxplots of attachment strength from each substratum. Medians are indicated by (■). Letters represent significant differences between means, as determined by a Tukey's posthoc test.

fleshy substrata by penetrating the tissues (see [Oliver, 1923](#); [Ravichandran and Rameshkumar, 2014](#)). In this way, the properties of the material may become important in determining attachment strength, since dislodgement could occur if tears form around anchoring points (i.e., hooks). Here, we demonstrate that *Idotea* are more strongly attached to some seaweed species than to rocks, that attachment strength to seaweeds can differ (Fig. 3), and that attachment strength correlates with the material breaking stress and thickness of seaweed tissues (Fig. 5). Isopods had higher attachment strength when dislodged from thicker and stronger seaweeds, even when only comparing seaweed species of the same morphology (i.e. unbranched, bladed forms: *Macrocytis*, *Mazzaella*, *Pyropia*, *Ulva*). Together, this evidence suggests that it is the seaweed tissues themselves that affect attachment strength. In this way, macroalgal material properties could limit the

distribution of invertebrate herbivores that live on them, making thinner and weaker seaweeds inaccessible at higher wave velocities.

4.2. Differences in attachment strength could limit substratum choice

We predicted that dislodgement from thinner and weaker seaweeds (e.g. *Ulva*; mean = 4.29 ms^{-1} , *Pyropia*; mean = 3.91 ms^{-1}) and from rock (mean = 2.96 ms^{-1}) would occur at a significantly lower velocity than from the thick phaeophycean algae, *F. distichus* (mean = 7.28 ms^{-1}) and *M. pyrifera* (mean = 6.04 ms^{-1} ; Fig. 4). In addition, these predicted velocities fall within the range of values commonly reported along wave-swept shores. [Denny \(2000\)](#) recorded velocities as high as 25 ms^{-1} on the most wave-exposed coastlines, and $5\text{--}10 \text{ ms}^{-1}$ are commonly reported values for maximum intertidal velocity, even in the Strait of Georgia, which is protected from offshore swell ([Anderson and Martone, 2014](#)). Previous wave measurements at our "Wizard Exposed" site were between 3 and 4 ms^{-1} ([Arsenault et al., 2001](#)). However, these measurements were taken mid-summer, when waves are expected to be the smallest.

Based on these findings, it is probable that differences in attachment strength can limit the distribution of *Idotea* along wave-swept coastlines. Isopods could be unable to attach to some seaweeds with

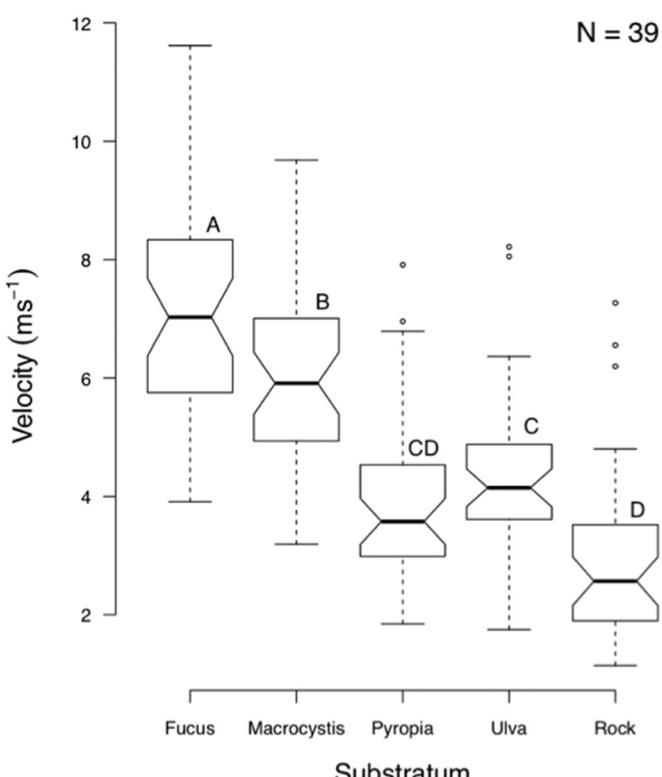


Fig 4. Boxplots of dislodgement velocity (ms^{-1}) from different substrata. Data presented here are pooled from all sites but represent a repeated measures design.

