“Home Sweet *Fucus*”: The Role of *Fucus distichus* as a Community Habitat Former at Low and High Margins of its Intertidal Range

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FHL 470: Research in Marine Biology
Spring 2021

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Keywords: *Fucus distichus*, canopy-forming seaweed, invertebrate communities, intertidal

Abstract

Fucus distichus is a common and ecologically important canopy-forming seaweed found on the rocky intertidal shores of the Northern Hemisphere. In addition to its role in primary production, *F. distichus* is a critical habitat former for many invertebrates. It provides both physical structure and protection from sunlight and high temperatures, preventing desiccation and heat stress in intertidal environments. In order to quantify the communities living on and under *Fucus*, we sampled quadrats along transects at the low and high ends of its intertidal zone at three sites on San Juan Island. We recorded counts of invertebrates and estimated percent cover of understory macroalgae and occasional epiphytes. We hypothesized that there would be differences in invertebrate assemblages occupying the low and high edges of *Fucus* and sought to compare these among sites. We hypothesized that there would be differences in species diversity and richness in the low and high assemblages. Across sites, we found that distinct groups of organisms occupy the low and high edges of *Fucus* and that *Littorina scutulata, Chthamalus dalli*, and *Semibalanus cariosus* contribute most to this dissimilarity. We also found that in general, the diversity of invertebrate and algal assemblages is higher in the low edge and lower in the high edge of the *Fucus* zone.

Introduction

It is widely known that *Fucus spp.* are important canopy-forming seaweeds in rocky intertidal ecosystems. Members of this genus are some of the most abundant organisms found in the intertidal shores of the Northern Hemisphere, and *Fucus distichus* is a cold-adapted species with a wide-reaching latitudinal and longitudinal distribution (Smolina et al. n.d.). Many studies have shown that canopy-forming algae can strongly influence intertidal community structure

(Ingólfsson 2008). *Fucus* blades provide physical habitat and protection for rich and diverse intertidal communities, and as a result of high biomass and productivity are an important food source for several intertidal organisms, namely limpets and amphipods (Graiff et al. 2015). Many invertebrates require *Fucus distichus* to survive harsh and variable intertidal conditions; it has been hypothesized that decreases in or disappearance of *Fucus spp.* could result in changes in the composition and biomass of vegetation-associated invertebrates, and that such changes have the potential to impact higher trophic levels in coastal ecosystems (Wikström and Kautsky 2007).

With climate change, it has been predicted that the vertical distribution of *Fucus* may be "squeezed" as a result of increased physiological stress due to abiotic factors at its upper limit and increased intensity of biotic factors at its lower limit (Martins et al. 2019). One important abiotic factor likely to restrict the upper limit of *Fucus* is temperature. In the near future, it is expected that heat waves will increase in frequency, intensity, and duration and that such unpredictable temperature changes may have detrimental impacts by inhibiting growth and photosynthetic processes (Graiff et al. 2015). Many intertidal species already live at or near their upper thermal tolerance limit, and it has been hypothesized that *Fucus spp.* from cold temperate habitats – such as *F. distichus* – will likely be more stressed in response to increased temperatures, which can have a negative impact on photosynthetic performance (Smolina et al. n.d.). Experiments have shown that *Fucus* is unable to acclimate to high temperatures; temperatures of 28 degrees C can cause mortality of *Fucus* individuals even after a short exposure time, and at greater than 26 degrees C, growth performance and yield of apices grown was greatly reduced (Graiff et al. 2015). Potential factors influencing the lower limit of *Fucus* include increased levels of submersion with global rising sea levels. Consistent submersion over a 42-day period leads to substantial deterioration of *F. distichus* individuals (personal observation). It is important to recognize that local populations of *F. distichus* may have divergent responses to site-specific environmental changes, and these predictions are only indicative of potential responses of the San Juan Island populations. It is unclear exactly how this structural zone shift may impact *Fucus*-associated invertebrates, but it is likely to affect the distribution and abundance of some species.

