The effect of variation in flow velocity on the growth morphology and susceptibility to herbivory of *Nereocystis luetkeana*

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Abstract

As biogenic habitat, *N. luetkeana* beds mediate interactions between the abiotic environment and biological dimensions of an ecosystem. Prevalent in existing literature is evidence for relationships between *N. luetkeana* blade morphology and flow velocity of the surrounding environment. In our project, we examined the effect of contrasting flow velocities on blade morphology of *N. luetkeana* from the San Juan Islands, WA, and further how blade thickness varied based on the blade's spatial characteristics. We also examined how flow regime and consequent blade morphology affects rates of herbivory via the kelp crab (*Pugettia producta).* Our results show that blades are thickest near their midline (lengthwise), and that blades closest to the central axis are thicker than those further away. Trends in linear models of our data indicate that blades exposed to higher flow velocities were narrower and less undulated than their low flow counterparts, which is consistent with existing literature. Our results show that kelp crabs preferred blades from an area of relatively high flow velocity. One explanation for this result is that narrow, flat blades are mechanically easier for kelp crabs to consume than wide, undulated blades. It is possible that the wide, undulated blade morphology is a morphological defense against herbivory for blades that experience low flow velocity, where kelp crab herbivory may be more prevalent. More research is needed to determine if blade morphology mediates the interaction between flow velocity and herbivory.

We would like to acknowledge that our research takes place on the traditional land of the first people of the San Juan Islands, the Coast Salish People past and present and honor with gratitude the land itself and the Coast Salish Tribes, including the Sooke, Saanich, Songhee, Lummi, Samish, Semiahmoo and Swinomish.

Introduction

Similar to other biogenic habitats, macroalgal communities are both economically (Tiwari and Troy 2015; Kim et al. 2015) and ecologically important (Simenstad et al. 1978, Tegner and Dayton 2000, Graham 2004). Macroalgae alter sediment regimes (Clarke 2002) and flow regimes (Jackson and Winant 1983). Furthermore, they are highly productive in coastal systems (Krause-Jensen and Duarte 2016) and provide ample habitat for organisms at multiple trophic levels (Smale et al. 2013). In the Salish Sea, kelp species are highly diverse, supporting food webs (Tallis 2009) and serving as an important cultural and commercial resource (Turner 2003, Kim et al. 2015). *Nereocystis luetkeana (Phaeophyta, Phaeophyceae, Laminariales),* commonly known as bull kelp, is the primary canopy-forming kelp in the Salish Sea (Berry et al. 2021). N. luetkeana is declining in the Salish Sea, and the cause of decline is currently unknown (Berry et al. 2021). We must seek a better understanding of how *N. luetkeana (Phaeophyta, Phaeophyceae, Laminariales) (bull kelp)* is influenced by abiotic factors, given its functional role in ecosystem landscapes and trophic structures (Carter et al. 2007).

Flow velocity is a substantial driver of macroalgal growth (Koehl et al. 2008), nutrient uptake (Stevens et al. 2003) and abundance (Kumagai et al. 2018). The impact of flow velocity on characteristics of kelp most often concerns blade morphology. Many studies show that several species of macroalgae display narrow, flat blades in areas of high flow velocity, and display wider, undulated blades in areas of lower flow velocity (Koehl and Alberte 1988, Hurd and Stevens 1997, Hurd et al. 1997, Koehl et al. 2008).

Differences in morphology have inherent trade-offs. For *N. luetkeana*, blades with more undulations tend to be more efficient at both nutrient and sunlight uptake (Hurd et al. 1997). Undulate blades increase turbulent flow and gas exchange, reduce self-shading (which occurs when flattened, clumped blades block sunlight) and orient the blade to increase photon capture (Hurd et al. 1997, Hurd and Stevens 1997, Koehl et al. 2008). Wide blades and greater undulations also increase drag, putting more strain on the stipe and making it less adaptive for individuals in high flow environments to display such traits (Koehl and Alberte 1988, Koehl et al. 2008). Varied thickness also has trade-offs; thicker blades are more resistant to breakage, while thinner blades make individuals more productive due to a higher surface area to volume ratio (Rodriguez et al. 2016). The results of Duggins et al. (2003) may reflect this phenomenon as multiple species of macroalgae were significantly thinner in areas of low flow. Across the aforementioned traits, blade morphology has been shown to be a plastic trait (Duggins et al. 2003, Koehl et al. 2008).

Our first objective was to see if variation in morphological traits of *N. luetkeana* blades is explained by flow velocity. We proposed the following hypotheses:

H0.1: Flow velocity will not be correlated with thickness, width or undulation.
H1: Increased flow velocity will be correlated with narrower blades.
H2: Increased flow velocity will be correlated with less blade undulation.
H3: Decreased flow velocity, or increased undulation, will be correlated with thinner blades.

We based these hypotheses on the following rationale: individuals in high flow environments will have narrower blades than those in low flow environments to reduce drag and relieve stress on the stipe (H1); Individuals in low flow environments will have more undulations than individuals in high flow environments to increase turbulent flow, gas exchange, and light exposure, increasing rates of photosynthesis and respiration (H2); Individuals in low flow, or with more ruffles, will be thinner to maximize surface area to volume to facilitate nutrient uptake, either due to more competition with phytoplankton or greater light accessibility compared to less-ruffled conspecifics (because ruffling helps individuals avoid self-shading) (H3).

