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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.

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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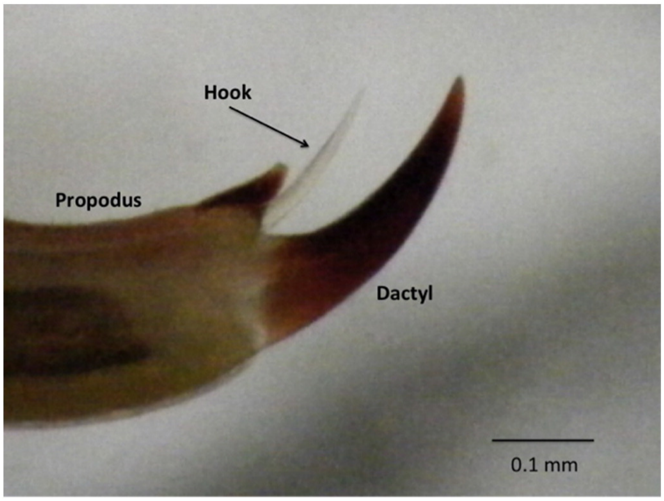

Fig 1. Hooked claws of *Idotea wosnesenskii* with propodus, dactyl and hook. Claws were excised by cutting mid-propodus.

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 exasparatus*, 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 tensometer (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.,