Our motivation for this study was to quantify and compare invertebrate assemblages found in the highest and lowest regions of the *Fucus distichus* zone to better understand the diversity of organisms that utilize this alga as habitat in the intertidal on San Juan Island. We aimed to determine invertebrate types strongly associated with a specific limit of the range, to begin to hypothesize about which species could be most impacted by a potential narrowed *Fucus* range in the future. We also estimated understory algal community assemblages; besides also potentially serving as a habitat substrate for invertebrates, these algae may rely on *Fucus* for desiccation prevention (Ingólfsson 2008). There are also competitive interactions to consider: canopy-forming species such as *Fucus* can have a suppressive effect on subtidal algal turf communities, yet areas with high amounts of turf algae can also limit recruitment and colonization of *Fucus* (Wikström and Kautsky 2007). When considering the habitat-forming role of *Fucus*, it is important to consider the direct and indirect impacts of other algae on both *Fucus* itself and invertebrate communities.

Methods

Field sampling:

We sampled transects at the high and the low limits of the *Fucus* zone at three sites on San Juan Island: Cattle Point (48.4499, -122.9633), Lime Kiln (48.5131, -123.1467), and

Cantilever Point (48.5462, -123.0098). Between May 20th-27th 2021, we sampled during low tide which generally occurred late morning to early afternoon during the week. We sampled 15 quadrats per transect; 15 in the high edge and 15 in the low edge for a total of 30 quadrats per site. A 25cm x 25cm quadrat was randomly placed along a 25m transect line on a region of the beach within each limit. We sampled at the highest and lowest possible areas of the *Fucus* zone. The high and low regions at a site were at the same horizontal location on the beach, parallel to each other and the water line. For each quadrat, we ensured the given area was well covered with *Fucus* and contained minimal bare rock. If it did not contain a sufficient amount of *Fucu*s cover, we chose a new quadrat. We examined the *Fucus* in the quadrat, counting motile and benthic invertebrates and estimating percent cover of other algae types. While our focus was on invertebrates, we estimate percent cover of macroalgae present because it likely additionally contributes to community structure. In order to minimize observer bias, members of our two-person team made sure to alternate between quadrats with one person counting and one recording. Because we followed the tides, our sampling occurred at different times of day with varied weather and temperatures. We noted these details because they may have an influence on the communities present on and under *Fucus* beds at a given time.

Analytical:

We performed several different forms of analyses to interpret our community assemblage data. All analysis was done in R Studio version 1.2.5033. To assess similarities among communities, we created Non-metric Multi-dimensional (NMDS) plots containing our data from high and low zones at each site, separately for invertebrate counts and algae percent cover. The closer the points, the more similar they are to each other. We also performed a SIMPER analysis for both invertebrates and algae to determine which species were contributing most to the dissimilarities among sites and between high and low zones. We manually calculated species richness for each height at each site, displaying these values in a bar chart. Lastly, we used a Simpson Diversity Index to quantify species diversity between high and low zones and among sites. Values range from 0-1, with higher values indicating higher diversity.

Results

1) NMDS

We found that the invertebrate assemblages living on and under *Fucus* at the high and low margins differed from each other across all sites. In other words, the assemblages in each margin contain different groupings of invertebrates and this difference is visible at all sites, as indicated by the distinct separation of colors in the plot. Assemblages at Cantilever Point were generally more variable; in particular, the low margin quadrats were quite different from each other at this site. By contrast, the assemblages in both the high and low *Fucus* margins at Cattle Point and Lime Kiln were more similar to each other within sites. In addition, overall organism assemblages were fairly similar between Cattle Point and Lime Kiln whereas assemblages at Cantilever were more dissimilar to the other sites.

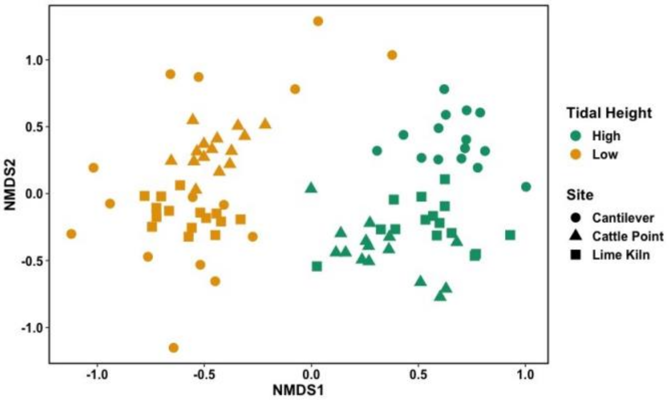

Figure 1 NMDS plot of invertebrates, stress value = 0.1944352. Each quadrat is represented by a shape, unique to the site it is from. High and low ends of the Fucus zone are represented by colors.

We found less clear differences among algal assemblages in quadrats between high and low margins and among sites. However, we found that algae in the low margin at Lime Kiln and Cantilever point were relatively similar. There was less consistency among high margins across the sites. Cattle Point assemblages in the high and low margins were fairly similar to each other. Thus, there was not a substantial difference in algal assemblages between high and low margins at Cattle Point. At the other sites, high and low margins were more different from each other.

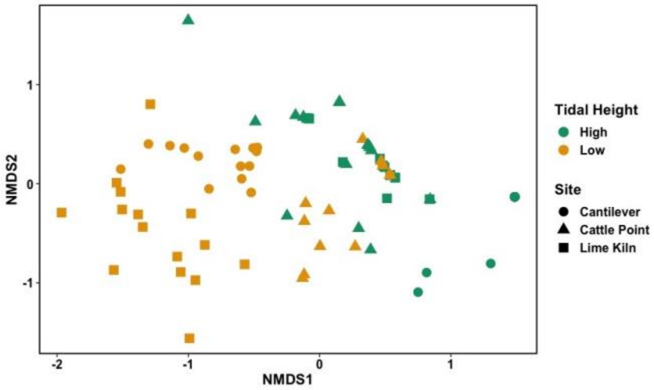

Figure 2 NMDS plot of algae, stress value = 0.1381868. Each quadrat is represented by a shape, unique to the site it is from. High and low ends of the Fucus zone are represented by colors.

2) SIMPER

At Lime Kiln, three species contributed to 70% of the dissimilarity between high and low margins: *Semibalanus cariosus*, *Littorina scutulata*, and *Chthamalus dalli*, from lowest to highest contribution. At Cattle Point, four taxa that contributed 70% of the dissimilarity between high and low were limpets, anemones, *Littorina scutulata*, and *Semibalanus cariosus*, from lowest to highest contribution. At Cantilever Point, three species that contributed 70% of the dissimilarity between high and low were *Chthamalus dalli*, *Balanus glandula*, and *Littorina scutulata*, from lowest to highest contribution. In general, the same organisms contributing to dissimilarity between high and low at individual sites contribute to dissimilarity between high and low across all sites on San Juan Island; meaning organisms that more strictly occupy the high and low margins are consistent throughout sites. These three species were *Littorina scutulata*, *Chthamalus dalli*, and *Semibalanus cariosus*.

As for algal communities, four understory algal types – upright reds, brownish mat, *Endocladia muricata*, and “Petrocelis” crust – contribute most to dissimilarity between low and high across all sites, from lowest to highest contribution. However, we cannot evaluate whether *Fucus* has a significant impact on this dissimilarity between margins.

3) Species Richness

Across sites, species richness was higher at the lower limit of the *Fucus* zone and lower at the higher limit of the zone.

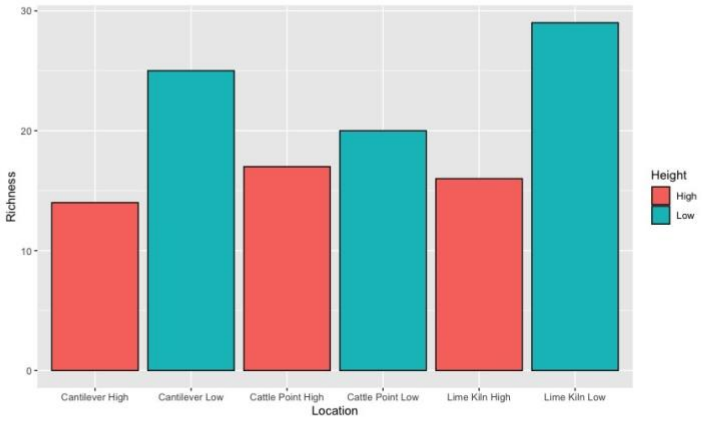

Figure 3 Species richness of low and high zones for each site.

4) Species Diversity: Simpson Index

Across all sites, the diversity of invertebrates was higher at the low margin of *Fucus* while the diversity was lower at the high margin. For individual sites, Cattle Point had the highest overall diversity of invertebrates, then Lime Kiln, while Cantilever Point had the lowest overall diversity.

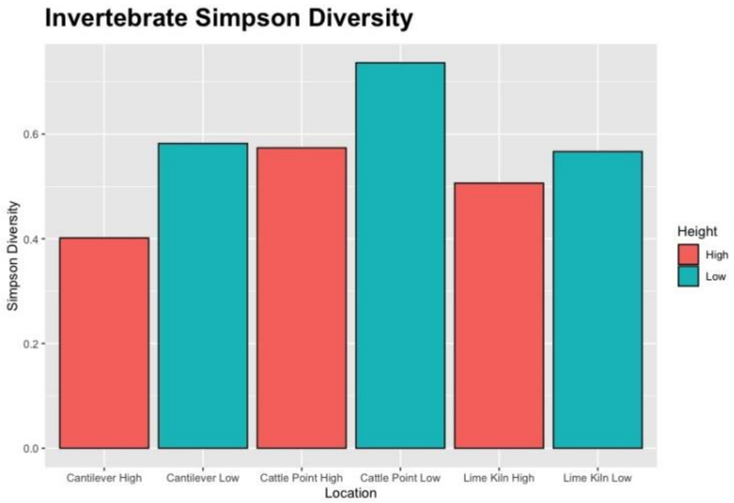

Figure 4 Species diversity (Simpson Index) of low and high zones for each site.

Diversity of algal assemblages showed a similar pattern of generally higher diversity in the low margin and lower diversity in the high margin. Lime Kiln showed the highest overall diversity of algae, while Cattle Point and Cantilever Point showed lower but similar levels of diversity. When invertebrates and algae are combined into one Simpson's Index, the overall trends in species diversity by site are the same: highest diversity at Cattle Point, followed by Lime Kiln, then Cantilever Point.

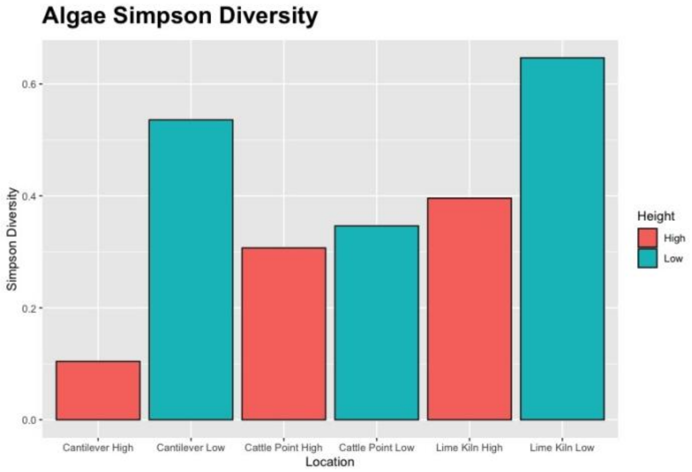

Figure 5 Species diversity (Simpson Index) of low and high zones for each site.

Discussion

Overall, we found distinct compositions of invertebrates in the low and high margins of the *F. distichus* zone, and this pattern was consistent across Cantilever Point, Lime Kiln, and Cattle Point. In addition, species richness and diversity of both invertebrates and understory algae were higher at the lower limit of the *Fucus* zone. Thus, we determined that different assemblages occupy the high and low edges of the *Fucus* band. The species that contribute most to this dissimilarity across sites – *Littorina scutulata, Chthamalus dalli,* and *Semibalanus cariosus* – occur more at one tidal height, whereas the other invertebrates were found more widely throughout the *Fucus* zone. Because these species more strictly inhabit either the high or low margins, they potentially could be affected by the predicted vertical narrowing of the *Fucus distichus* range in the future.

With a narrowed band of this key canopy-forming alga, there are potential broad-scale effects on intertidal community structure. Several studies have shown examples of declines in species diversity when a keystone canopy-forming alga decreases in abundance. For example, during and after the Pacific Marine Heatwave of 2014-2016 in the northern Gulf of Alaska, declines in macroalgal cover – mostly *F. distichus* – lead to greater homogenization of community structure in rocky intertidal regions, as barnacle and mussel cover increased in its place (Weitzman et al. 2021). The removal of another dominant, canopy-forming alga *Hormosira banksia* in southern New Zealand resulted in a decline in diversity of 44% and 36% at two sites relative to controls, with very few invertebrates present (Lilley and Schiel 2006). A study by Wikström and Kautsky in 2007 found that in general, certain species abundances were lower and biomass was halved when *F. vesiculous* was experimentally absent. By contrast, sites with *Fucus* contained a specific community of invertebrates of high biomass (Wikström and

Kautsky 2007). All of these instances demonstrate the importance of canopy-forming algae, such as *F. distichus*, to intertidal community structure. While these studies involve monitoring impacts due to the absence or presence of the alga, our study aimed to quantify differences in assemblage composition and diversity specifically in the high and low margins of *Fucus*.

Of course, implications for invertebrate and understory algae communities in the future largely depend on the response of *Fucus* beds to climate-induced stressors. In general, the ability of *Fucus* to compete in the intertidal is determined largely by growth rates, reproductive output, and defense towards biotic and abiotic factors (Wahl et al. 2011). Several studies have indicated the range of *Fucus* in the intertidal may narrow in the future; in the Baltic Sea, the lower limit of *F. vesiculosus* has already shifted upward, likely due to increased eutrophication levels and competition (Wahl et al. 2011). Here on San Juan Island, because other algal types tend to be more abundant and diverse in the lower edge, we hypothesize that perhaps with a rising sea level these algae could replace *Fucus* and thus have an impact on invertebrate assemblages. Abiotic factors will likely suppress the upper limit of the *Fucus* range. It has been demonstrated that intense desiccation combined with high temperatures and light can increase mortality of *Fucus spp*., and juveniles are most susceptible (Wahl et al. 2011). However, there are also physiological adaptations that could protect against these effects. For instance, *Fucus spp.* have shown several defense mechanisms including high concentrations of phlorotannins to protect against UV rays, as well as herbivore-induced chemical defense in *F. distichus* (Wahl et al. 2011). In addition, the resilience of *F. distichus* has been demonstrated experimentally where intense pulse disturbances involving complete clearing of canopies resulted in short-term synchronous increases in biomass (Klinger and Fukuyama 2011). However, it is important to note that many climate-induced disturbances are gradual and many factors compound their intensity.

Our study aimed to quantify and compare diversity of invertebrates inhabiting low and high margins of the *Fucus* zone, and while we were able to conclude that these assemblages do in fact differ, many other factors likely influence their composition. Observationally as we sampled quadrats, we noticed high variability in the patchiness and morphology of *Fucus* individuals depending on their location in the range and the site. *Fucus* canopies modify intertidal habitats by increasing spatial complexity, which in turn maintain large aggregations of invertebrates (Lilley and Schiel 2006). On a smaller scale, other studies of rockweeds demonstrate that rather than only biomass, structural details of plant length, circumference, and density are important predictors of associated community structure (Kay et al. 2016). Subtle variations in the three-dimensional structure of canopies therefore likely influence the communities present. A future study could quantify differences in *Fucus* bed density and individual morphology in low and high margins, then connect these trends to invertebrate and algal assemblage composition.

Acknowledgements

I'd like to thank Terrie Klinger and Joe Duprey for guidance on both this study and report. Additionally, thank you to the Mary Gates Endowment for supporting my quarter at Friday Harbor Labs which greatly expanded my knowledge and fueled my curiosity for marine ecosystems.

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