We also considered that thickness may vary within an individual specimen or within areas of an individual blade. We hypothesized the following:

H0.2: Blade thickness will not be correlated with blade area or position.
H4: Blades will be thicker near the central axis and thinner towards the margins.
H5: Medial blades will be thinner than lateral blades.

We based these hypotheses on the following rationale: Blades will be thicker near the central axis to resist breakage, and blades would be thinner towards blade margins either because of diffuse growth at the margins or because of increased nutrient uptake (H4); medial blades will be thinner than lateral blades due to lower flow velocities, similar to the *N. luetkeana* specimens that experience slower flow in the middle of a bed than at the edge of a bed (H5).

Few studies have examined the effect of flow velocity on herbivory. “Herbivory is a significant factor in the regulation of kelp growth (Franco et al. 2017), and several predator-prey mechanisms maintain the balance of the kelp forest. Given that kelp forests are one of the most productive ecosystems in temperature oceans (Stenneck et al 2003), herbivory pressure has a substantial effect on the rest of the ecosystem. One of the more well-studied interactions is the predator-prey interaction between otters and sea urchins as top-down factors to regulate kelp growth (Estes et al. 1989). However, the importance of other biotic and abiotic factors in the regulation of kelp growth are infrequently studied. An example of these less highlighted interactions is the role of omnivorous crustaceans as top-down factors that control the productivity of kelp forests. The crustacean species we used to emulate top-down control of kelp growth is the kelp crab (*Pugettia producta*). Kelp crabs are widely distributed throughout the west coast of the United States and are usually associated with *Macrocystis pyrifera (giant kelp)* and *Nereocystis* kelp forests (Rudy Jr et al. 2013). These brachyurans are the largest from the genus *Pugettia* and serve as a main consumer of *N. luetkeana* in the San Juan Islands (Dobkowski 2017). Both the large size and appetite for *N. luetkeana* makes this species an excellent candidate for this experiment.

With the wide distribution of *N. luetkeana* and its even greater variety of grazers, *N. luetkeana* does not seem to have any commonly used chemical defenses such as phlorotannins (Dobkowski et al. 2017). We predict that induced defenses (morphological or chemical) in *N. luetkeana* will depend on the level of flow velocity. This prediction is based on the horizontal patterns of distribution and abundance in the rocky intertidal, as predation and physical processes are negatively correlated with each other (Underwood and Chapman 2000). Previous studies on the role of herbivores and varying hydrodynamic forces have also shown that macroalgal herbivores are less successful in areas of high flow (Duggins et al. 2001). To elaborate, kelp from the low flow environment will be less likely to be consumed due to previous acclimatization to predation from kelp crabs. In contrast, kelp from high flow environments are not acclimatized to kelp crab predation, causing them to have less defenses resulting in increased likelihood to be consumed by kelp crabs. We propose that *N. luetkeana* from areas of high flow velocity will experience greater herbivory in lab feeding experiments because they possess fewer anti-herbivory mechanisms compared to *N. luetkeana* from areas of lower flow. Thus, we proposed the following hypotheses:

H0.3: *P. producta* will have no preference for blades from sites with varying flow velocities.
H6: *P. producta* will prefer *N. luetkeana* from an exposed site compared to a more sheltered site.

We conducted feeding experiments to determine whether the kelp crab *Pugettia producta* has a preference for N. luetkeana blades at two sites with contrasting flow velocities. We measured several morphological characteristics of blades from these sites. Any morphological differences we observed between *N. luetkeana* blades in areas of high and low velocity may be part of *N. luetkeana*'s induced defense against herbivory in that area. Our results will help elucidate the impact of flow velocity on *N. luetkeana* morphology and herbivory, and help us further understand the role of morphology in anti-herbivory defenses.

Materials and Methods

Study Locations

We collected *N. luetkeana* specimens from two distinct areas in the San Juan Islands, Washington USA (Figure 1). Our first site, Point Caution (PC) (48.563°, -123.022°), experiences relatively low flow conditions (~ ½ knots) compared to our second site, Turn Rock (TR) (48.512°, -122.927°), which experiences relatively high flow conditions (~2 knots) due to a lack of coastline protection (NOAA Tide Predictions, accessed 2 June 2021).

