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RESEARCH ARTICLE

Coastal upwelling may strengthen the controls of herbivory and light over the population dynamics of *Hedophyllum sessile* in the Oregon rocky intertidal

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Abstract

Survival of early life history stages is critical to the successful establishment of benthic populations. Although light availability and herbivory are likely to influence the passage of marine macroalgae through a “recruitment bottleneck” at the sporeling stage, the interactive effect of these factors on subsequent community patterns of macroalgae is not well studied. We experimentally tested the effect of light and grazing on sporelings of the common intertidal kelp *Hedophyllum sessile*. Studies were conducted at two sites along the Oregon coast: Strawberry Hill (an intermittent upwelling region) and Cape Blanco North (a persistent upwelling region). Herbivory and light availability were manipulated and kelp performance metrics (density and length) were measured monthly from May to November 2019. We found that the effects of herbivory and light availability were pronounced at Cape Blanco North but negligible at Strawberry Hill. At Cape Blanco North, herbivory had strong but opposing effects on the density and length of *H. sessile*. Kelp density was higher in treatments without herbivores while kelp length was greater in treatments with herbivores. Responses also differed with the life history stage. Herbivory had negative effects on juvenile kelp but positive effects on adult kelp while light availability had opposing effects on the length of juvenile and adult kelps. The length of juvenile kelps was higher in shaded treatments while the length of adult kelps was higher in unshaded treatments. Our study highlights the potential importance of coastal geophysical processes (and subsequently, nutrients) in modifying herbivore and light effects on population dynamics of *H. sessile*, and how these dynamics may be further influenced by different characteristics of the kelp (i.e., demographic traits and life history stages).

KEYWORDS
bottom-up, coastal upwelling, herbivory, kelp populations, life history stage, light availability, Oregon, rocky intertidal, shading, top-down

TAXONOMY CLASSIFICATION
Population ecology

1 | INTRODUCTION

Species occurrence and persistence in an ecosystem are based on its recruitment success (Santelices, 1990). Recruitment of marine macroalgae is a complex process that involves dispersal, settlement, germination, and survival. Due to different physiological and morphological requirements, each life stage (gametophytes and sporophytes) of benthic macroalgae is subjected to varying environmental influences (i.e., light, nutrients, temperature, and water quality). Survival of early life history stages is critical to the successful establishment of benthic populations (Vadas et al., 1992). Within each stage, biological interactions such as herbivory can interact with environmental factors to increase variance in recruitment (Deysher & Dean, 1986). Light can have a strong effect on macrophyte performance, and the combination of light availability and herbivory can control the passage of marine macroalgae through a "recruitment bottleneck" at the sporeling stage. However, the influence of these interactive effects on subsequent community patterns of macroalgae is not well studied (Lotze et al., 2001).

In marine intertidal communities, extensive studies show that benthic grazers play an important role in determining macroalgal assemblages (Poore et al., 2012; Sellers et al., 2020). Changes in bottom-up inputs such as nutrient levels or propagule supply can affect the reproduction, settlement, and growth of macroalgae and the activities of herbivores and, hence, the interactions between them (Lubchenco & Gaines, 1981). For example, molluscan herbivores were found to have the greatest effect on Laminariales in intertidal rocky reefs (Poore et al., 2012). These grazers can consume spores and juveniles of macroalgae, thereby reducing their biomass (Coleman et al., 2006; Hawkins & Hartnoll, 1983; Jenkins et al., 2001). Moreover, Chenelot and Konar (2007) found that grazing by limpets produced greater damage on tissues of juvenile subtidal kelp *Nereocystis* than on older individuals. If this grazing strategy intensifies beyond a threshold, herbivores can reduce population density, decrease community diversity, and alter early community succession patterns (Benedetti-Cecchi & Cinelli, 1993; Lubchenco, 1978).

Despite the key role of water clarity in controlling the abundance and distribution of macrophytes, the community effects of benthic shading by phytoplankton blooms are less well known (Dennison, 1987; Dennison et al., 1993; Short & Wyllie-Echeverria, 1996). For example, Cosper et al. (1987) showed that decreased light penetration caused by "brown tide" algal blooms led to a substantial decline in biomass of temperate seagrass *Zostera marina*. Furthermore, experimental manipulation of shading to imitate light attenuation from dense phytoplankton blooms was found to reduce the growth rate and percent cover of intertidal kelp *Hedophyllum sessile* (Kavanaugh et al., 2009).

In upwelling ecosystems, nutrient pulses indirectly can underlie competition between phytoplankton and benthic macroalgae. Nutrients stimulate summer phytoplankton blooms which increase the turbidity of the water column, shading intertidal substrata (Kavanaugh et al., 2009). Such shading may create a "recruitment bottleneck" for the annual spring cohort of algal sporelings due to decreased light availability. Those sporelings passing through the bottleneck will grow into adults, thereby establishing the macroalgal community.

