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NOTE

ROLE OF SURFACE WOUNDS AND BROWN ALGAL EPIPHYTES IN THE COLONIZATION OF *ASCOPHYLLUM NODOSUM* (PHAEOPHYCEAE) FRONDS BY *VERTEBRATA LANOSA* (RHODOPHYTA)[1]

Caroline M. Longtin and Ricardo A. Scrosati[2]

Department of Biology, Saint Francis Xavier University, Antigonish, Nova Scotia B2G 2W5, Canada

Ascophyllum nodosum **(L.) Le Jol. forms extensive beds in wave-sheltered, rocky intertidal habitats on the northwestern Atlantic coast. This fucoid seaweed is host to an obligate red algal epiphyte,** ***Vertebrata lanosa*** **(L.) T. A. Chr. [=*Polysiphonia lanosa* (L.) Tandy], and two facultative brown algal epiphytes,** ***Elachista fucicola*** **(Velley) Aresch. and** ***Pylaiella littoralis*** **(L.) Kjellm. Although** ***V. lanosa*** **can occur throughout most of the length of host fronds, it largely predominates in midfrond segments. The two brown algal epiphytes are restricted to distal segments. Through field experiments conducted in Nova Scotia, Canada, we tested the hypothesis that surface wounds are required for the colonization of distal segments of host fronds by** ***V. lanosa*****. Distal tissues normally have a smooth surface because of their young age (*A. nodosum* fronds grow apically). By creating small wounds that mimicked grazing wounds distributed elsewhere on host fronds, we demonstrated that** ***V. lanosa*** **can colonize distal frond segments during the growth and reproductive season (summer and autumn). Approximately half of the artificial wounds were colonized by** ***V. lanosa*** **during this time. The experimental exclusion of both brown algal epiphytes from distal frond segments did not affect colonization by** ***V. lanosa*****. Thus, we conclude that the absence of surface irregularities on distal segments of host fronds, specifically small wounds, is the main factor explaining the absence of** ***V. lanosa*** **there. We propose that further experimental work clarifying epiphyte distribution in host beds will enhance our ability to understand the functional role of epiphytes in intertidal ecosystems.**

Key index words: ***Ascophyllum nodosum*****; colonization;** ***Elachista fucicola*****; epiphytism; intertidal zone;** ***Pylaiella littoralis*****; recruitment;** ***Vertebrata lanosa***

[1]Received 12 August 2008. Accepted 28 January 2009.
[2]Author for correspondence: e-mail rscrosat@stfx.ca.

Epiphytes are important components of rocky intertidal communities. They have positive effects on many animals by providing food and habitat to them (Mazzella and Alberte 1986, Johnson and Scheibling 1987, Pavia et al. 1999, Karez et al. 2000, Viejo and Åberg 2003). On hosts, effects are often negative, as epiphytes can decrease the host's growth and reproduction, by limiting carbon uptake and reducing light penetration, and the host's survival, by increasing drag (Sand-Jensen 1977, D'Antonio 1985, Howard 1986, Arrontes 1990, Buschmann and Gómez 1993, Kraberg and Norton 2007). Some epiphytes are actually parasitic on their hosts, reducing the host's fitness by translocating nutrients from it (McRoy and Goering 1974, Callow et al. 1979, Penot et al. 1993). Because of the widespread presence of epiphytes on marine rocky shores, unraveling the factors that affect their distribution is relevant to understand how communities are structured in these habitats. This is important to point out because experimental work on the distribution of rocky intertidal organisms has traditionally focused on species that are primary-space holders (Menge and Branch 2001).

Most epiphytes are facultative and are not associated with a specific host (Wahl and Mark 1999), but some species are obligate epiphytes on certain hosts (Levin and Mathieson 1991, Garbary and Deckert 2001). On the northwestern Atlantic coast, the brown seaweed *A. nodosum* (*Ascophyllum* hereafter) often forms extensive beds in rocky intertidal habitats subjected to a low degree of wave exposure. This species is host to an obligate red algal epiphyte, *V. lanosa* (*Vertebrata* hereafter), and two facultative brown algal epiphytes, *E. fucicola* (*Elachista* hereafter) and *P. littoralis* (*Pylaiella* hereafter; Lobban and Baxter 1983, Garbary et al. 1991, Levin and Mathieson 1991, Cardinal and Lesage 1992, Chopin et al. 1996). These species differ in distribution along *Ascophyllum* fronds. While *Vertebrata* occurs throughout most of the length of host fronds, it largely predominates in midfrond segments. Conversely, the two brown algal epiphytes are restricted to distal segments of host fronds, with *Pylaiella* showing a higher seasonal variability in abundance than *Elachista* (Longtin et al. 2009). The low degree of epiphytism in basal frond segments is thought to result from the abrasion stress that is likely caused by the high biomass packing there (Lobban and Baxter 1983). Explaining the distribution of epiphytes in distal and midsegments seems to be more complex, however, as both physical and biological factors appear to be involved. The present study focuses on factors affecting the distribution of *Vertebrata*.