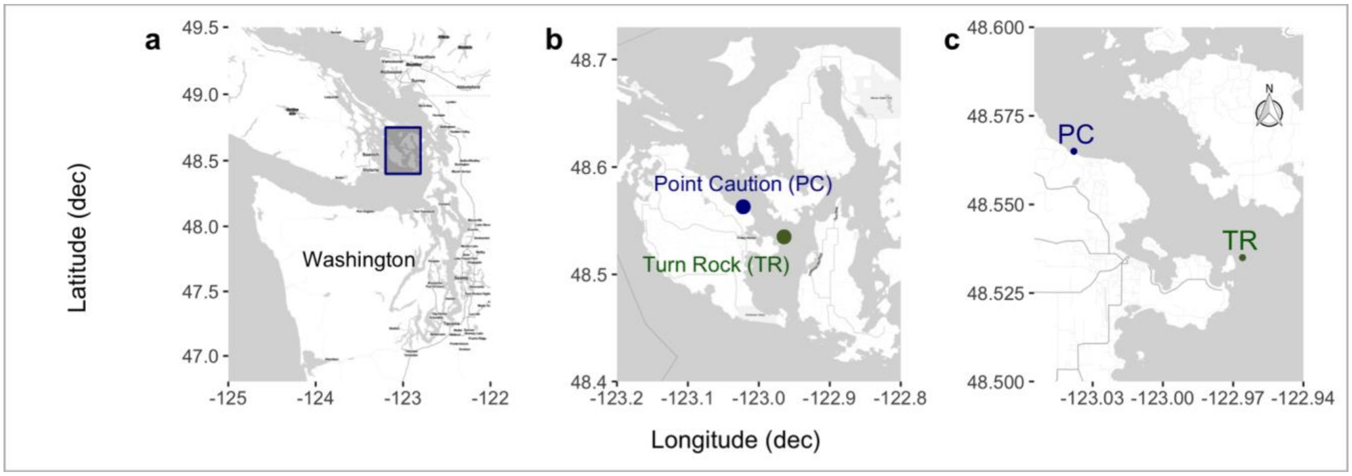

Figure 1: Map of our study site at different scales: the Salish Sea (a), the San Juan Islands (b), and San Juan Island (c).

Morphology Measurements

N. luetkeana individuals were collected from both sites specified above from June 29 to July 1, 2021. 5 individuals were collected from TR, and 3 individuals were collected from PC. Four full blades were removed from each individual: two medial blades, as defined as a blade close to the kelp's central axis, and two lateral blades, as defined as the two blades farthest from the central axis on either side. For each of these blades, we measured four morphological characteristics: width, thickness, undulation length and blade length. The width of each blade was measured ~50 cm above the origin, or point at which the blade widens to a flat surface (as described by Koehl et al. 2008). We measured thickness at three points along each blade by making two cross sections on either side of the blade's central axis (0.5 cm away from the blade's margin) and one cross section in the middle of the blade. Each cross section was done roughly 30 cm above the blade's origin for continuity. To measure undulation, we first measured linear length—the total length of the blade along the specimen's central axis. Then, we measured one flattened edge (with all undulations pressed flat) 25 cm away from the midpoint of the entire blade's length to simulate undulation length. We divided undulation length by 25 cm to assign each blade an undulation score.

To determine which significant relationships existed between morphological characteristics, we performed Unpaired Welch Two Sample t-tests between covariates, which assume unequal variances between both tested groups (Rasch et al. 2011). Before performing the t-test, we made quantile-quantile plots to ensure that our data was normally distributed. Our t-tests addressed the following questions: first, is undulation score correlated with site or blade position; second, is width correlated with site or blade position; and third, is thickness correlated with site, blade position, blade area, or undulation score?

We explored several different linear models in RStudio (RStudio Team 2020) to look for trends in morphological characteristics of *N. luetkeana*. First, we examined trends in blade thickness (Table 1). Our most simple model only included blade area (the central or marginal portion of the blade) as an explanatory variable. Our other models included both blade position and site as covariates. Our most complex model included both blade area and blade position nested in our site variable, allowing blade area and position to have differential effects on thickness at different sites. Using the best fit model of thickness, we also tested whether undulation affected thickness (Table 1). We then examined trends in undulation, total length, and width (Table 2). The simplest models tested whether each characteristic was explained by site alone. The next models tested whether the characteristic could be explained by a combination of site and another morphological characteristic, among other specifications. We compared data support for models based on delta AIC (Akaike 1973). All models were fit using the lme4 package (Bates et al. 2015). We assessed goodness of fit using the residual diagnostic tests in the DHARMa package; if the model failed one of the tests, it was discounted (Hartig 2020).

Herbivory Experiments

Initially, we collected *P. producta* from Friday Harbor lab docks via net during both high and low tides. A total of 12 specimens were collected across a five-day period (June 27 to July 1, 2021). Specifically, crabs with at least one intact chela and as many legs as possible were selected. Afterwards, all kelp crabs were placed in a throughflow saltwater holding tank. Fresh algae were offered daily at 11AM consisting of green, red and brown that was collected at the dock of Friday Harbor Labs.

N. luetkeana blades were collected from TR (48.512°, -122.927°) and west of PC (48.563°, -123.022°). The blades from TR were grown in high flow velocity while the PC blades were grown in low flow velocity. Selected blades were then wiped down before weighing to eliminate potential epiphytes and bacteria, as studies have shown *Pugettia sp* reliance on chemical cues in the water column to search for food (Zimmer-Faust and Case 1982). 6 blades of kelp from each location -a total of 12 blades- were first weighed in grams to record the pre-exposure weight. Blades longer than 30 cm were selected to eliminate food limitation bias as studies have shown the use of visual cues to locate food in brachyurans (Knudsen 1964). In addition, smaller blades (<30 cm) were used as trial experiments have shown that kelp crabs could consume the whole blade of kelp within 24 hours.

Each crab was starved for 24 hours before the initiation of the experiment to ensure no influence of previous gut content on food selection. Afterwards, a whole blade from each environment was placed into the experimental container measuring 58.42 cm x 124.46cm x 15.23 cm with one kelp crab. The use of whole blades instead of cut pieces was to imitate in-situ conditions and to account for morphology as a method of herbivory resistance. Another tank of exact dimensions and no kelp crab was then set up to account for growth and natural tissue loss of *N. luetkeana* during the 24-hour experiment period. Natural growth of the bull kelp was not accounted for due to the 24-hour experiment period consistent with previous study conducted by Dobkowski et al. (2017). After the 24-hour feeding period, each kelp was removed, wiped down again and weighed to determine mass consumed by each kelp crab. The average, standard deviation, minimum and maximum biomass change was calculated along a one-tailed T-test and graphed RStudio (RStudio Team 2020) to show relative difference in herbivory resistance between the two different kelp localities. We performed a Paired Welch Two Sample t-test on the mass change (g) between PC blades and TR blades. Before performing the t-test, we made quantile-quantile plots to ensure that our data was normally distributed.