Grazing intensity is often also correlated with nutrient availability. High nutrients can stimulate the growth of benthic macroalgae, which through bottom-up effects can increase grazing intensity (Menge et al., 1999; Worm et al., 2000). In areas with high upwelling and frequent phytoplankton blooms, molluscan herbivores (snails, chitons, and limpets) can graze down sporelings and thus can also create a recruitment bottleneck (Lotze et al., 2000; Lotze & Worm, 2000), causing changes in community composition. Thus, the combination of shading and grazing may reduce sporeling survivorship, ultimately reducing adult density.

The Oregon rocky intertidal ecosystem is an excellent natural laboratory for the study of environmental and biological processes shaping kelp population dynamics due to its exposure to strong environmental gradients (i.e., temperature, desiccation, and coastal upwelling) over short spatial scales. Spiecker and Menge (2022) showed that the intertidal kelp, *Hedophyllum sessile*, had higher percent cover, maximum length, and growth rates in the southern region (Cape Blanco) where coastal upwelling was more persistent and nutrient levels were higher. Yet, kelp density was equivalent to or lower than that in the northern regions (Capes Foulweather and Perpetua). Because both light and grazing have been shown to be important factors affecting intertidal kelp, and are readily manipulated (e.g., using shades and exclusion methods), we designed a study to determine their effects on kelp density and length.

We hypothesized the following: (1) Grazing: Herbivores will preferentially graze on juvenile kelps, thereby reducing kelp population density, and will shorten juvenile kelp length. However, adult kelp performance metrics largely will be unaffected. (2) Light availability: Shading will reduce the density, and shorten the length of all kelp individuals. (3) Grazing x light availability: The interactive effects of high grazing and low light (i.e., at nutrient-replete and shaded regions) will be synergistic. That is, high grazing and low light combined will reduce density and shorten kelp more than each effect individually. We also hypothesize that the combined effects will be most severe for the juvenile kelps. (4) Upwelling: Compared to the intermittently upwelled site (in the Central coast region), the persistently upwelled site (Southern coast region) will have intensified grazing and lower light availability through bottom-up direct and indirect effects of upwelled nutrients, thus amplifying their detrimental effects on the kelp.

2 | METHODS

2.1 | Study system

We tested the effect of herbivory and light availability on established individuals and new recruits of *Hedophyllum sessile*, a common intertidal kelp species, at two sites along the Oregon coast.

Strawberry Hill is on Cape Perpetua [central Oregon] (44.25°N, 124.12°W) and Cape Blanco North is on Cape Blanco [southern Oregon] (42.84°N, 124.57°W). Kelp performance metrics (length and density) were measured monthly from April 2019 to November 2019 at Strawberry Hill. Because of delays due to logistical and weather difficulties, from June 2019 to November 2019 at Cape Blanco North, these capes differ in physical, biological, and geological features (Menge et al., 2015). Cape Perpetua is bordered by a relatively wide continental shelf, has retentive currents, experiences more intermittent upwelling, has lower dissolved inorganic nitrogen and higher phytoplankton levels, and is dominated by sessile invertebrates and non-canopy and turf-forming algae in the low zone. Cape Blanco's continental shelf is relatively narrow, experiences more persistent upwelling, has higher dissolved inorganic nitrogen levels, and is dominated by macrophytes in the low zone

2.2 | Experimental design

At both sites, 20 × 20 cm plots were established in the low zone where *H. sessile* and coralline species (e.g., *Bossiella plumosa* and *Corallina vancouveriensis*) were abundant. We specified this association because *H. sessile* relies on geniculate corallines to provide structural complexity for settlement (Barner et al., 2016). The fully crossed randomized block experiment consisted of two treatment factors with four replicates or blocks (light availability and herbivory) (Appendix S1: Figure S1). Each treatment factor had two levels: light availability (no shade/shade) and herbivory (present/absent).

Light level (shade) was manipulated using black plastic mesh (¼-in mesh openings and neutral spectral density). The mesh imitated natural shading by phytoplankton in the water column and attenuated light levels reaching benthic surfaces (e.g., Bertness et al., 1999; Kavanaugh et al., 2009). The mesh was attached to a PVC frame using cable ties. Stainless-steel all-thread support rods were inserted approximately 15 cm into holes drilled into the bedrock, and the rods were cemented into the holes with Z-spar marine epoxy (Koppers Splash Zone A-788 kit). The shading mesh was elevated approximately 20 cm over the rock surface using the rods to minimize wave resistance but allow access to the plots and reduce abrasion of the algae by the mesh at high tide. The mesh was also approximately 10 cm^2 wider than the plot to minimize edge effects (Appendix S1: Figure S1).

To quantify light levels in shaded vs. unshaded plots, at each site we placed four HOBO light/temperature sensors (ONSET Computer Corp., Part #: UA-002-64) underneath the mesh in the shaded treatments, and four sensors were placed near unshaded treatments. Light/temperature sensors were recorded continuously at 30-min intervals. Using the resulting data, we estimated that during a full tidal cycle (including immersion and emersion periods), the mesh attenuated light level at an average of 64% and 59% (i.e., 100 − [mean shaded light intensity/mean unshaded light intensity]*100) throughout the experiment at Strawberry Hill and Cape Blanco North, respectively.