The limited abundance of *Vertebrata* in distal frond segments might result from the low availability of suitable microsites for colonization there. *Ascophyllum* grows apically, resulting in a gradient from young, mostly unbranched, smooth surfaces in distal frond segments to older surfaces with several wounds, branch axils, and lateral pits (formed when receptacles shed) in midsegments (Åberg 1996). Surface irregularities are thought to promote *Vertebrata* recruitment because they interrupt the streamlined shape of the host thallus, possibly creating hydrodynamic conditions that favor spore settlement and survival (Lobban and Baxter 1983, Pearson and Evans 1990, Garbary et al. 1991, Levin and Mathieson 1991). Settling in wounds might also protect spores from being removed by a periodic antifouling mechanism in *Ascophyllum* known as skin shedding (Filion-Myklebust and Norton 1981). Field observations have indeed noted *Vertebrata* clumps occurring in wounds formed in older tissues by herbivory and wave action (Lobban and Baxter 1983, Garbary et al. 1991, Levin and Mathieson 1991). However, such observations do not conclusively demonstrate that the absence (or limited number) of wounds in young, distal segments of *Ascophyllum* fronds is the main factor limiting *Vertebrata* colonization there, as other physical factors (e.g., high irradiance) might be more important. For this reason, we tested the hypothesis that wounds promote *Vertebrata* colonization in distal frond segments by conducting a field experiment that created numerous wounds there, similar to those naturally occurring in older segments.

The predominance of the two brown algal epiphytes (*Elachista* and *Pylaiella*) in the distal segments of *Ascophyllum* fronds suggests that those epiphytes might also explain the virtual absence of *Vertebrata* there. This could be so if *Elachista* and *Pylaiella* preempted space (they reproductively mature before *Vertebrata*; Longtin et al. 2009) or competitively excluded *Vertebrata* at early developmental stages. Therefore, we also tested the hypothesis that the experimental removal of both brown algal epiphytes enhances colonization by *Vertebrata*.

The study was conducted between June and November 2007 at a wave-sheltered, intertidal boulder field in Tor Bay Provincial Park (45°11.123′ N, 61°20.578′ W), on the Atlantic coast of Nova Scotia, Canada. This area is similar in wave exposure and topography to 12 other boulder fields we visited along 80 km of coastline between Drum Head (45°08.709′ N, 61°35.958′ W) and Green Point (45°12.771′ N, 61°10.682′ W). The average site-wise cover of *Vertebrata* (0.5%–1.3%, $n = 30$ quadrats per site), *Elachista* (0.5%–0.9%), and *Pylaiella* (0–0.1%) measured across the *Ascophyllum* bed at the midintertidal zone was similar among those sites. Thus, our study site can be considered as representative of this region. Surface-seawater temperature varies between monthly mean values of −0.3°C and 16.9°C in this region, while seawater salinity varies between monthly mean values of 29.5‰ and 31.4‰ (Fisheries and Oceans Canada 2008). In the summer and autumn of 2005, at Tor Bay Provincial Park, we measured a maximum seawater temperature of 20.5°C (September) and a maximum salinity of 35‰ (October). During the same period, the maximum water velocity (an index of wave exposure) ranged between 3.2 and 5.6 $m \cdot s^{-1}$ in wave-sheltered habitats at Tor Bay Provincial Park (Scrosati and Heaven 2007).

At our study site, we established two 40 m transect lines across the midportion of the *Ascophyllum* zone, where this species is most abundant on the shore (0.95 m of elevation above chart datum). We used one transect line to start one trial of the experiment between 5 and 12 June 2007. At that time of the year, *Vertebrata* begins to form reproductive structures (Kaczmarska and Dowe 1997, Longtin et al. 2009). To test for the generality of our findings, we started a second experimental trial on the other transect line between 16 and 18 July 2007, when *Vertebrata* reproduction peaked (Longtin et al. 2009).