Results

Consistent with our hypotheses, blade area and blade position were significantly related to thickness; central blades were thicker ($p < 0.0001$), as were medial blades ($p = 0.004$) (Figure 2). We observed no significant relationship between site and undulation score, width, or thickness.

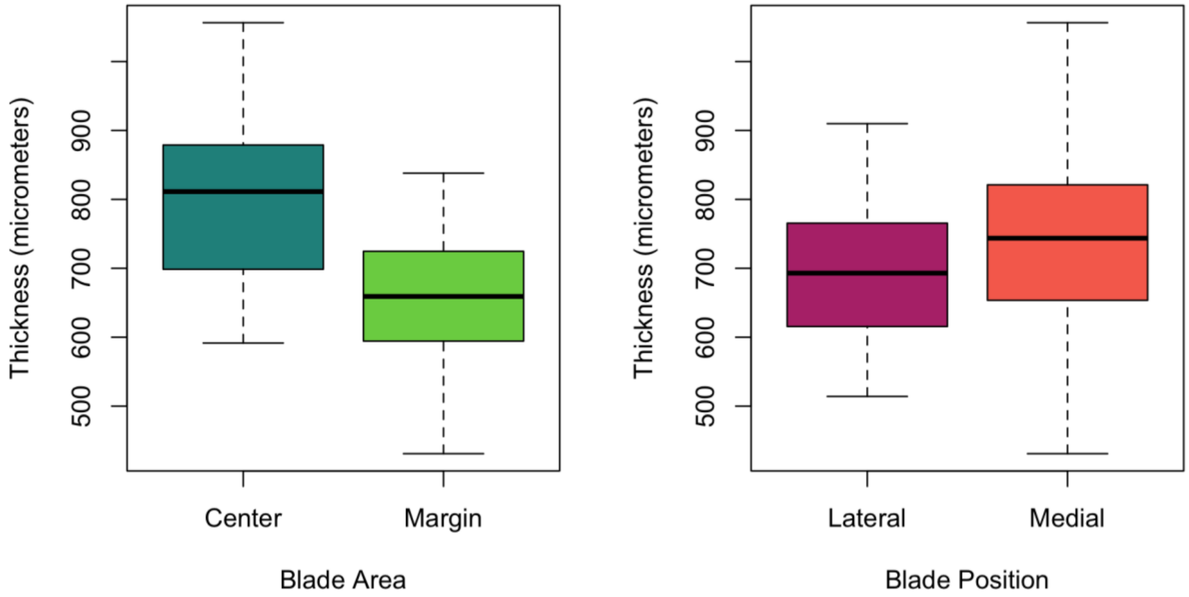

Figure 2: Comparison of thickness between blade area (central or marginal) and blade area (lateral or medial).

We observed significant differences in the amount of *N. luetkeana* consumed by kelp crabs based on the site from which blades originated. During feeding experiments, the mass change of blades from TR was significantly greater than that of blades from PC ($p = 0.02$) (Figure 3), indicating that blades from TR were consumed in greater amounts than blades from PC. This is consistent with our hypothesis that more kelp will be consumed from TR compared to PC due to environmentally driven difference in chemical/morphological construction.

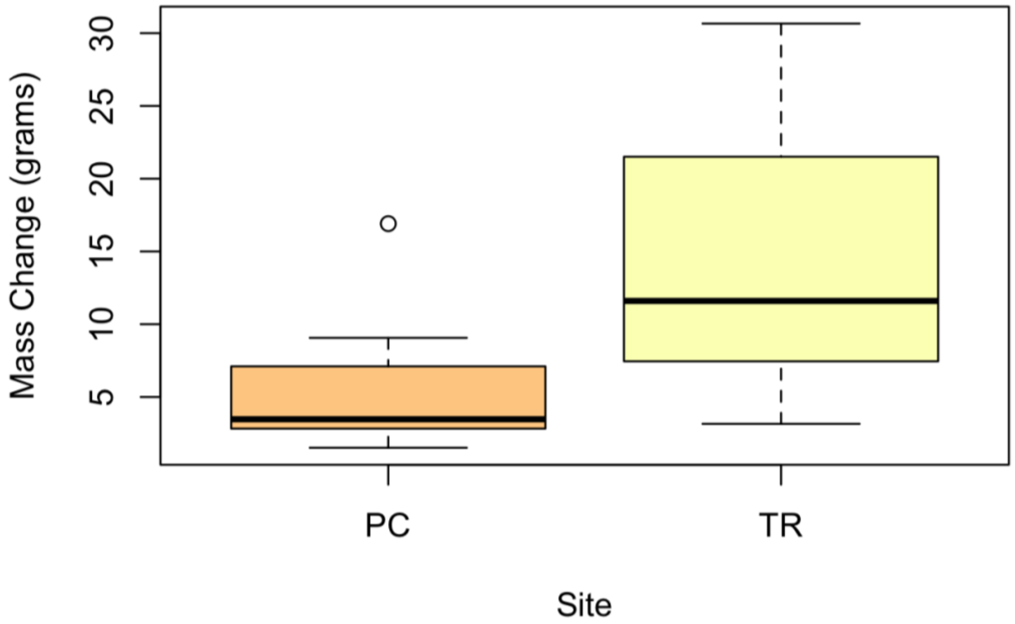

Figure 3: Boxplot of the mass change (g) due to kelp crab consumption of *N. luetkeana* blades from PC and TR.

