The Scientific Naturalist

Ecology, 0(0), 2019, e02791

Between a rock and a soft place: surfgrass colonizes sediments without attachment to rock

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Manuscript received 26 March 2019; revised 18 May 2019; accepted 28 May 2019. Corresponding Editor: John Pastor.

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Citation: Stephens, T. A., B. B. Hughes, K. J. Kroeker, M. Hessing-Lewis, Z. Monteith, M. Morris, and W. W. Raymond. 2019. Between a rock and a soft place: surfgrass colonizes sediments without attachment to rock. Ecology 00(00):e02791. 10.1002/ecy.2791

Key words: anchoring; attachment; ecotype; habitat; plasticity; rhizome; root; seagrass; surfgrass.

The complex coastline that stretches from Southeast Alaska, USA, to the Salish Sea hosts an expansive and verdant bathtub ring of seagrasses. Their presence is facilitated by the geographic complexity of the region, which promotes a variety of suitable substrates that are appropriate for seagrass recruitment (mud to sands to rock within small spatial scales). Seagrasses are marine flowering plants that have evolved at least three times from land plants back to the sea (Les et al. 1997). Although several adaptations have allowed for them to recolonize marine environments, they still rely upon rhizome and root structures for nutrient uptake and storage, gas exchange, and anchoring to substrates. These structures are reminiscent of their terrestrial ancestors, by which the rhizomes and roots of most species form belowground networks in soft sediments but sometimes exhibit plasticity in anchoring strategy, where a minority of species can also colonize rocky substrates. In such instances, attachment is secured via the secretion of an adhesive, mucilage from the plant's roots (see Appendix S1: Table S1). Of the 72 species of seagrass, there are only five (genus *Phyllospadix*) described to use rock as an obligate substrate (summarized by Balestri et al. 2015). Their niche is further differentiated from other seagrasses in that they prefer habitat with higher wave exposure and, as such, they are commonly referred to as surfgrasses.

In the temperate North Pacific, surfgrasses and eelgrass (*Zostera marina*) can dominate shallow seascapes. While preparing for research that targeted eelgrass communities in Southeast Alaska, comprehensive scouting efforts across soft-sediment embayments on Prince of Wales Island unearthed what looked to be surfgrass, without attachment to rock, intermixed with shoots of eelgrass of typical morphology (Fig. 1). The surfgrass was, in fact, later identified as *Phyllospadix serrulatus* and considereda peculiar find considering explicit descriptions of its life on the rocks. After communicating with regional seagrass experts, we learned that (1) this phenomenon is acknowledged colloquially but a popular notion was that it is rare and that surfgrass rhizomes are typically adhered to rock below the apparent sediment layer, (2) surfgrass growing in sediments without attachment to rock was noted elsewhere in Alaska and British Columbia, and (3) drop-video recordings and other opportunistic observations highlight that sediment-dwelling surfgrass is present at sites in Washington (WA DNR 2019) and elsewhere in British Columbia (Fig. 2) but the nature of belowground anchorage was not confirmed (i.e., attached to rock below the sediment, or not). A formal observation of *P. serrulatus* growing "on a muddy sediment" exists in the literature but, again, the specific anchorage mechanism is unclear (Phillips and Meñez 1988). Additionally, it is important to note that surfgrass species other than *P. serrulatus* were identified growing in sediments in British Columbia, Canada, Washington, USA, and even California, USA (see Appendix S1: Table S2), but we focus on *P. serrulatus* here due to sheer prevalence and consistency across our collected observations. In general, sites where we found sandy ecotypes of surfgrasses were characterized by coarser and/or compacted sediments (consolidated sands, sometimes with pebble, gravel, or cobble) and were likely subject to slightly elevated hydrodynamic forcing via wind fetch compared to adjacent, *Zostera*-only areas.

For other seagrass species that are plastic in substrate selection, intraspecific morphological features can vary between ecotypes. For example, *Posidonia oceanica*, which predominantly grows in sands or vegetative matte (accumulated rhizome and sheath material), displays reduced leaf number, reduced shoot size, and higher shoot density when growing on rock compared to sand (Short 1983,