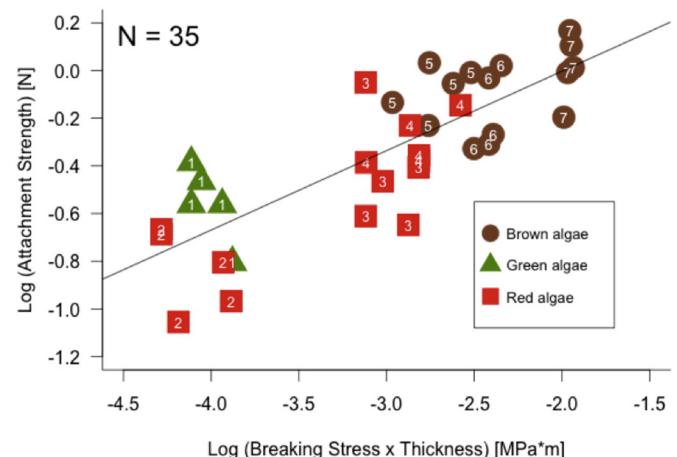


Fig 5. The effect of material properties on attachment strength. Breaking strength \times thickness served as the greatest predictor of isopod attachment strength ($\text{Log}[\text{Attachment Strength}] = 0.3331 * \text{Log}[\text{Breaking Stress} \times \text{Thickness}] + 0.6634$). Seaweed species are numbered for visualization: (1) *U. lactuca*, (2) *Pyropia* sp., (3) *M. splendens*, (4) *C. exasperatus*, (5) *M. pyrifera*, (6) *F. distichus*, and (7) *E. menziesii*.

enough force to resist drag and lift. This would, in turn, prevent them from using this habitat.

In this study, we only address drag as a wave-induced force. However, the forces of acceleration reaction, and lift could also contribute to dislodgement (see [Lau and Martinez, 2003](#)). The compounding of these forces with drag could further limit the distribution of isopods, causing dislodgement at even lower velocities.

4.3. Ecological implications

As implied by its common name, “the rockweed isopod”, *I. wosnesenskii* is often found on rockweed (*Fucus*). Previous studies, however, have reported a feeding preference of this species for seaweeds in the genus *Ulva* over *Fucus* species ([Van Alstyne et al., 2006](#)). This is presumed to be a result of the phlorotannin chemical defenses produced by *Fucus* spp. It has been suggested that these compounds can reduce assimilation efficiency of *Idotea* species ([Jormalainen et al., 2004](#)). Despite this, *Idotea* at wave-exposed sites in Barkley Sound appear to be largely restricted to *F. distichus* and some kelp species, with small isopods sometimes found on strong coralline algae (pers obv.). The differences in attachment strength between substrata could influence habitat and food choices for *I. wosnesenskii*. As a result, *I. wosnesenskii* likely face a trade-off between nutritional requirements and risk of dislodgment on sites with greater wave velocities. This could also drive differences in algal community structure between exposed and sheltered sites.

[Miller et al. \(2007\)](#) found that the intertidal snail *Littorina keenae* can survive dislodgement and return to shore. It remains unclear how often dislodgement results in death for *I. wosnesenskii* and, given their swimming abilities, it is very likely that at least a proportion of *Idotea* could find refuge subtidally after dislodgement. Despite this, habitat limitation such as that described here (Section 4.2) could have important consequences on intertidal communities, by preventing herbivory on seaweeds to which animals are unable to attach. This could be advantageous for weaker seaweeds, in that herbivores cannot easily take hold. However, damage to the thallus may be detrimental, if it led to a subsequent loss of tissue due to crack propagation (see [Denny et al., 1989; Mach et al., 2007](#)).

4.4. Conclusions and future directions

I. wosnesenskii are well adapted to live along exposed shores with high macroalgal abundance. Hooks anchor isopods into seaweed substrata, allowing for sufficient attachment strength to survive large wave velocities. *I. wosnesenskii* can only weakly attach to rock and, as a result, rely heavily on seaweeds to avoid dislodgement, and may swim between macroalgae in search of food or a mate. Seaweeds differ in their abilities to support isopods, and this ability depends on their material properties. Patterns in attachment strength investigated in this study could drive trade-offs in food choice and attachment, leading herbivores on exposed shores to live on less palatable algae. This, in turn, could drive shifts in community composition between wave-exposed and -protected areas.

Future work should include field-based investigations that directly examine the extent to which wave-exposure may limit seaweed use by this species, and determine whether this could drive a difference in food usage between wave-exposed and sheltered sites. Studies to come could also explore seasonal differences in habitat use, since wave velocities at one site often vary seasonally. Additionally, future work could investigate other invertebrate species, that attach to algal hosts by similar mechanisms, to further improve our understanding of flow-mediated herbivore-host interactions.

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