While we found few significant morphological relationships, our models indicate trends consistent with our hypotheses. Thickness was best modeled by blade area and blade position; site was not supported as a covariate (Table 1). Thickness was lower on blade margins (± SE = 23.16, t = -4.98, df = 67, $p < 0.001$), and higher in medial blades (± SE = 26.04, t = 2.11, df = 67, $p = 0.039$) (Figure 2). We found that undulation did not affect blade thickness, regardless of blade area (± SE = 3.55, t = -0.995, df = 266, $p = 0.32$) (Table 1). Our best supported model of undulation included site and total length nested in site, where total length differed in its effect on undulation by site (Table 2). Blades at TR had fewer undulations (± SE = 2.41, t = -2.58, df = 11, $p = 0.026$) and total length was negatively correlated with undulation at PC (± SE = 0.012, t = -2.76, df = 11, $p = 0.018$). For blade width, we chose our second most supported model, because our most-supported model failed residual diagnostic tests. This model also included site and nested total length (Table 2). Blades were more narrow at TR (± SE = 1.96, t = -2.61, df = 11, $p = 0.024$) (Figure 3) and total length did not affect blade width (± SE = 0.0035, t = -1.21, df = 11, p = 0.25). For total length, our best supported model had two covariates: site and width (Table 2). This model indicated no relationship between total length and site (± SE = 79.19, t = 0.77, df = 12, $p = 0.45$) or total length and width (± SE = 18.89, t = -1.73, df = 12, $p = 0.11$).

Table 1: Models of blade thickness. *Indicates a nested interaction. The delta AIC of the last two models were analyzed separately from the first six models.

Model Specification	**AIC**	**delta_AIC**
thickness ~ blade area	862.27	2.49
thickness ~ blade area + blade position	859.77	0
thickness ~ blade area + blade position + site	861.50	1.73
thickness ~ blade area*site + blade position	863.39	3.62
thickness ~ blade area + blade position*site	860.92	1.15
thickness ~ blade area*site + blade position*site	862.81	3.04
thickness ~ undulation*blade area + blade area + blade position	3289.33	1.95
thickness ~ undulation + blade area + blade position	3287.33	0

Table 2: Models of three morphological characteristics: undulation, width, and total length. Delta AIC was calculated within each group of models pertaining to a distinct response variable.

Model Specification	**AIC**	**delta_AIC**
undulation ~ site	63.08	4.34
undulation ~ site + width	61.79	3.05
undulation ~ site + width*site	61.81	3.06
undulation ~ site + total length	62.98	4.24
undulation ~ site + total length*site	58.74	0
undulation ~ site + total length*site + blade position*site	61.90	3.16

width ~ site	55.24	3.98
width ~ site + undulation	53.95	2.69
width ~ site + undulation*site	55.83	4.57
width ~ site + total length	53.90	2.64
width ~ site + total length*site	52.63	1.37
width ~ site + total length*site + blade position*site	51.26	0
total length ~ site	183.86	1.33
total length ~ site + undulation	183.77	1.24
total length ~ site + undulation*site	184.37	1.84
total length ~ site + width	182.52	0
total length ~ site + width*site	184.48	1.95
total length ~ site + width*site + blade position*site	187.69	5.16

Discussion

Contrary to our original predictions, the spatial properties of each blade (blade area and position) proved to be greater determinants of morphological characteristics (width, undulation and thickness) than flow velocity.

Medial blades were significantly thicker than lateral blades. Previous studies have not compared the thickness of medial versus lateral blades. However, existing literature does address differences in morphology based on blade position in the wider macroalgal bed. If individuals in the center of kelp beds are buffered in some way by surrounding conspecifics—driving differences in their morphology—then similar variation might be observed between medial and lateral blades, which are relatively more exposed. Stewart et al. (2009) found that in the summer months, the macroalgae *Macrocystis pyrifera* was both denser and faster-growing on the edge of the kelp bed versus the center of the bed. Stevens et al. (2019) found that the biomass of central-bed *M. pyrifera* blades was lower than that of marginal-bed blades, confirming higher density on bed margins but not variation in thickness. If we extrapolated these results to our medial-lateral blade comparison, we would expect lateral blades to be denser and faster-growing. However, we would also need to know if increased growth rates and density were correlated with thickness in *N. luetkeana*. There may be a trade-off between high growth rate and blade thickness if sunlight or nutrients are limited. Stephens and Hepburn (2016) found that *M. pyrifera* blades enriched with nitrogen grew thicker, not longer. Higher nutrient availability towards the central axis of *N. luetkeana* may explain increased thickness in medial blades.