Herbivory was manipulated by coating a square band of Z-spar marine epoxy (Koppers Splash Zone A-788 compound) placed around each plot with copper-based antifouling paint (Pettit Trinidad SR Antifouling Bottom Paint) (Appendix S1: Figure S1). Previous research has shown that such paint excludes “flat” grazers such as limpets and chitons (Cubit, 1984; Farrell, 1988; Menge, 2000; Menge et al., 1999; Paine, 1984; Sousa, 1979). The experiments were monitored monthly when damaged shades were repaired and fouling organisms were removed. To maximize the time available for experimental setup and monitoring at the low intertidal zone of these experiments, we did not establish paint controls. Since prior experiments in this system that did include such controls never found a paint artifact (e.g., Guerry & Menge, 2017; Menge et al., 1999; B. Menge, unpublished data), we believe this omission did not affect the robustness of our results.

Response variables in the experiment were monthly estimates of kelp density and length of each individual kelp thallus. Density was measured by counting all individual kelp present in the plots, including both the established ones and new recruits. The length of each individual was measured as the distance between the holdfast and the tip of the longest blade. Kelp density and length increments were standardized by subtracting the initial mean value at the beginning of the experiment (T_0) from the mean value at subsequent time points (T_n) for each replicate. These replicates then were averaged for each increment ($T_n - T_0$).

At both sites, we measured chlorophyll-a levels every month during the sampling period using bottle samples taken from the surf zone (Menge et al., 1997). We also quantified the abundance of small mobile species using the transect–quadrat method (e.g., Lubchenco & Menge, 1978; Menge, 1976). Surveys were conducted annually in the low intertidal zone (i.e., tidal height ± ~0.7 m) in June or July. The method involves visual sampling in 10 haphazardly chosen 0.25 m^2 quadrats per each of two to three sectors per site (e.g., Menge et al., 2011). Quadrats were spaced at ~3-m intervals along 30 m transects placed in the center of each zone parallel to the water's edge. Mobile organisms were then counted in each 0.25 m^2 quadrat to provide density estimates. We present data from 2016 to 2019 (Appendix S1: Table S1).

2.3 | Statistical analyses

To assess the effects of treatment and site on performance metrics of *H. sessile* (i.e., density and length), we used hierarchical linear mixed models (HLMM) to account for the fixed and random effects. Site, treatment, and the Site x Treatment interaction were fixed effects, and month and block were random effects. Restricted maximum likelihood and Kenward–Roger approximation corrections were used to minimize small sample size bias and prevent inflation of type I error rates. Model assumptions appropriate for each model (independence, homoscedasticity, and normality) were examined visually and all met the criteria except for the models analyzing kelp density and length of blades >10 cm. Models that violated the assumptions were log10 transformed. Transformed data were back-transformed to acquire interpretable least square means and standard error (using the delta method for SE; Ver Hoef, 2012)

Least square mean methods (LSM) were used for the multiple pairwise comparisons. Corrections were not applied for these comparisons because the contrasts were planned a priori with an intention of comparing the observed results with prior results in the literature. Furthermore, reducing the type I error for null associations may increase the type II error for those associations that are not null, which is a concern when important differences may be deemed non-significant (Feise, 2002; Perneger, 1998; Rothman, 1990). Thus, instead of corrections, we report precise *p*-values and standard errors. Software and code used for the analyses were SAS Enterprise Guide (SAS Institute Inc. 2013, Version 7.1, Procedure: MIXED)

3 | RESULTS

3.1 | Kelp density

The response of *H. sessile* density differed greatly between sites, with strong responses of density to herbivory and no response to light at Cape Blanco North but no response to either treatment at Strawberry Hill (Appendix S1: Tables S2A,B; Figure 1a,b). On average, at Cape Blanco North in unshaded plots, the *H. sessile* density increment was 2.99 ± 0.41 lower in +herbivore than in −herbivore treatments (LSM; $p_{(+\text{He}/-\text{Sh vs. }-\text{He}/-\text{Sh})} = .0009$). In shaded plots, the *H. sessile* density increment was 4.44 ± 0.77 lower in +herbivore than in −herbivore treatments ($p_{(+\text{He}/+\text{Sh vs. }-\text{He}/+\text{Sh})} < .0001$). In −herbivore treatments, density tended to increase more in shaded than unshaded plots (Figure 1b) but the difference was not statistically significant (Appendix S1: Table S2B, $p = .25$).

3.2 | Kelp length

At Cape Blanco North, similar results occurred with kelp length, except that on average thalli were longer, not shorter, with grazing and the effect of light remained negligible (Appendix S1: Tables S3A,B; Figure 2b). In contrast, neither herbivory nor light was important at Strawberry Hill (Figure 2a).

A more detailed analysis of Cape Blanco North results yielded more nuanced results with respect to herbivore and light treatments (Appendix S1: Tables S3A,B; Figure 2b). In unshaded plots, the average *H. sessile* length increment was 6 ± 1.57 cm greater in +herbivore than in −herbivore treatments (Appendix S1: Table S3B, LSM; $p_{(+\text{He}/-\text{Sh vs. }-\text{He}/-\text{Sh})} = .0002$). In shaded plots, the average kelp length increment was 5 ± 1.57 cm greater in +herbivore than in −herbivore treatments (Appendix S1: Table S3B, LSM; $p_{(+\text{He}/+\text{Sh vs. }-\text{He}/+\text{Sh})} = .0018$).

Partitioning kelp recruit lengths into "adult" (>10 cm length) and "juvenile" (<10 cm length) size categories (Van Alstyne et al., 1999, 2001) offered additional insight into the roles of herbivory and light. Across the growth season in unshaded −herbivore plots, the number of juveniles increased from June to August and declined in September (Figure 3a; yellow bars), while the number of adults

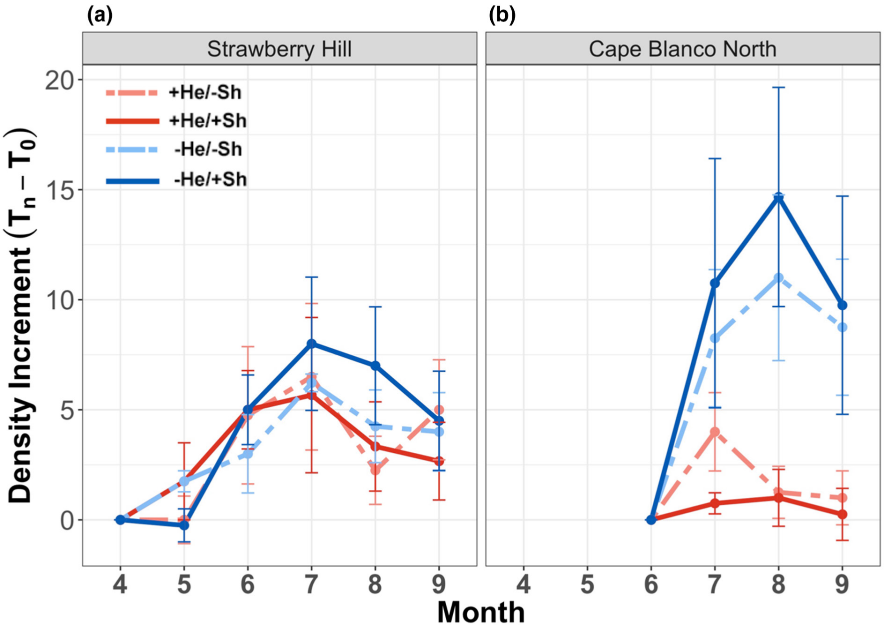

FIGURE 1 The effects of herbivory and light availability on *Hedophyllum sessile* density across months. Average density increment (number of individuals per 0.04 m^2) at (a) Strawberry Hill and (b) Cape Blanco North. Kelp density increments were standardized by subtracting the initial mean value at the beginning of the experiment (T_0) from the mean value at subsequent time points (T_n) for each replicate. These replicates then were averaged for each increment ($T_n - T_0$). All of the values are reported using arithmetic mean ± standard error. Treatments are denoted by the following: herbivore present/unshaded (+He/−Sh) = light red two dashes, herbivore present/shaded (+He/+Sh) = red solid, herbivore absent/unshaded (−He/−Sh) = light blue two dashes, and herbivore absent/shaded (−He/+Sh) = blue solid.

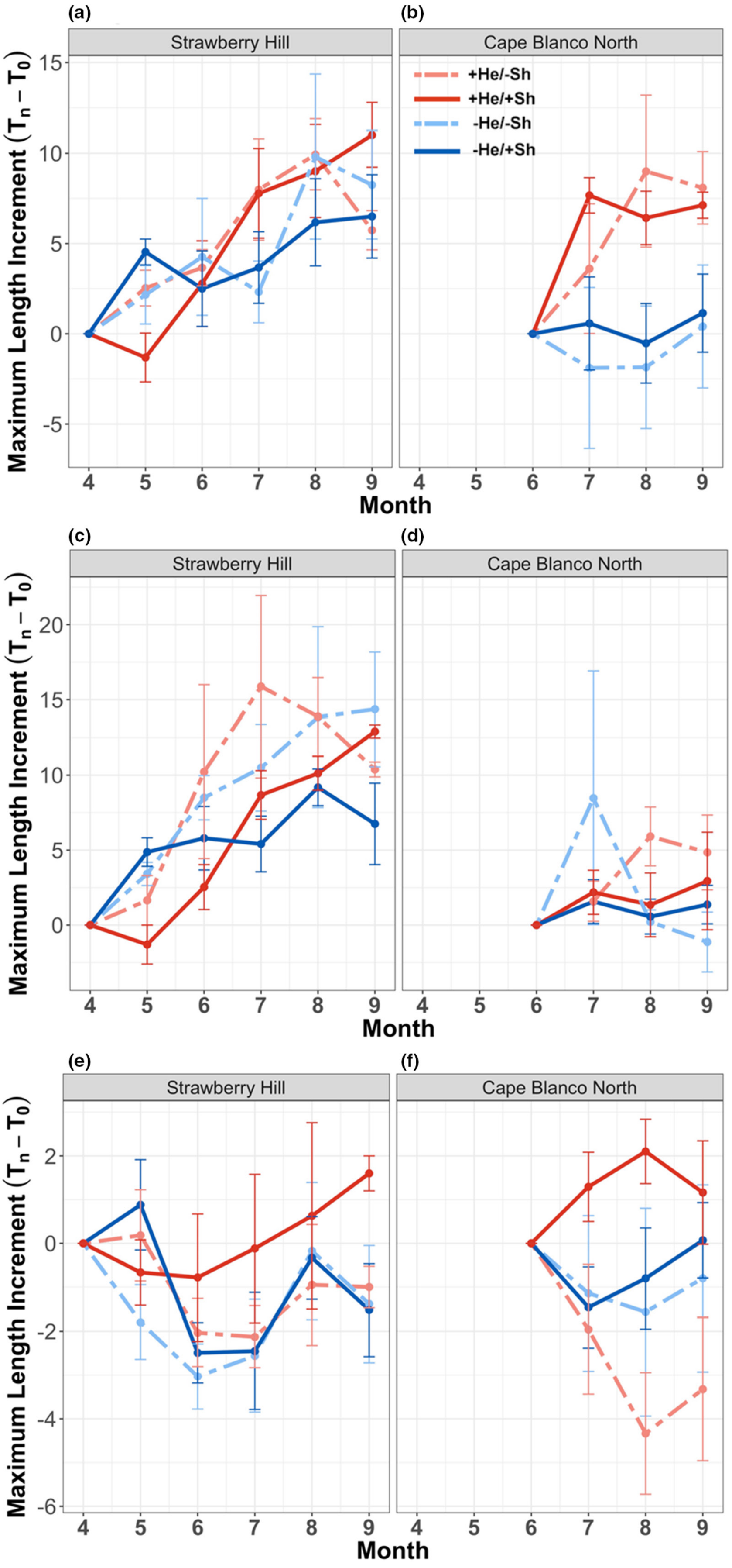

FIGURE 2 The effects of herbivory and light availability treatments on *Hedophyllum sessile* length across months. All sizes: Average length increment (centimeters per 0.04 m^2) for all kelp individuals at (a) Strawberry Hill and (b) Cape Blanco North. Large kelp (>10 cm): Average change in length (centimeters per 0.04 m^2) at (c) Strawberry Hill and (d) Cape Blanco North. Small kelp (<10 cm): Average change in length (centimeters per 0.04 m^2) at (e) Strawberry Hill and (f) Cape Blanco North. See Figure 1 caption for further details.

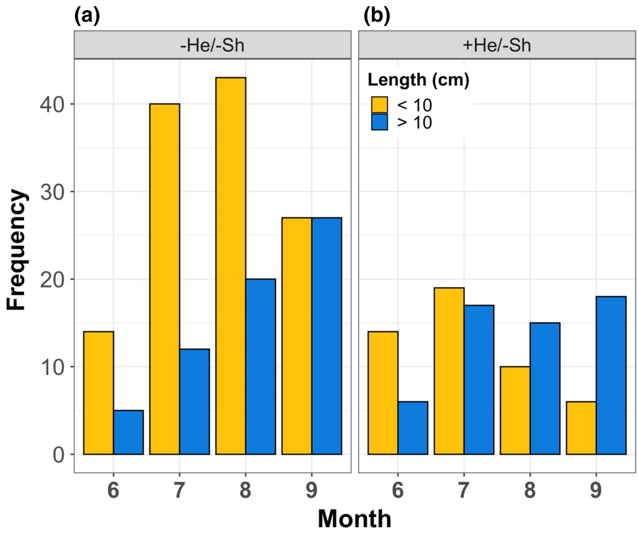

FIGURE 3 *Hedophyllum sessile* frequency per month in the Cape Blanco North unshaded plots without and with herbivores. Frequency (counts of length values per month) in (a) the herbivore absent/unshaded plots (−He/−Sh) and (b) the herbivore present/unshaded plots (+He/−Sh). Length size bins are as follows: Less than 10 centimeters = yellow solid, and over 10 centimeters = blue solid.

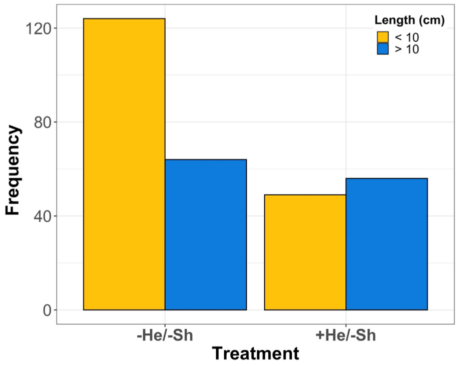

FIGURE 4 *Hedophyllum sessile* frequency across months in the Cape Blanco North unshaded plots without and with herbivores. Frequency (counts of length values across months) in the herbivore absent/unshaded plots (−He/−Sh) and the herbivore present/unshaded plots (+He/−Sh). See Figure 3 caption for additional details.

increased from June through September (Figure 3a, blue bars). In unshaded +herbivore plots, the number of juveniles increased from June to July and decreased from July to September while the number of adults increased from June to July and then persisted at a similar frequency from July through September (Figure 3b). This latter trend suggests that new recruits were grazed, thus limiting the number of juveniles growing into adults.

Combining across months indicates that herbivory effects in unshaded plots differed by size category (Figure 4). That is, juvenile kelp were more abundant in −herbivore plots and less abundant in +herbivore plots, indicating that grazing reduced juvenile abundance, while adults were less abundant in −herbivore plots and more abundant in +herbivore plots, indicating that grazing may facilitate adult abundance.

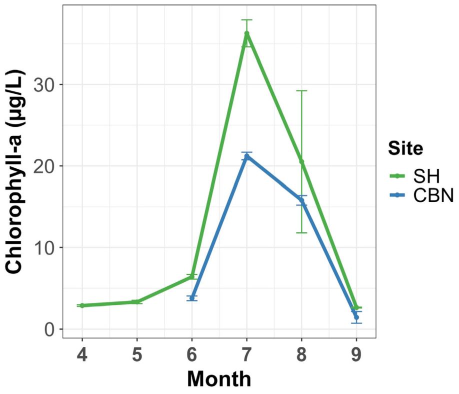

FIGURE 5 Chlorophyll-a levels at Strawberry Hill and Cape Blanco North throughout the experiment. All of the values are reported using arithmetic mean ± standard error. Sites are Strawberry Hill = green and Cape Blanco North = blue.

The division of experimental kelp individuals into juvenile and adult categories provided the first evidence of a light effect (Appendix S1: Tables S4A,B; Figure 2d,f). That is, while the effects of herbivory that emerged above remained the same, the effects of light availability became important but were opposite for the juveniles and adults. For adults, in unshaded +herbivore plots, the average length increment was 4.00 ± 0.80 cm greater than in unshaded −herbivore plots (LSM; $p_{(+\text{He}/-\text{Sh vs. }-\text{He}/-\text{Sh})} = .0035$), but only 2.23 ± 0.43 cm greater than in shaded −herbivore plots (LSM; $p_{(+\text{He}/-\text{Sh vs. }-\text{He}/+\text{Sh})} = .0732$). That is, shading tended to reduce the size advantage of adults (Figure 2d).

For juveniles, length increment was greatest in shaded +herbivore plots (Appendix S1: Tables S5A,B; Figure 2f). The average length increment of juveniles was 3.05 ± 0.86 cm greater in shaded +herbivore plots than in unshaded +herbivore plots (LSM; $p_{(+\text{He}/-\text{Sh vs. }+\text{He}/+\text{Sh})} = .0005$), and 1.53 ± 0.83 cm greater in shaded −herbivore than in unshaded +herbivore treatments (LSM: $p_{(+\text{He}/+\text{Sh vs. }-\text{He}/+\text{Sh})} = .0674$). That is, juvenile *H. sessile* tended to grow more in shaded +herbivore plots than in unshaded −herbivore plots (Figure 2f).

3.3 | Chlorophyll-a levels

Chlorophyll-a levels were consistently higher at Strawberry Hill than Cape Blanco North throughout the growing season, with levels at both sites peaking in July (Figure 5).

3.4 | Herbivore densities

The total abundance of the three grazer taxa (limpets *Lottia* sp., the chiton *Katharina tunicata*, and the sea urchin *Strongylocentrotus purpuratus*) was slightly greater at Cape Blanco North than at Strawberry

Hill (Appendix S1: Table S1). Limpet density was similar between sites with 11.8 ± 2.4 per 0.25 m^2 at Cape Blanco North and 19.9 ± 4.2 per 0.25 m^2 at Strawberry Hill. *K. tunicata* density also was similar between sites with 1.2 ± 0.1 per 0.25 m^2 at Cape Blanco North and 0.8 ± 0.1 per 0.25 m^2 at Strawberry Hill. However, *S. purpuratus* density was much higher at Cape Blanco North with 13.6 ± 1.6 per 0.25 m^2 compared to 0.6 ± 0.1 per 0.25 m^2 at Strawberry Hill.

4 | DISCUSSION

Survival and growth of important habitat-forming rocky-shore kelps are known to vary with abiotic and biotic variables (Davison & Pearson, 1996; Harley et al., 2012; Lubchenco & Gaines, 1981). Furthermore, interactions between a species and its environment can be species, life history stage, or even specimen specific. Our findings show that in addition to coastal geophysical processes, demographic traits (i.e., density as a representation of population survival, and length as a representation of growth) and life history stages (i.e., juvenile and adult) of *H. sessile* are crucial to understanding the mechanisms underlying kelp population dynamics in the Oregon rocky intertidal upwelling ecosystem. More specifically, differentiating our experimental results based on demographic traits and life history stages of the kelp revealed nuanced differences in the effects of herbivory and light availability.

A caveat to our conclusions is that we were unable to replicate our study at the site within-region scale. This limits inferences we can make with respect to geophysical modulation of regional effects of herbivory and light availability on kelp populations. However, extensive research has shown that, both physically and biologically, sites within each of these regions are very similar and very different between regions (Menge et al., 2015; Menge & Menge, 2013). That is, Strawberry Hill has similar dynamics and abundance patterns to those at other Cape Perpetua sites (Yachats Beach, Tokatee Klootchman) and Cape Blanco North has comparable similarities to other Cape Blanco sites (Cape Blanco South, Rocky Point). Thus, despite the fact that we cannot test regional (cape) effects in this study, we are confident that our study highlights the potential importance of coastal geophysical processes (and subsequently, nutrients) in modifying herbivore and light effects on population dynamics of *H. sessile*, and how these dynamics may be further influenced by different characteristics of the kelp (i.e., demographic traits and life history stages). Nonetheless, additional research with site-based replication would be welcome.

4.1 | Between-site differences

We found that the effects of herbivory and light availability were pronounced at Cape Blanco North but negligible (or non-significant) at Strawberry Hill. Why did results differ so greatly between sites? As suggested above, variation in geophysical features (i.e., coastal upwelling and continental shelf width) between these two sites may provide a mechanistic explanation for these results (Menge et al., 2015, Menge & Menge, 2013).

Because the continental shelf at Cape Blanco North is narrow (18–20 km) and the location of the study site at the tip of a prominent headland locally enhances the stronger upwelling winds, persistent coastal upwelling and strong offshore transport occur. At sites like Strawberry Hill, the continental shelf is wide (60–65 km), and the coastline is more or less linear. Here, upwelling is less persistent and currents are retentive. Average Coastal Upwelling Transport Indices (CUTI) from 1988 to 2020 show that upwelling is 4.5–6 times stronger and more persistent at Cape Blanco North (average CUTI for central (44°N) and southern Oregon (42°N): 0.062 ± 0.007 and 0.48 ± 0.01 (mean ± *SE*), respectively) (https://mjacox.com/upwelling-indices/).

Nutrient pulses, combined with retentive currents, at Strawberry Hill, can stimulate dense phytoplankton blooms, thereby lowering light availability (Kavanaugh et al., 2009). As a result of the between-site difference in currents and intensity of phytoplankton blooms (as reflected by chlorophyll-a levels sampled during our study), average light levels in unshaded plots during the immersion period were 34% lower at Strawberry Hill compared to Cape Blanco North (Strawberry Hill: 1722.53 lux and Cape Blanco North: 2303.63 lux).

The between-site difference in the strength of herbivory is more puzzling. Prior studies found that grazing impacts in the low zone were generally greater at Strawberry Hill and a nearby site, and weaker at Cape Blanco North and nearby sites (Freidenburg et al., 2007). In these experiments, the response variable was the percent cover of algae colonists (mostly diatoms, microalgae, and ephemeral algae) to cleared bare rock. In the present study, we focused on established recruits and adults of *H. sessile* occurring mostly in geniculate coralline algae (the favored recruitment substratum; Barner et al., 2016) rather than on early succession to cleared plots. In Freidenburg et al. (2007), limpets were the main grazers. In the present study, the occurrence of the kelp holdfasts in coralline algal turfs likely inhibited limpet grazing to some extent, and it is possible that the primary grazers were the large chiton *Katharina tunicata* and/or the sea urchin *Strongylocentrotus purpuratus*, for both of which *H. sessile* is a preferred alga (Burnaford, 2004; Dethier & Duggins, 1984; Paine & Vadas, 1969). However, the abundances of *K. tunicata* were similar between Cape Blanco North and Strawberry Hill, suggesting densities of the chiton may not be the most likely explanation for greater herbivory at Cape Blanco North. The higher urchin density at Cape Blanco North suggests that these grazers may have been responsible for the stronger grazing effects on kelp density at the southern site.

At Cape Blanco North, herbivory had strong but opposing effects on the density and length of *H. sessile*. Kelp density was higher in treatments without herbivores, while kelp length was greater in treatments with herbivores. Upon closer inspection of responses of different kelp life stages, we found that herbivores grazed directly on juvenile kelp thalli but likely on diatoms and microalgae attached to adult blades. Because young and old macroalgal tissues often have different palatability or anti-grazing characteristics, grazers usually preferentially graze on juvenile kelps over adults (Heaven & Scrosati, 2004; Taylor et al., 2002; Van Alstyne et al., 1999, 2001; Watson & Norton, 1985), thereby likely contributing to the negative density response (i.e., low density) to our treatments with herbivores. Furthermore, juveniles surviving grazing may benefit from grazing effects through reduction in density-dependent competition (Choi & Norton, 2005; Steen & Scrosati, 2004). In contrast to juveniles, adults likely benefit from grazing because grazers, in this case most likely small limpets and snails that forage on kelp blades, can remove light-intercepting epibionts from the fronds (D'Antionio, 1985; Duffy, 1990) and reduce the abundance of surrounding macroalgal competitors (Duffy & Hay, 2000), thereby minimizing shading.

Differentiation of adult and juvenile kelps provided further insight into the influence of light and grazing on *H. sessile*. Analyses using average length across all thalli (combining both juvenile and adult kelps) found that light had no effect on kelp length. This result is contrary to studies showing that shading (e.g., light attenuation by dense phytoplankton blooms) can reduce the growth and abundance of macrophytes (e.g., Dennison, 1987; Kavanaugh et al., 2009; Phillips et al., 1978). Analyses separating juvenile and adult life history stages, however, suggested nuanced differences in light effects. That is, juvenile kelp length was higher in the shaded +herbivore treatment than in the unshaded treatments, suggesting light inhibition, and the opposite was true for adult kelps in the unshaded +herbivore treatment.

The negative effects of light on juvenile kelps and positive effects of light on adult kelps may be explained by differences in physiological and morphological adaptations. Kelp can acclimate to different light conditions by means of different processes (e.g., changes in pigment content, regulation of photosynthesis, and changes in bio-optical tissue properties). For example, Xu et al. (2015) showed that both the maximum potential quantum efficiency of photosystem II and effective photosystem II quantum yields increase as the giant kelp *Macrocystis pyrifera* develops. Adaptations related to ontogeny have already been described for other Laminarians, showing, for example, that individuals have different age-dependent enzymatic capacities (Küppers & Kremer, 1978). As such, turnover rates of enzymatic proteins may cause differences in the photoacclimation and photoprotection responses of juvenile vs. adult sporophytes of *M. pyrifera* that will ultimately influence growth, as shown for other macroalgal species (Li et al., 2014; Vergara-Jara et al., 2010; Wahl et al., 2011). Furthermore, Altamirano (2017) reported low productivity and even mortality of juvenile sporophytes of *M. pyrifera* growing at either higher or lower irradiances to which they could not adapt. In short, adult kelps can utilize light more efficiently and have well-developed photoacclimation and photoprotection strategies in place against high light levels, thus potentially allowing the adult kelps in our study to grow or increase in length more as opposed to the juvenile kelps.

The strong negative response of juvenile kelps in the unshaded +herbivore treatments may be explained by exposure to light and its associated desiccation effects. Desiccation results in important losses of cellular water content, mainly triggered by the emersion periods from daily tide changes and exposure to high light (Abe et al., 2001; Burritt et al., 2002; Dring & Brown, 1982; Pearson et al., 2000; Shafer et al., 2008). Adult kelps can respond to desiccation stress and retain moisture by forming dense aggregations (Johnson et al., 1998) and closed canopies (Choi & Norton, 2005). However, juvenile kelps do not employ the same anti-desiccation adaptations as their adult counterparts. Several studies show that high density has negative effects on juvenile kelps (Choi & Norton, 2005; Steen & Scrosati, 2004). In short, juvenile kelps may be more prone to the harmful effects of desiccation than adult kelps and the juvenile kelps in our study may rely on shading to grow or increase in length.

Variability in coastal upwelling regimes has been shown to indirectly intensify grazing activity (Menge et al., 1999; Worm et al., 2000) and lower light availability (Kavanaugh et al., 2009) through bottom-up propagation of upwelled nutrients. Because of the strong bottom-up propagation at Cape Blanco North, herbivores (i.e., higher grazer density and grazing intensity) may negatively influence kelp populations through a reduction in their numbers. However, they may positively influence kelp individuals within the population by removing their surrounding competitors. At Strawberry Hill, in contrast, retentive currents may create intense phytoplankton blooms that persist throughout the spring/summer season and overwhelm the shading treatment, thus rendering the treatment ineffective in manipulating light availability. Furthermore, the area had a very low urchin density which may explain the lack of herbivore effects on kelp.

AUTHOR CONTRIBUTIONS

Barbara Spiecker: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); project administration (lead); resources (lead); software (equal); supervision (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Bruce A. Menge:** Conceptualization (supporting); funding acquisition (lead); resources (supporting); software (equal); writing – review and editing (supporting).

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CONFLICT OF INTEREST

The authors do not have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data (Spiecker & Menge, 2022) are available in Dryad: https://doi.org/10.25349/D9V61R.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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