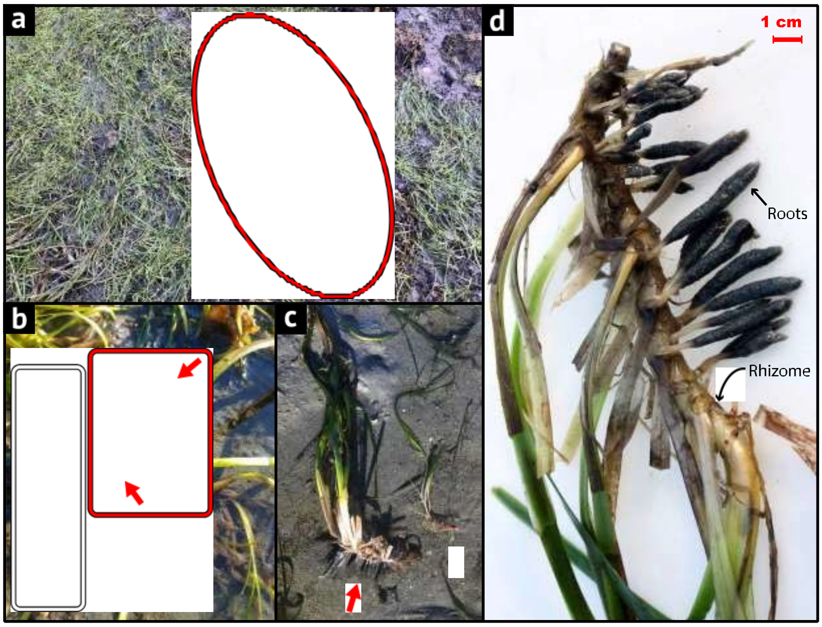

Fig. 1. Examples of sand ecotypes of *Phyllospadix serrulatus*; red shapes and arrows highlight *P. serrulatus* and all white shapes and arrows highlight *Zostera marina*. (a) Patchy colonization of *P. serrulatus* rooted in sandy sediment, with occasional cobble; seagrass outside of the red oval is primarily *Z. marina*. Location: southwest Fish Egg Island, Prince of Wales Island, Alaska, USA. (b) The red arrows annotate old leaves/sheaths on *P. serrulatus*, which is often useful in identifying *P. serrulatus* without uprooting individual ramets. (c) A notable difference in size for these uprooted examples *P. serrulatus* and *Z. marina*, which were growing immediately adjacent to each other in the intertidal; approximatel~~y~~ 0.05 m MLLW (mean lower low water). (d) The morphology of the rhizome and roots from a sand ecotype of *P. serrulatus*, showcasing the finger-like conglomerations of sand and mucilage around each root.

Giovannetti et al. 2008). We did not empirically compare the morphometrics of rock and sand ecotypes of *P. serrulatus* but observations suggest that shoots in sands grow less densely and are wider relative to their length compared to those growing on rock. The most striking feature noted for sand ecotypes of *P. serrulatus*, however, were the roots, the majority of which still secreted the adhesive mucilage used for attachment to rocks. In the absence of rock, these secretions formed finger-like conglomerations of a sand–mucilage complex around each root (Fig. 1d), theoretically better anchoring surfgrass in sediments. Considering that rhizome extension in *P. serrulatus* is likely slow due to rhizome thickness (Marba and Duarte 1998), these bulbous anchors could be critical in stabilizing the establishing seedling recruits until they are able to build a stronger rhizome network via clonal growth. This would be particularly appropriate for individuals that recruit along the upper edge of *Z. marina* beds where wave energy is elevated, which was the most common location that we found *P. serrulatus* established. Occasionally, *P. serrulatus* also grew in patches located inside the seagrass bed, without necessarily extending to the edge of the meadow. Regardless of the location, both surfgrass and eelgrass often grew intermixed instead of forming distinct bands (e.g., Fig. 1a, b). It is possible, however, for *P. serrulatus* to grow in monospecific stands (see Appendix S1: Table S2; north Fish Egg Island 2, Alaska) but the majority of our observations are limited to eelgrass sites due to the objectives of the initial research.

There are two mechanisms by which seagrasses recruit in soft sediments: seed dispersal and clonal growth. The winged morphology of *Phyllospadix* seeds keeps them aloft to track water movement (see Blanchette et al. 1999), likely transporting them from nearby rocky to soft-sediment sites. Because the seeds are negatively buoyant, deposition via sinking in these lower energy habitats is likely after currents dissipate. Additionally, it is common to find unattached seaweeds that have floated into these low energy sites; seeds could be attached to such thalli (Turner 1983) and later deposited in eelgrass beds. Entire reproductive shoots can also be transported before releasing seeds if they are still buoyant (Reusch et al. 2000, Harwell and Orth 2002). Alternatively, it is possible that *P. serrulatus* may colonize sediments via clonal, rhizomatous extension from adjacent populations on rocky reefs or outcrops. Indeed, sand ecotypes were sometimes observed growing at or near the lateral edges of seagrass beds where nearby reef/rock served as a physical barrier to the beach.