We also found that the center of the blades was thicker than the margin of the blades. This is consistent with existing literature on undulation in *N. luetkeana* blades. Koehl et al. (2008) found that the edges of undulated blades grew more quickly than their midlines. Undulated blades are thinner than flat blades because high blade thickness prevents elastic buckling (Koehl et al. 2008). Because undulation is much less pronounced in the center of the blade compared to the margins, the center does not have to be as thin to support its morphology. While thin sections of blades and consequent undulation increases light exposure and gas exchange (Hurd et al. 1997, Hurd and Stevens 1997, Koehl et al. 2008), thick sections of blades provide structural integrity and resist breakage (Rodriguez et al. 2016). Thus, thinner margins and thicker centers may be adaptive for *N. luetkeana*.

As to why thickness did not vary with site, existing literature does not suggest a uniform pattern between thickness and flow velocity across macroalgal species. Gerard and Mann (1979) found that sugar kelp *Saccharina latissima* from protected sites had significantly thinner blades than those from exposed sites, while Gerard (1987) found that the central and marginal blade thickness of *S. latissima* was unaffected by differences in mechanical loading (where weights are attached to blades). Molloy and Bolton (1996) examined the split-fan kelp *Laminaria pallida* in different levels of water motion, and found that blades were thicker when exposed to high flow velocity. Considering *N. luetkeana* in particular, Coleman et al. (2020) found no relationship between thickness and mechanical loading. The response of individual thickness to flow velocity may be species-specific; in that case, our results are consistent with existing literature on *N. luetkeana.*

Coleman et al. (2020) also found that increased mechanical loading caused *N. luetkeana* blades to become narrower and less undulated, in agreement with existing literature (Koehl and Alberte 1988, Koehl et al. 2008). We are uncertain as to why flow velocity did not affect the width or undulation of blades in our study. Our study had several limitations. Firstly, there was a bias in blade length, where blades less than ~50 cm were not used to standardize the length of blade at which width was measured. Secondly, we were unable to account for whether blade deterioration was due to natural causes or herbivory. Third, width measurements were not standardized. Each blade width was measured 50 cm above the blade origin, and not at a distance proportional to the blades length. Furthermore, it is also possible that our sample did not include enough con-specific variation; we only collected blades from 5 individuals at TR, and 3 individuals at PC. While multiple blades were collected from each individual, these are not true replicates. It is possible that with a larger sample size, we would have a more accurate view of morphological variation in width and undulation between the two sites. This is likely the case, because linear models of our data point to trends consistent with existing literature on flow velocity and morphology.

Trends in undulation between the two sites show that blades at TR (high flow velocity) were less undulated than blades at PC (low flow velocity), which echoes existing literature (Koehl and Alberte 1988, Koehl et al. 2008). Our models indicate that blades were narrower at TR than at PC, in agreement with previous studies. The models also indicate that in the low flow environment, longer blades were less undulated. This agrees with Coleman and Martone (2020), who found that *N. luetkeana* blades with less undulation were longer than those with more undulation. Our models also showed that blade length was unexplained by flow velocity or width. This deviates from Coleman and Martone (2020), who found that long, flat *N. luetkeana* blades arose under increased mechanical loading. However, models of blade length should be considered cautiously, given the limitations mentioned above. Generally, the trends we observed in width and undulation agree with past literature concerning the effect of flow velocity on *N. luetkeana* morphology.

Blade morphology may have mediated the interaction between flow velocity and kelp crab herbivory. In our feeding experiments, the mass of *N. luetkeana* blades from TR decreased significantly more than the mass of blades from PC ($p = 0.02$). We were able to reject the null hypothesis given df= 10 with 95% confidence interval.

Assuming that deterioration rates were equal for blades from both sites, blades from TR were consumed significantly more than blades from PC. Previous papers on the usage of both chemical and morphological traits as herbivore deterrents by tropical algae shed light onto the what could be responsible phenomenon observed in this study. In the tropics, algae usually use a combination of secondary metabolites and morphological defenses, such as a calcified thalli, to ward off potential predators (Valerie and Hay 1986).

The method used by kelp crabs to consume blades during our experiment highlights the interaction between morphology and herbivory. While feeding, our kelp crabs tore small strips, with both chelae, lengthwise from the margin of each blade. This feeding method often left notch-like marks on the kelp blade. Dobkowski et al. (2017) study also noted similar shredding behaviors in which the crabs shredded algae of different morphology (*Nereocystis* sp., *Macrocystis* sp., *and Egregia* sp.) in choice experiments. Eventually, the blades from TR were completely fragmented. In contrast, *N. luetkeana* from PC remained intact through the feeding experiment. The feeding method of kelp crabs influences the *N. luetkeana* biomass lost via mechanical damage, and it is possible that blade morphology mediates this interaction.

N. luetkeana blade morphology may serve as an adaptive trait against mechanical erosion and herbivore consumption. Blades from TR tended to be narrower and less undulated than blades from PC. These stream-lined characteristics may have made blades from TR easier to consume, given the strip-tearing method used by kelp crabs; it is possible that undulations (an uneven surface) make the tearing-method more energetically demanding. While collecting field samples, we did observe that blades from PC had more overall damage than blades from TR. So while *N. luetkeana* from PC may be less appealing to kelp crabs, it has possibly developed morphological deterrents in response to significantly higher rates of herbivory than exist at TR. Further research should address whether flow velocity alone drives gradients in herbivory of *N. luetkeana*.