We determined the effects of host surface wounds and brown algal epiphytes on *Vertebrata* recruitment using a randomized complete block design (Krebs 1999), considering an *Ascophyllum* thallus as a block and randomly selecting four fronds (with intact apices) of 60–80 cm in length in each block. An *Ascophyllum* thallus consists of a crustose holdfast and a number of fronds that display variable levels of branching (David 1943, Cousens 1985). On each transect line, we randomly selected 50 blocks. Then, we applied four treatments to each block, one treatment per frond creating all possible combinations of artificial wounds present/absent and brown algal epiphytes present/absent. A wounding treatment consisted of the creation of 10 wounds located 1 cm apart along the surface of host fronds, five on each of the two youngest internodes. In *Ascophyllum,* the distance between consecutive air bladders is referred to as an internode (Cousens 1982, Sharp 1986). The wounds that we created mimicked those formed by amphipods, isopods, and snails (Lowell et al. 1991). We used tweezers to remove a hemispherical section, ~1–2 mm in diameter, of *Ascophyllum* tissue along the lateral surface of *Ascophyllum* fronds, similar to those created by Lowell et al. (1991). A nonwounding treatment consisted of leaving the host frond unmanipulated. A brown-epiphyte exclusion treatment consisted of removing *Elachista* and *Pylaiella* clumps once per month by gently pulling them from the surface of *Ascophyllum* fronds using fine-point forceps. A brown-epiphyte inclusion treatment consisted of leaving the host frond unmanipulated, bearing the natural abundance of brown algal epiphytes.

In November 2007, 1 month after *Vertebrata* reproduction had declined substantially (<10% of *Vertebrata* clumps were then reproductive; Longtin et al. 2009), we counted the number of *Vertebrata* recruits on each replicate. For wounding treatments (with and without brown algal epiphytes), we counted only the recruits located in the artificial wounds. For nonwounding treatments (with and without brown algal epiphytes), we used a ruler to record whether recruitment had occurred at 10 (smooth) surface microsites located 1 cm apart along the two youngest internodes. We calculated the proportion of colonized microsites for each of the four experimental treatments by dividing the number of occupied microsites on each replicate by the number of measurements (10) taken on each replicate.

For statistical analyses, we did not use the data from nonwounding treatments (with and without brown algal epiphytes) because all measurements were zero, as no *Vertebrata* recruitment occurred in those replicates. We analyzed the effects of the presence of brown algal epiphytes on *Vertebrata* recruitment on wounded fronds separately for the June and July trials, using one-way analyses of variance (ANOVA) with blocking (Krebs 1999). The blocking factor was nonsignificant for the June trial, so for that trial we compared the proportion of colonized wounds between fronds with and without brown algal epiphytes using a Student's *t*-test. When the blocking factor is nonsignificant, it should be removed from the analysis because it would otherwise decrease the relative efficiency of the test (Krebs 1999). The assumptions of normality and homogeneity of variance (Sokal and Rohlf 1995) were tested using normal quantile plots and Levene's test, respectively. The assumptions were met for the June trial, but the data from the July trial were arcsine-transformed to meet them. We performed all statistical analyses using JMP 5.1 for Macintosh (SAS, Cary, NC, USA).

During both the June and July trials, recruitment of *Vertebrata* occurred on the wounds we created on *Ascophyllum* surfaces, but never on unwounded surfaces of the host. On average, nearly half of the wound microsites were colonized by *Vertebrata* by November 2007 (Fig. 1). For both the June ($t_{12} = 0.21$, $P = 0.84$) and July ($F_{1,11} = 1.73$, $P = 0.22$) trials, the proportion of colonized wounds did not differ significantly between host fronds where the brown algal epiphytes (*Elachista* and *Pylaiella*) were excluded and the fronds where such epiphytes were left in place. The artificial wounds were only occupied by *Vertebrata*; no *Elachista* or *Pylaiella* recruits were observed there. The block (host thallus) factor was not significant for the June trial ($F_{1,6} = 1.40$, $P = 0.35$), but significant for the July trial ($F_{1,11} = 11.60$, $P = 0.0002$), indicating that the overall colonization rate for *Vertebrata* (combining values for the frond with brown algal epiphytes and for the frond without brown algal epiphytes in each block) may differ among host thalli across the study site depending on the timing of availability of wounds.

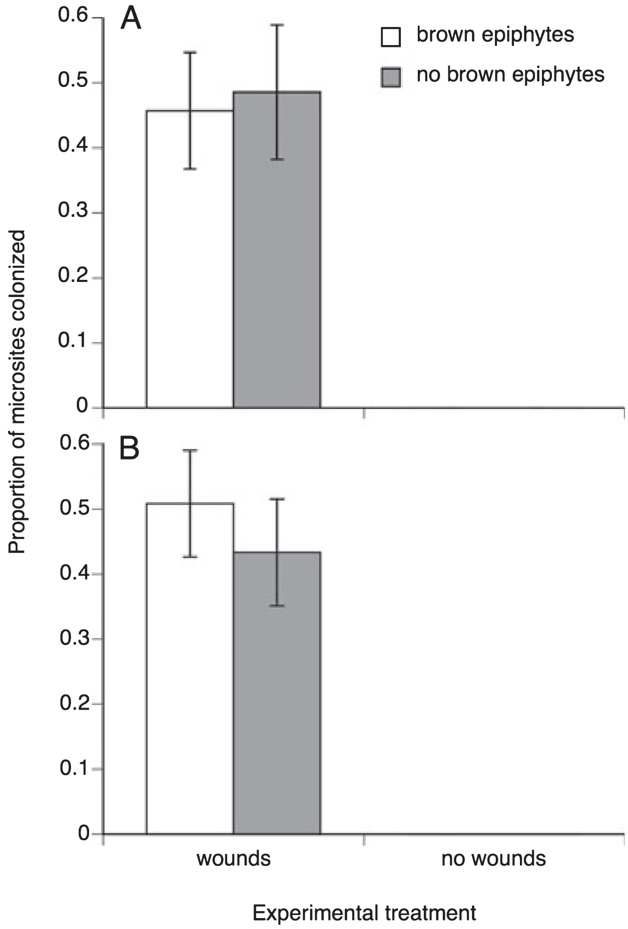

Fig. 1. Proportion of wounded and unwounded microsites (mean ± SE) colonized by *Vertebrata lanosa* when *Elachista fucicola* and *Pylaiella littoralis* (brown algal epiphytes) were present and absent on distal segments of *Ascophyllum nodosum* fronds for the (A) June and (B) July experimental trials. For both trials, the proportion of wounds colonized by *V. lanosa* did not differ significantly between the exclusion and inclusion treatments of brown algal epiphytes.

Our results therefore support the model that the virtual absence of *Vertebrata* clumps on distal segments of *Ascophyllum* fronds is largely a result of an absence of surface wounds in such young tissues. The brown algal epiphytes seem to play no role, as the existing clumps in the *Ascophyllum* bed were unable to produce recruits in the wounds, even though these epiphytes were also reproductive during the experiments (Longtin et al. 2009). Also, their presence in the distal segments with wounds did not affect the colonization rate of *Vertebrata*. Thus, given the absence or scarcity of other types of surface irregularity (branch axils and lateral pits after receptacle shedding) in distal segments of host fronds (Åberg 1996), the smooth nature of the surface of such tissues, probably together with the process of skin shedding (Filion-Myklebust and Norton 1981), represents an effective barrier against *Vertebrata* colonization.

In a laboratory setting using a flow tank, Pearson and Evans (1990) recorded a high abundance of *Vertebrata* individuals settling on the smooth, uninterrupted surface of test *Ascophyllum* fronds. Such a result is contrary to field observations (Lobban and Baxter 1983, Garbary et al. 1991, Levin and Mathieson 1991) and to the results of our two field experiments. Explaining this discrepancy between laboratory and field results is not straightforward, but a major difference is that the water flow was unidirectional in Pearson and Evans's (1990) tank, without including any waves or eddies. At the intertidal zone, however, water turbulence would be expected to prevent spores from settling on smooth surfaces of hosts (Vadas et al. 1990, Brawley and Johnson 1991, Fletcher and Callow 1992, Granhag et al. 2007). Surface irregularities, on the other hand, create good deposition eddies for spore settlement (Lobban and Baxter 1983, Callow et al. 2002). In the end, algal spores that settle in protected microsites are sheltered from desiccation (González and Goff 1989) and dislodgement by waves and water currents (Pearson and Evans 1990, Vadas et al. 1990, Brawley and Johnson 1991, Fletcher and Callow 1992).

Future experimental work on this host–epiphyte system should address other components of the puzzle explaining epiphyte distribution. For example, why are *Elachista* and *Pylaiella* restricted to the distal segments of host fronds? Would they be excluded competitively by *Vertebrata* in midsegments, or would light requirements simply not be met for them in midsegments, where irradiance is normally lower than in distal segments (Longtin et al. 2009)? Furthermore, future research should address the role of herbivores as a balance between promoting epiphyte recruitment by creating colonization microsites and limiting epiphyte recruitment by grazing on them.

Fronds of host macroalgae in dense stands represent environmental gradients, showing differences in, for example, light penetration and abrasion stress from holdfasts to frond tips. In biological communities, environmental gradients are known to contribute greatly to explain the distribution of species (Bruno et al. 2003). Our study has shown that, in host–epiphyte systems, physical features of host fronds may be equally important in determining species distribution.

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