Once recruited, does surfgrass compete with eelgrass? In our sites, there was apparent competition for space due to physical overlap with obvious intermixing of species. Space occupation by seagrasses is closely controlled by rhizome growth strategies, where branching angle and branching density inform upon spreading efficiency.

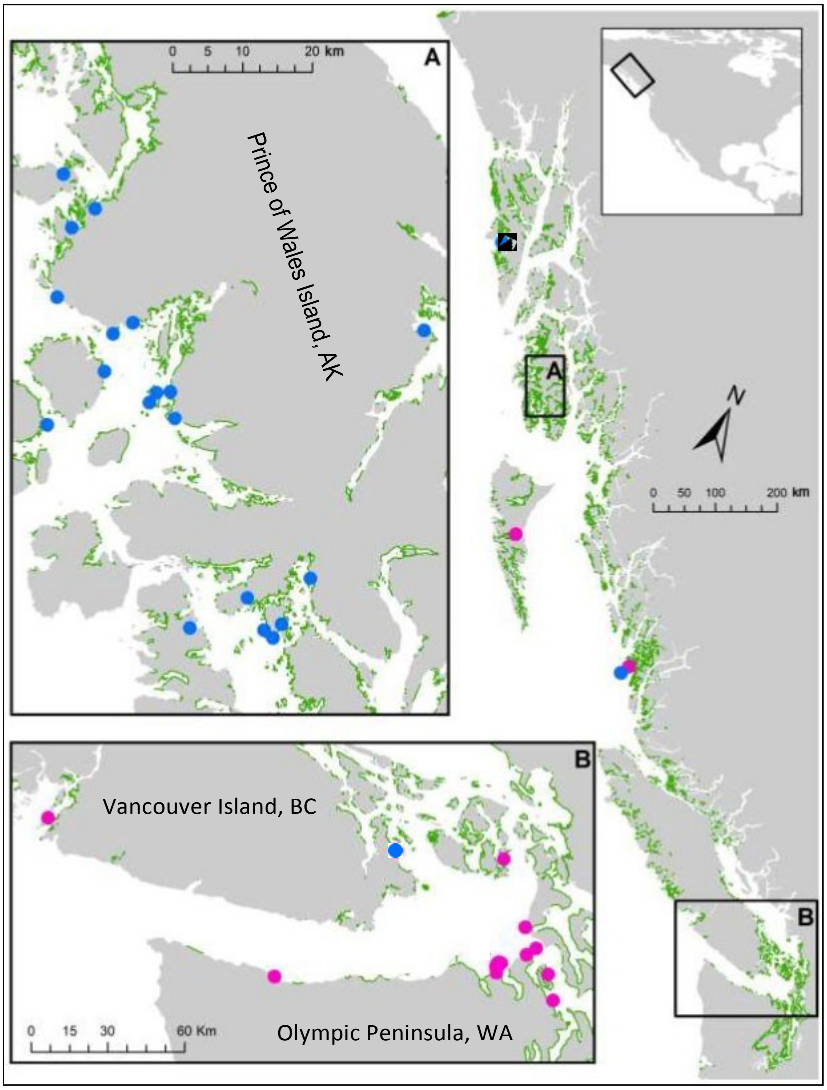

FIG. 2. Location of opportunistic observations of *Phyllospadix* growing in sediments, ranging from southeast Alaska (AK), through British Columbia (BC), Canada, to Washington (WA), USA. Due to the clustering of observations in two regions, better spatial resolution of sites is shown for Prince of Wales Island (Inset A) and the Salish Sea (Inset B). The blue points symbolize surfgrasses that were confirmed to be growing without any attachment to rocky substrates, the pink points symbolize surfgrasses that were growing in sands but the nature of attachment was not confirmed (i.e., could have been attached to rock below the apparent sediment layer). The single triangle (Sitka, AK) represents *P. serrulatus* that was attached to rock but the roots were buried by sand. The green line that follows the shoreline shows where seagrass has been observed by ShoreZone (NOAA 2009). These locations represent multiple species from the genus *Phyllospadix* (nearly all *P. serrulatus*), the species at each location are recorded in Appendix S1: Table S2. Note that ShoreZone is the best current synthesis of existing, coastwide, seagrass presence but data were collected macroscopically and, therefore, does have limitations when considering small-scale presence/absence.

P. serrulatus has thicker rhizomes and dense branching compared to *Z. marina,* and therefore may have lower spreading efficiency and higher space-filling capacity (see Marba and Duarte 1998). How this translates into physical competition requires empirical description of growth strategies over time. Currently, it does not appear that *P. serrulatus* is a dominant competitor for space. This assumption could be confounded by the longevity of *P. serrulatus* ramets in sediments (see Marba and Duarte 1998) or by the regional pattern indicative of the evolutionary and ecological history of *Phyllospadix* populations in soft-sediment habitats.

The potential evolutionary history that frames *Phyllospadix* occupation of soft sediments is two-fold: (1) the sandy ecotype is a vestige of an ancestral, sediment-dwelling *Phyllospadix* line that was more similar in habitat preference compared to taxonomic sister groups like *Zostera*, ultimately evolving to recruit upon rock, or (2) sandy ecotypes are descendent from modern rock-dwelling populations of *Phyllospadix* spp. and have recolonized sediments, independently. Either of these scenarios is novel and lend themselves to potentially ground-breaking investigations concerning evolutionary processes specific to marine angiosperms, or to evolutionary theory, and its interaction with benthic habitat type, in general. The latter may be especially true when considering the apparent latitudinal patterns displayed in Fig. 2 (note that this manuscript serves to report observations of a newly identified ecotype for *Phyllospadix*, not the full extent of this ecotype reported across this region). Is it possible that there is a latitudinal effect on niche differentiation and trait evolution of this genus? This is a question that still plagues evolutionary biologists today, and *Phyllospadix* may provide a unique opportunity to explore these concepts further. More formal efforts in determining the full extent of sandy ecotypes are necessary to address such.

It may be that the scientific community has not previously described surfgrasses growing in soft-sediment environments because appropriate habitat is likely most prevalent along the remote coastlines of British Columbia and Southeast Alaska. This region lies in stark contrast to coastal counterparts at lower latitudes in that the region is walled by mountainous terrain and is not easily accessible. Furthermore, the large and complex coastline allows for significant spatial heterogeneity (due to variation in exposure, substrates, freshwater input, etc.). The combination of these two attributes leads to a lack of habitat-based monitoring necessary to comprehensively build representative inventories of community composition in this region. Cryptic species or strategies (e.g., sand ecotype of *Phyllospadix*) are especially overlooked when monitoring is difficult. For most of our observations, it must be reiterated that we visited sites that were suitable for and dominated by *Z. marina* due to the research objectives of independent teams, and it is possible that beds composed of only surfgrass could exist in soft sediments that are not colonized by eelgrass. Regardless, we do not know the history of *P. serrulatus* colonization of soft-sediment habitats. What are the evolutionary selective forces that have created this phenomenon, are these vestigial populations or a recent adaptation? Do the energetic and subsidy requirements differ for each ecotype? If so, what are the implications to productivity, fitness, and resilience of populations? Do the ecosystem services of surfgrass (e.g., carbon burial, biogenic habitat) differ compared to *Zostera*? Clearly, focused observation efforts are necessary to better assess the breadth of this alternative lifestyle in surfgrasses.

Acknowledgments

We thank the following experts for sharing everything they know, or information that they had heard, about *Phyllospadix* growing in sands: Helen Berry, Matthew Bracken, Colleen Burge, Bart Christiaen, Megan Dethier, Jeff Gaeckle, Kevin Hovel, Fiona Tomas Nash, Thomas Mumford, Jay Stachowicz, Susan Williams. We also thank those that assisted in the field: Cathy Mattson (AK), Maggie Shields (AK), Angeleen Olson (BC), Derek Vanmaanen (BC), Kyle Hall (BC), Ondine Pontier (BC), Ben Millard-Martin (BC), Ross Whippo (BC), Tristan Blaine (BC), Carolyn Prentice (BC), Krystal Bachen (BC), Tyrel Froese (BC), Gillian Sandlier-Brown (BC), and Rhea Smith (BC). Access to field sites on Prince of Wales Island was supported by an NSF BIO-OCE grant awarded to Ginny Eckert (NSF #1635716); observations in British Columbia were supported by the Hakai Institute and the Tula Foundation.

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Data Availability

Data are available on the Knowledge Network for Biocomplexity: https://doi.org/10.5063/F1PK0DF9

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2791/suppinfo