Internal and external chemical cues may also have influenced our results. One secondary metabolite that might influence feeding preference in temperate environments is phlorotannin; if blades from PC produced phlorotannin as a chemical defense, kelp crabs may have avoided them. Swanson and Fox (2007) found that *N. luetkeana* produced higher levels of phlorotannin in carbon-enriched environments, suggesting that chemical defenses secreted by our specimens may have influenced herbivory preferences. However, Dobkowski et al. (2017) found that when given *N. luetkeana* and *M. pyrifera*, kelp crabs still consumed *N. luetkeana* despite its elevated levels of phlorotannins. These results reveal heavier reliance on physical or environmental anti-herbivory characteristics, rather than chemical defenses, such as flow velocity and morphology. That being said, the study also stated that results were correlative, and not all secondary metabolites are used for defense against herbivores. More testing with isolated metabolites should yield more accurate interpretations.

Our results may also be explained by the difference in C:N ratio preference of kelp crabs. Herbivores such as kelp crabs are limited by nitrogen (Mattson 1980). Kelp crabs might select for kelp with a low C:N ratio, shifting the results of this study. Since there were no chemical compositions tests on the kelp in our study, we cannot conclude the role of C:N ratio between the two localities (PC and TR) influencing the difference consumed by the kelp crabs. Future studies on the effects of C:N ratios can shed light on the topic of nutritional preference of kelp crabs in the Salish sea and be applied to other locations.

One substantial limitation of our herbivory experiments is that the shapes (length, width, thickness) of blades used from TR and PC were still uneven, even though all blades were >50 cm long. Additional experiments can involve more standardized selection and measurement protocols to ensure kelp size consistency and blades from a diversity of thalli in each collection location.

Our results elucidate the influence of flow velocity on the morphology of *N. luetkeana* blades, and in a larger sense, the landscape of subtidal habitats. Furthermore, we show that abiotic conditions, and resulting morphological characteristics, may mediate trophic interactions between macroalgae and herbivores. This is of particular relevance for marine biodiversity in Puget Sound, WA. Demersal crustaceans, such as kelp crabs, are commonly consumed by juvenile rockfish in the genus *Sebastes* (Murie 1995). Juvenile rockfish also take refuge within beds of macroalgae for protection from predation (Larsen 1972). Declining rockfish populations in Puget Sound due to historic exploitation (Williams et al. 2010) create a negative feedback loop, where increasing abundances of kelp crabs reduce macroalgae biomass, which in turn leads to higher juvenile rockfish mortality who no longer have a sheltered habitat. Due to increased herbivory, anti-herbivory morphologies may become more prevalent in *N. luetkeana* populations. Given each population's abiotic environment, not all populations may be able to evolve these morphologies, and may turn to other defenses (secondary metabolites, etc.) to resist increased herbivory pressures.

Whether due to abiotic or biotic shifts, changes in macroalgal structure matter. Kelp forests, like the ones formed by *N. luetkeana*, are integral to their ecosystems. They are nurseries for juvenile fishes (Holbrook et al. 1990, Tegner and Dayton 2000), sheltered regions for commercially important fishes (Bologna and Steneck 1993), and ecosystem engineers (Jones et al. 1994), altering the nutrient, sediment and flow regimes of their environment. These ecosystem services are under threat from a variety of sources. High wave action due to increasingly frequent storms thins kelp forests (Reed et al. 2011). The now-familiar phenomenon of overgrazing by uncontrolled sea urchin populations—a consequence of overfishing—results in homogenous urchin barrens (Steneck et al. 2002). Further, the physiological stress induced by changing ocean chemistry is correlated with increased disease prevalence in macroalgae (Teagle et al. 2017). Given the diversity of ecological roles played by macroalgae, the health of macroalgal communities affected by these threats reflects the health of their environment as a whole. We should invest in understanding the complex role macroalgal landscapes play in coupling natural processes for the sake of maintaining productive ecosystems.

Acknowledgements

We are grateful for the contributions of Tom Mumford, Wilson Freshwater and Miranda Roethler for their significant assistance throughout our project. Secondly, Ross Whippo contributed greatly to our data collection efforts. We would also like to thank Friday Harbor Labs for giving us the opportunity to use their facilities to conduct our experiment.

H.C. conceived of the project's morphology component, and S.W. conceived of the project's herbivory component. S.W. and H.C. both carried out *N. luetkeana* sampling, H.C. carried out the majority of morphology measurements, and S.W. carried out the feeding experiments. H.C. created figures and performed all data analysis. S.W. wrote sections concerning herbivory, H.C. wrote sections concerning morphology and broad subject overview, and both worked together to merge sections.

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Supplementary Material:

1) Herbivory Data:

	Weight before (g)		**Weight after (g)**	
Crab Trial	**Low flow**	**High flow**	**Low flow**	**High flow**
1	64.37	42.47	61.69	33.13
2	81.33	75.61	75.63	68.18
3	93.71	89.34	85.2	58.68
5	49.98	71.76	52.23	64.29
6	192.05	120.74	189.08	107.45
7	97.42	130.1	88.36	106.3
8	184.17	127.51	167.26	124.36
9	96.69	200.86	98.198	191.72
10	77.52	197.35	73.14	171.13
11	70.05	111.33	66.87	108.04
12	52.57	104.13	49.1	92.53

2) Morphology Data: Thickness

margin_1	**margin_2**	**center**	**Site**	**Blade_position**
25.1	25.3	32.3	TR	L
23.9	25.1	32.2	TR	L
25	26.4	31.7	TR	L
21.8	22	25.4	TR	L
28.1	26.8	29.9	TR	L
17.2	24	25.5	TR	L
22	21.6	23	TR	L
21.5	23.9	22.9	TR	L
26	26	29	TR	M
14.4	16.2	21	TR	M
24.8	24	31.4	TR	M
25.5	32	36.9	TR	M
25	19	26	TR	M

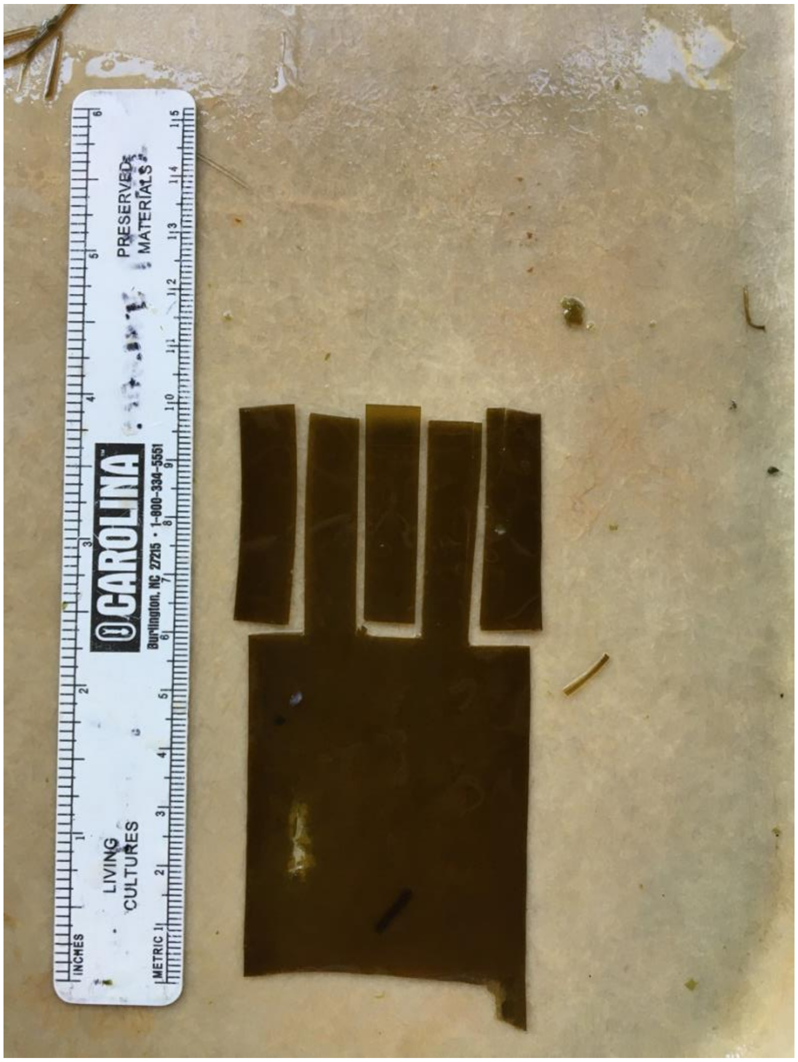
29.5	30	32.1	TR	M
22	29.5	31	TR	M
24.9	23.1	28.8	TR	M
23	27.8	28.8	TR	M
18.7	21.5	22.8	TR	M
23.5	24.7	26.8	TR	M
19.8	16.7	22.1	PC	L
30.9	20.5	29.8	PC	L
20.5	21	29.2	PC	L
23.5	28.8	30.8	PC	L
23	19.9	22	PC	L
21.6	19.6	26.9	PC	L
19.6	19.7	24.7	PC	L
19.3	20.1	22.7	PC	L
20.5	23	24.9	PC	M
22	18.1	21.9	PC	M
21.9	24.9	31	PC	M
32.1	26.2	28.5	PC	M
24	22.4	27	PC	M
22	22.5	36.1	PC	M
30.5	26	37.5	PC	M_short
28	29	32.4	PC	M_short

3) Morphology Data: Width + Undulation

blade.position	width	Total Length	Ruffle Length	Site.Indiv
M	6.1	279	27	TR.1
M	3.6	125	NA	TR.1
M	3.4	206	25	TR.2
M	3.9	231	26	TR.2

M	5.3	523	25	TR.3
M	4.9	371	25	TR.3
M	4.5	374	27	TR.4
M	5.2	328	25	TR.4
M	5	376	26	TR.5
M	6.2	372	26	TR.5
M	10.2	110	28.3	PC.1
M	8.2	228	25	PC.1
M	8.3	208	29.5	PC.2
M	9.3	157	27.5	PC.2
M		45	NA	PC.3_short
L	7.6	256	25	TR.1
L	5.1	149	28	TR.1
L	5.8	312.2	27.5	TR.2
L	4.1	289	27	TR.2
L	4.2	591	25	TR.3
L	5.1	469	25	TR.3
L	5.6	200	25	TR.4
L	4.5	296	25	TR.4
L	9.5	284	27	TR.5
L	6.8	106	25	TR.5
L				
L	7.4	319.6	26.5	PC.1
L	4.6	95	25.1	PC.1
L				
L	8.7	125	26.8	PC.2
L	10.4	84	26	PC.2
L				
L	11.3	93	32.9	PC.3
L	8.8	46		PC.3_short

4) Cross Section Area:



5) Undulation: