Local environmental conditions predict spatial transitions in seaweed community composition in a rocky intertidal ecosystem

by

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Abstract

Kelp forests are considered the most vulnerable temperate marine ecosystems to climate change, and recent marine heatwaves have caused considerable kelp losses. Globally, heat stress has induced phase shifts from kelp to more heat-tolerant turf algae ecosystems with less structural complexity, resulting in a loss of food, habitat, and productivity. Currently, the relationships between temperature and intertidal kelp and turf species in the Northeast Pacific is not thoroughly understood, as majority of research has focused on subtidal kelp abundances over temporal scales. Here, I investigated how a spatial temperature gradient of ~6 ^{o}C, combined with local variation in wave energy at sites within Barkley Sound, Vancouver Island, B.C., influences the abundance of kelp and turf algal species in the rocky intertidal. High kelp cover was primarily observed at sites with the lowest water temperatures, and at sites with high wave energy relative to other sites with similar local temperatures but low wave energy. Accordingly, I found that the percent of kelp cover, as well as kelp diversity (measured as species richness, Simpson diversity, and Shannon diversity) were all significantly negatively influenced by temperature, and positively influenced by wave energy. No kelp species were found at sites above 15.8°C, and *Egregia menziesii* was the only species to be found across all sites that contained kelp. These results indicate that kelp is negatively influenced by increasing temperatures, and that high wave energy may act to ameliorate heat stress. In contrast, turf cover was significantly negatively correlated with kelp cover, such that turf cover was significantly greater at sites with higher temperature and lower wave energy. The results indicate that on a spatial scale, an increase in temperature, combined with variation in wave energy, significantly drives the absence of kelp species, and further the dominance of less structurally complex turf algae. These significant effects of local environmental variation could have implications for how

climate change may be negatively influencing the structural complexity of seaweed communities in the rocky intertidal.

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Introduction

Kelp (brown algae in the Order Laminariales) are globally important foundation species that thrive in nutrient rich temperate waters (Steneck *et al.*, 2002). Kelp provide the largest biogenic structures of any marine benthic system, and subsequently form the base of complex, productive ecosystems, in which they provide both habitat and food to a wide diversity of coastal organisms (Christie *et al.*, 2009; Teagle *et al.*, 2017). Kelp forest ecosystems also provide several critical social, economic, and ecological services, including aquaculture, fishing, tourism, coastline protection, climate control, and carbon sequestration (Vásquez *et al.*, 2014; Krause-Jensen and Duarte, 2016; Eger *et al.*, 2021). Since kelp function to ameliorate environmental stress for marine communities, these species have been predicted to increase in importance in maintaining ecosystem function in periods of environmental stress (Bruno *et al.*, 2003; Wernberg *et al.*, 2018).

As a result of increasing levels of anthropogenically-sourced atmospheric greenhouse gases, the world's oceans have warmed substantially, and marine heatwaves have also increased in frequency and intensity (Bindoff *et al.*, 2019). These respective chronic and acute heat stressors have negatively impacted kelp ecosystems globally, causing drastic declines in the local biomass and diversity of kelp species (Filbee-Dexter *et al.*, 2016, 2020; Thomsen *et al.*, 2019; Wernberg, 2021). Thermal stress-related kelp mortality is attributed to the physiological impacts of heat stress, as increasing temperature causes oxidative stress and induces damage to kelp tissue, resulting in a reduction of growth, increased dislodgement, reduced photosynthetic growth and reduced reproduction rates in a species-specific manner (Simonson *et al.*, 2015; Mabin *et al.*, 2019; Nepper-Davidsen *et al.*, 2019; Hollarsmith *et al.*, 2020). The immediate impacts of heat are not always apparent, as heat stress can induce depletion of nutrient reserves, reduction of metabolic capacity, and reduced genetic diversity at the population level, causing a lag in negative responses to temperature (Gerard, 1997; Wernberg *et al.*, 2018; Fernández *et al.*, 2021).

In many instances, kelp-dominated ecosystems (e.g. **Figure 1A,C**) have shifted towards turf algal seascapes (e.g. **Figure 1B,D**) as a result of chronic and acute heat stress (Filbee-Dexter and Wernberg, 2018; O'Brien and Scheibling, 2018; Wernberg, 2021). Ocean warming favours the proliferation of algal turfs, which are a broad category of more heat-tolerant algal species defined as dense communities of short-bladed algae with less structural complexity than kelp (Connell *et al.*, 2014). In North America, the primary observations of shifts from kelp to turf ecosystems have been in the Northwest Atlantic subtidal ecosystems, largely driven by multi-decadal increases in sea temperature, as well as severe marine heatwaves (Filbee-Dexter *et al.*, 2016; Dijkstra *et al.*, 2017; Feehan *et al.*, 2019).

Understanding whether a degraded turf algal state can be considered an 'alternative stable state' from kelp has been considerably well-researched, however the answer is specific to the context of the environmental drivers of the shift, as well as the possible feedback mechanisms at play (Filbee-Dexter and Wernberg, 2018). Feedback mechanisms involving the inhibition of kelp proliferation could suggest that a discontinuous phase shift has occurred, in which the forward shift has a different threshold level than the reverse shift to the original state, displaying a trend of hysteresis (Filbee-Dexter and Wernberg, 2018). For example, the formation of a turf reef can limit space for kelp settlement on rocky substrate (Connell and Russell, 2010), high sediment accumulation on subtidal turf reefs can reduce rates of germination and survival of recruits (Gorman and Connell, 2009), and due to lack of space on the rocky substrate, weak attachment of kelp recruits to turf blades may occur (Feehan *et al.*, 2019). Unlike shifts from kelp to urchin barren states, which have been well described as discontinuous (Konar and Estes, 2003; Filbee-

Dexter and Scheibling, 2014), shifts to turf reefs are not consistently described as such. The direct driver of the phase shift may be more significant, as rapid environmental changes drive collapse of kelp to turf reefs, which do not persist in the initial conditions (Filbee-Dexter *et al.*, 2016; Krumhansl *et al.*, 2016). Due to the constancy of climate change, these marine environments are likely to not be recovered in the same way that urchin barrens can be recovered by a rebound in predators of the herbivores that caused the initial decline (Filbee-Dexter and Scheibling, 2014; Filbee-Dexter and Wernberg, 2018). It is therefore useful to understand the environmental drivers that maintain dominance of kelp and turf to infer how turf ecosystems persist post-phase shift.

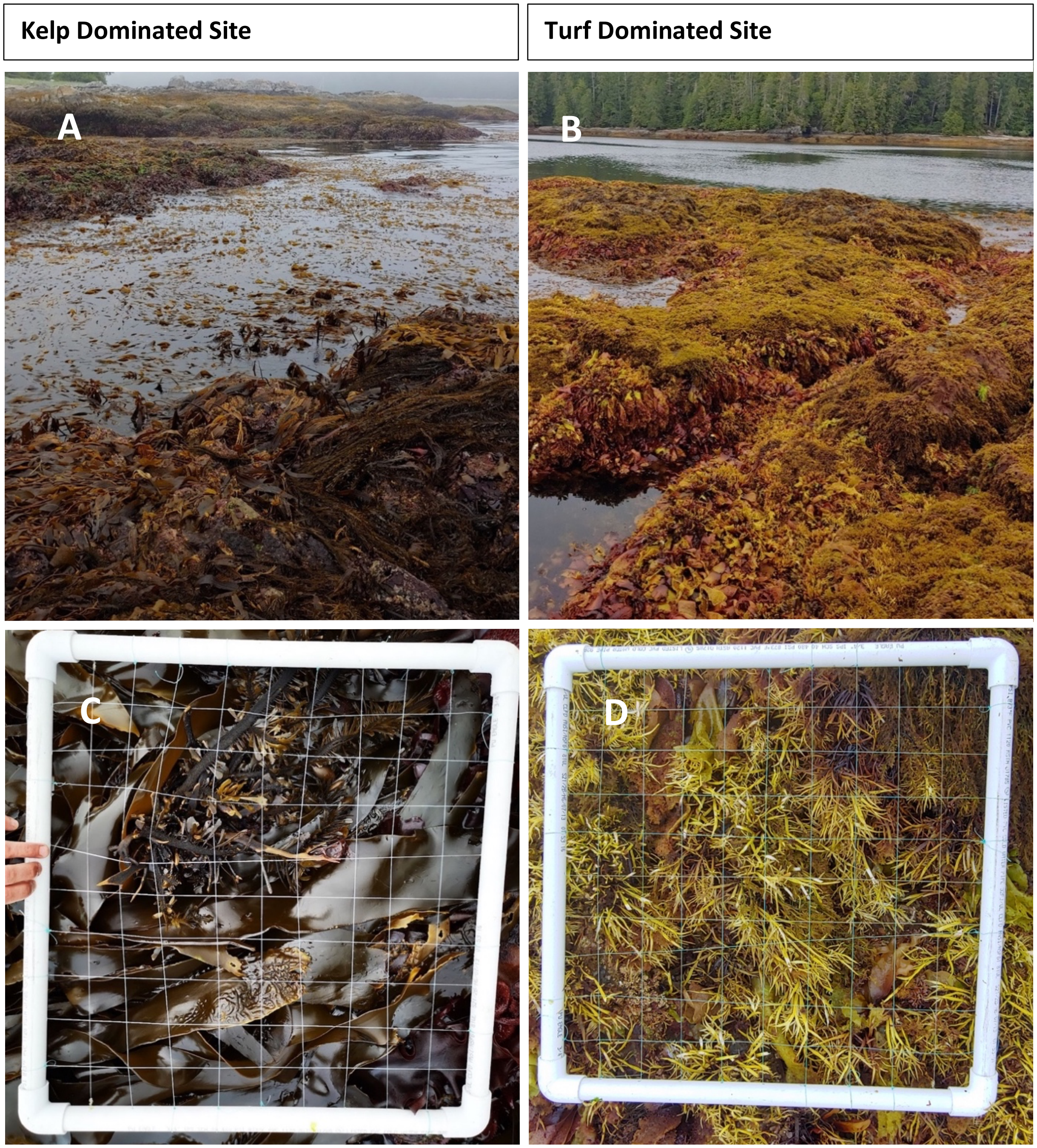

Figure 1. Images of an intertidal field site dominated by A) kelp and B) turf algae, and quadrats placed over substrate dominated by C) kelp (*Egregia menziesii* and *Hedophyllum sessile*) and D) turf algae (*Prionitis sp.* and *Neogastroclonium subarticulatum*).

Shifts to turf dominated ecosystems have negative consequences in terms of ecological productivity, as well as the structural complexity of habitats (Copertino *et al.,* 2005; Filbee-Dexter and Wernberg, 2018). Notably, shifts to turf have resulted in the reduction of annual net production per area by two to seven times, relative to the production of canopy-forming kelp (Copertino *et al.*, 2005). In addition to reduced productivity, turf algal shifts have reduced the structural complexity of ecosystems, resulting in habitat homogenization globally (Filbee-Dexter and Wernberg, 2018; Dijkstra *et al.*, 2019; Pessarrodona *et al.*, 2021). Even after correcting for increased surface availability, structural complexity of macroalgae has been shown to influence the number of species in a habitat (Matias *et al.*, 2010). Depending on the algal species assemblage, shifts to seascape structures that are architecturally more homogenous could have significant impacts on the availability of refuge from predators, as well as reduction in abundance of organisms that historically inhabited the region prior to the ecological shift (Graham, 2004; O'Brien *et al.*, 2018; Dijkstra *et al.*, 2019).

Given the projected increase of global average sea surface temperature (SST) under climate change (Bindoff *et al.,* 2019), and the value of canopy-forming kelp forests, there is a need to understand the environmental conditions that influence transitions from healthy kelp-dominated communities to less desirable turf seascapes. Shifts from kelp to turf ecosystems due to increasing SST have not yet been observed on intertidal ecosystems in the Northeast Pacific (Steneck *et al.*, 2013; Filbee-Dexter *et al.*, 2016). Despite greater exposure to environmental stress in the rocky intertidal relative to the subtidal regions, the mechanisms that maintain kelp and turf presence the intertidal are less understood (Filbee-Dexter and Wernberg, 2018; O'Brien and Scheibling, 2018). Persistence of kelp under environmental stressors can also vary spatially due to differences in fine scale environmental and biotic processes such as temperature and wave energy (Carnell and Keough, 2014; Krumhansl *et al.*, 2016; Cavanaugh *et al.*, 2019; Starko *et al.*, 2019). Unlike other marine foundational species, variation in local, rather than global, stressors dominate the dynamics of kelp distributions (Krumhansl *et al.*, 2016; Starko *et al.*, 2019). Thus, studying the influence of local temperature and wave energy on seaweed presence on the rocky intertidal of the Northeastern Pacific significantly contributes to our understanding of how kelp communities respond to environmental stress, and the conditions at which turf algae dominate in these regions.

In this study, I examined the additive effects of local gradients in temperature and wave energy on the composition of seaweed species in the rocky intertidal zone of Barkley Sound, Vancouver Island, B.C, in the traditional territory of the Huu-ay-aht Peoples. Using field imagery of the benthos taken 1m above the Canadian Chart Datum (hereafter "datum"), I analyzed the benthic cover at sites (n = 31) throughout the sound. Barkley Sound has a natural summer sea surface temperature gradient from the entrance of the sound to the inner region, with wave-sheltered and wave-exposed coastline at varying distances from the opening of the sound (**Figure 2**). Average water temperature and maximum air temperature were measured *in situ*, and wave energy was measured by proxy as the upper elevational limit of barnacles. I investigated whether these local-scale environmental variables could predict the diversity and percent cover of kelp. I tested the hypothesis that kelp diversity and percent cover is negatively correlated to temperature, as kelp are heat sensitive algal species that deteriorate under heat stress (Mabin *et al.*, 2019). I further hypothesized that kelp cover and diversity would be greater at sites exposed to higher wave energy, as water motion has a positive influence on the growth rate of kelp (Millar *et al.*, 2020). Finally, I hypothesized that turf cover would respond in an opposing manner to kelp cover, as it is an opportunistic, heat tolerant species that dominates the substrate in the absence of kelp (Filbee-Dexter and Wernberg, 2018).

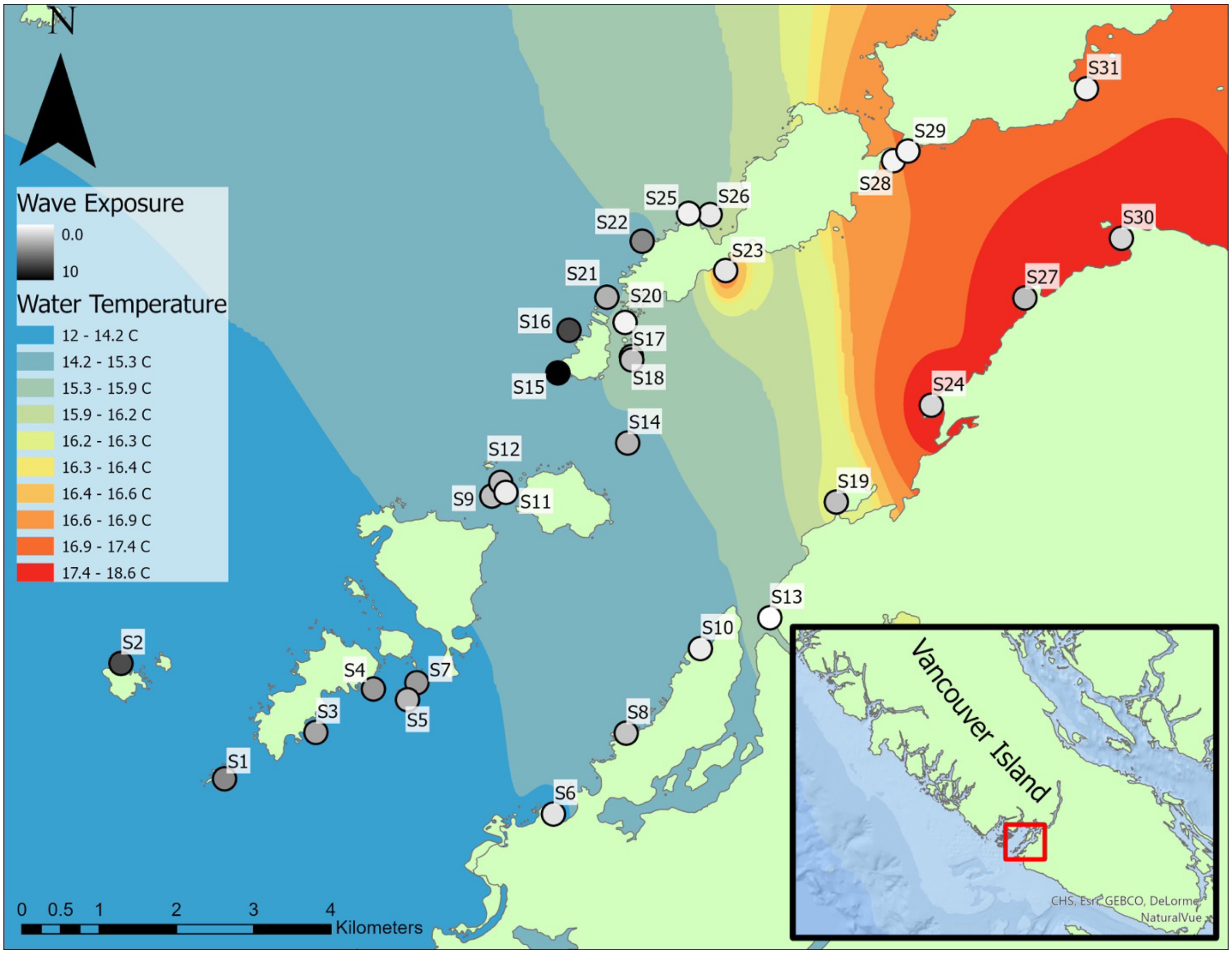

Figure 2. Map of (n=31) study sites in Barkley Sound, Vancouver Island, B.C, in the traditional territory of the Huu-ay-aht peoples. A colour gradient of average water temperature measured at each site from July 23 to August 7, 2021 is displayed, and relative wave exposure measured using barnacle height as proxy is displayed in greyscale for each site.

Methods

Study Site and Data Collection

Throughout the summer of 2021, 31 intertidal monitoring sites were surveyed along the rocky coast of Barkley Sound, Vancouver Island, in the traditional territory of the Huu-ay-aht Peoples (**Figure 2**). Barkley Sound is 30km wide and consists of over 1000km of rocky shoreline with wave-sheltered and wave-exposed coastline at varying distances from the opening of the sound (Starko *et al.,* 2019). At each site, ten to thirteen 0.25 m^2 quadrats were placed every meter along a transect that was laid out at 1m above datum, and a photograph of the quadrat and underlying benthos was taken. This tidal elevation (1m) was chosen to be well within the intertidal zone at which kelp will grow if present. A shallow hole (~1 cm) was drilled into the rock 1m above datum at each site, and temperature loggers (EnvLoggers, ElectricBlue) were placed inside and secured to the substrate with Z-Spar Epoxy. Loggers were set to record temperature every 10 minutes, and recorded data from July 23 to August 7, 2021, recording both air and water temperature depending on the height of the tide relative to the logger. The upper elevational limit of barnacles (varying from ~3-6m above datum) gives an indication of the extent to which waves splash up the shore. For this study the zonation patterns of barnacles were measured and used as a proxy for wave action, as in Starko *et al.,* 2019. Importantly, this proxy also correlates with other map-based proxies that estimate exposure to open swell (Neufeld *et al.*, 2017). At each site, the distance between the barnacle upper limit and datum was measured using either a stadia rod and sight level, or a weighted transect at sites that were steep (i.e. mostly vertical).

Image Analysis

For analysis of the benthic quadrat images, I first removed photos of unusable quality as well as duplicates for each of the 31 sites. I then used the software Adobe Photoshop Lightroom (Version 3.4) to align and crop photos of each quadrat, such that the quadrat tubing was not visible, and each image represented 0.25 m^2 of substrate. In total 367 images were selected and cropped for further analysis.

The composition of the benthos, including invertebrates, abiotic substrates, seagrass, and various algal species in the Phylum Rhodophyta (red algae), Phylum Chlorophyta (green algae), and Class Phaeophyceae, Phylum Ochrophyta (brown algae), was quantified using the opensource, web-based software CoralNet. Although this software is primarily used for coral reef photo-quadrat annotation, both coral reefs and the rocky intertidal consist of mostly sessile organisms, making this software applicable to quantifying seaweed community composition. A point-intercept method was used to uniformly generate 81 points per photo, as displayed in **Figure 3**. Since the performance of the CoralNet automated analysis-algorithm is not effective for algal species (Paul and Rani, 2021), I manually identified the points in each image to genus or species if possible. Due to similarity in features across species of filamentous algae, and limited resolution in photographs for identification, these algae were categorized into one group. Points that were unidentifiable due to obstructions were labelled as unclear, and an additional category was used to identify thick red branching algae in cases where the species was unclear due to poor image quality.

Benthic Cover Analysis Categories

For benthic cover analysis, 47 substrate tags were categorized into kelp, other canopy-forming brown algae, canopy-forming red algae, turf algae, encrusting algae, invertebrates, and abiotic substrates (**Table A1**). Prior to analysis, quadrats with the highest number of unclear points and unclear red algae points were removed, such that 10 photographs with the most identifiable points were represented for each site. Unclear points were removed from each remaining quadrat, and the percent cover for each category was scaled to reflect the percent of identifiable points per quadrat.

Although the broader understanding of algal turf has been that it is a layer of low-lying algae, the definition of algal turf has long been poorly described or too variable across the literature to allow viable comparisons across marine ecological studies (Connell *et al.*, 2014). According to the few common characteristics in the literature, I defined ‘turf’ in this study as algae that densely covers the rocky intertidal, with >1 aggregated thalli and short blades (<15cm). Ecosystems with these traits lack structural complexity, providing less habitable areas for marine organisms (Pessarrodona *et al.*, 2021). To contribute to a greater understanding of phycological ecology, researchers have been recommended to provide details of the morphology and taxonomy of species defined as 'turf' (Connell *et al.*, 2014). Thus, the definition of 'turf' for this study includes the following 17 red algae species that are categorized as bushy, coarse branching, and filamentous (Connell *et al.*, 2014): *Acrosiphonia sp., Ahnfeltiopsis sp., Gelidium sp., Grateloupia sp., Halosaccion glandiforme, Hymenema sp., Mastocarpus sp., Mazzaella affinis, Microcladia sp., Nemalion helminthoides, Neogastroclonium subarticulatum, Neorhodomela sp., Odonthalia sp., Polyneura sp., Prionitis sp., Pyropia sp.*, articulated coralline algae species, and red algae categorized as filamentous. Also defined as turf are the green algae species *Ulva sp.,* and the brown algal species *Leathesia marina* and *Colpomenia sp.* Examples of turf species are shown in **Figure 3C** and **D**.

In contrast to turf algae, canopy-forming algae in this study were defined as relatively tall (>15cm), structurally complex species that provide sufficient habitat for rocky shore organisms. Canopy-forming algae were separated into three broad categories: (1) eight species of kelp in the order Laminariales: *Alaria marginata, Costaria costata, Egregia menziesii, Eisenia arborea, Hedophyllum sessile, Laminaria setchellii, Lessionopsis litoralis,* and *Macrocystis pyrifera*; (2) two other canopy-forming brown algae species: *Fucus disticus* and *Sargassum muticum;*(3) two canopy-forming red algae: *Mazzaella splendens,* and *Chondracanthus sp.* Kelp were differentiated from other canopy-forming species in this study for separate analysis given their unique ecological significance and heat sensitivity (Christie *et al.*, 2009; Mabin *et al.*, 2019). Examples of different kelp species are shown in **Figure 3A** and **B.**

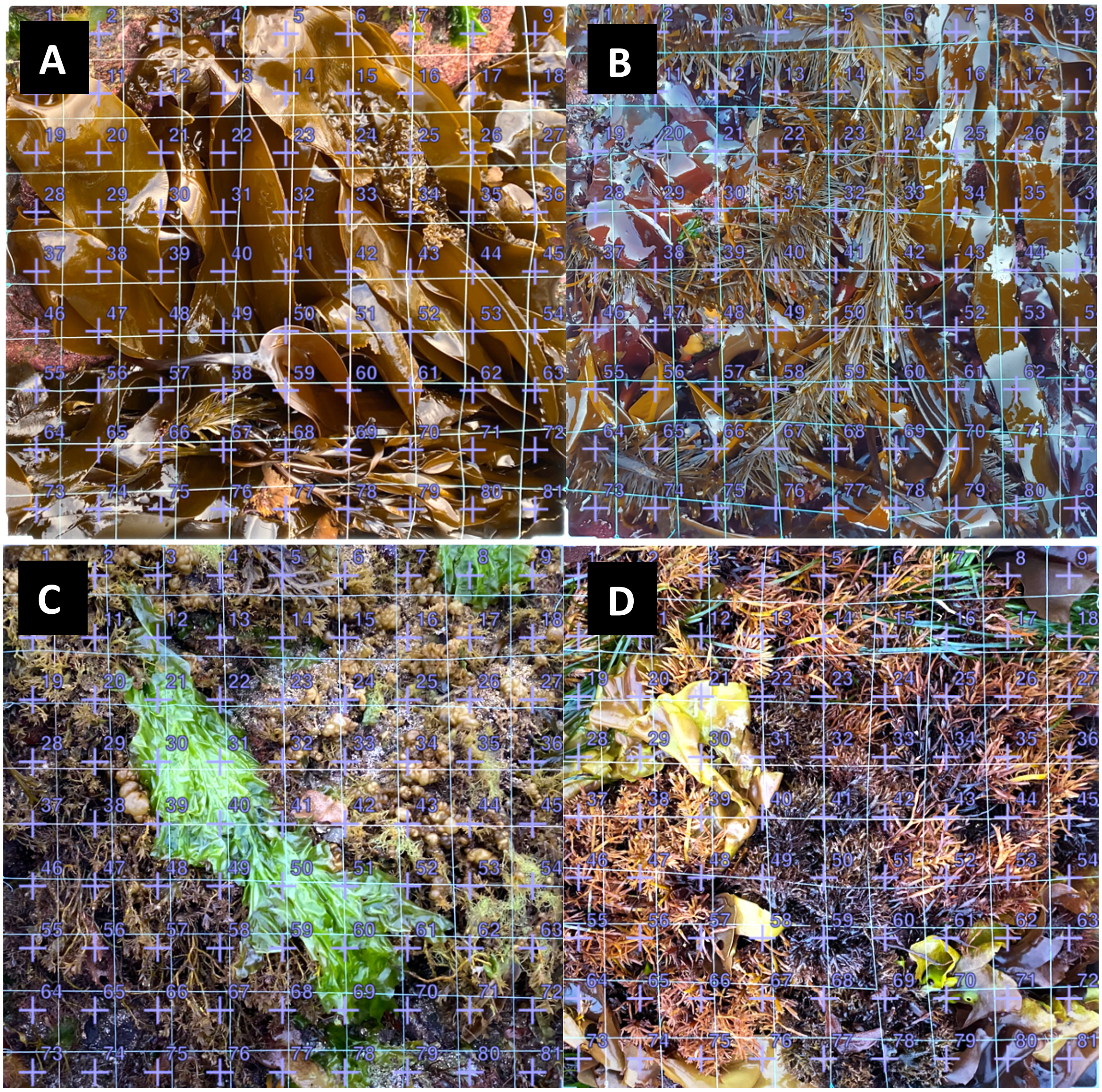

Figure 3. Photo-quadrats of different species of seaweed observed in Barkley sound, with 81 identification points (purple) on each image. Notable species under these points include **A)** Kelp species: *Hedophyllum sessile* (11,12,13), *Laminaria setchelli* (50,59,60), *Lessionopsis littoralis* (69,70,78,79); **B)** Kelp species: *Egregia menziesii* (4,5,6,14), *Alaria marginata* (56, 61,70); Red canopy-forming species: *Mazzaella splendens* (19,20,21,28); **C)** Turf algal species: *Ulva sp.* (21,30,31), *Leathesia marina* (34), *Neogastroclonium subarticulatum* (47,48,49); **D)** Red canopy-forming species: bleached *Mazzaella splendens* (20,21,29); Turf algal species: *Prionitis sp.* (37,38,47), *Mazzaella affinis* (49, 50,59); Seagrass species: *Phyllospadix sp.* (19).

Environmental Variable Quantification

For temperature, I first paired the data recorded from the *in-situ* temperature loggers with tidal data to extract the time periods at which the tide descended below the loggers at each site to extract air and water temperature. Water temperature was measured as the average temperature across all time periods that the logger was submerged during the two weeks of temperature recording. Air temperature was measured as the average daily maximum temperature at each site from July 26th to July 29th 2021, which were the four days when the tide was below the loggers for a significant amount of time during the day. Maximum air temperature was used instead of average temperature to capture the acute heat stress exerted on the organisms out of water. Variation in air temperature is likely driven by variation in exposure to direct sun, thus differences in air temperature may largely reflect the aspect of each site relative to the sun. It should be noted that the temperature logger for Site S15 was placed on a mussel bed, which may have led to an overestimate in the average daily maximum air temperature at that site.

Relative wave exposure at each site (measured as maximum barnacle height along the rocky shore) was quantified on a scale from 0-10 by subtracting the barnacle height at each site by the lowest height found across sites, dividing by the range of observed barnacle heights, and multiplying by ten.

Kelp Diversity Metrics

Statistical analyses, diversity calculations, and graphing were all performed using RStudio with R version 1.4.1103 (R Core Team, 2020).

To assess diversity for the kelp species, I calculated three different diversity indices. Species richness, Shannon Diversity Index, and Simpson Diversity Index were all chosen to investigate the influence of environmental variables on kelp diversity to obtain a range of metrics that accounted for both evenness and rareness of species. Species richness was calculated as the number of species summed across all quadrats at each site. Shannon Diversity Index and Simpson Diversity Index were both calculated in RStudio with the "vegan" package, using the average percent cover for each of the eight species at each site (Oksanen, 2020).

The Shannon Diversity Index (H) uses the equation $H = -\Sigma p_i * ln(p_i)$, where p_i is the proportion (n/N) of individuals of one species (n) divided by the total number of individuals of all species (N). Shannon Diversity was used to quantify the abundance distribution for the number of different species, such that a lower value represents lower diversity and higher dominance of abundant species. This index measures uncertainty about the identity of species, but tends to be biased by species richness and sample size (Hurlbert, 1971).

The Simpson Diversity Index (D) uses the equation $D = 1 / \Sigma(p_i)^2$, where p_i is the number individuals of the *i*th species (n) divided by the total number of individuals found (N). Simpson Diversity was used to quantify diversity in terms of evenness, such that a high value represents even abundance between species present, which is attributed to higher diversity. This index is less biased by species richness, meaning rare species have less of an effect than Shannon Diversity Index (Hurlbert, 1971). Sites with zero kelp species were set to a Simpson Diversity index of zero since calculations result in a value of one, despite no species being present.

Statistical Analyses

First, the relationship between the environmental variables was calculated as the correlation coefficient, and the strength and p-values of these relationships were visualized using a correlogram developed using the "corrplot" package (Taiyun Wei and Viliam Simko, 2021). The normality of environmental variables was tested using a Shapiro-Wilk test. Based on the non-normality of relative wave energy data, a Spearman correlation test was used for the calculation of p-values.

To examine the influence of water temperature, air temperature and wave energy on the percent cover of kelp and turf, respectively, I used the linear model function in the R "stats" package to perform regression analyses (R Core Team, 2020). Univariate models were fit using each of the three environmental variables as a predictor, and multivariate models were fit for all possible combinations of the three environmental variables. Models were tested with interaction terms but were not significant enough to be reported (most results had a p-value >0.05). I used a Shapiro-Wilk test to evaluate residuals for normality for each univariate model. All linear models were then compared using Akaike Information Criterion for small sample sizes (AICc) in the "AICcmodavg" package, and the best model for each dependent variable was determined as having the lowest AICc (Mazerolle, 2020).

To understand the relationship between kelp cover and turf cover, I tested the correlation using the package "ggpubr" (Kassambara, 2020). Normality was tested for percent cover data, and a Spearman's rank correlation was used based on the non-normality of kelp cover. A linear model of kelp and turf cover was also conducted using the R "stats" package (R Core Team, 2020). Given the non-normality of the model based on a Shapiro-Wilk test, square root transformed turf cover was used as the predictor for kelp cover.

Assessments of kelp Shannon Diversity Index and kelp Simpson Diversity Index were conducted in a similar manner as kelp and turf percent cover, using AICc values to determine the best linear model with water temperature, air temperature, and wave energy as possible predictors. Much like percent cover data, the diversity indices were calculated using average percent cover of each of the eight kelp species for each site, thus the data was independent, and linear mixed models were not used.

Kelp species richness was analyzed using a generalized linear model (GLM), with a Poisson distribution and link log function, using the "stats" package (R Core Team, 2020). Since kelp species richness was quantified as the sum of species per site, the Poisson distribution, which is used to model count data, was chosen for the GLM (Muller and Stewart, 2006). The lowest AICc value was used to determine the best GLM for species richness.

To further examine the influence of water temperature, air temperature, and wave energy on the species composition for all biota at each site, I also calculated Bray-Curtis distances across sites. The dissimilarity matrix was visualized as a Principal Coordinates Analysis (PCoA) using the "ape" package (Paradis and Schliep, 2019).

Ethics Statement

Field sampling conducted on the traditional territory of the Huu-ay-aht First Nations (HFN) was done so with permission from the HFN.

Results

Environmental Conditions of Barkley Sound

As visualized in the map of Barkley Sound (**Figure 2)**, a sea surface temperature gradient of ~6 ºC on average was recorded by the temperature loggers across the different sites. As expected, this gradient of increasing water temperature manifested across 16 km from the outer region of the sound to the inner region (**Figure 4A**). Relative wave energy varied throughout the sound with a general increase from the inner to outer region, however a broad range of relative wave energy occurred at sites ~1000m from the entrance, within the temperature range of 14-16°C (**Figure 4B)**. The average maximum air temperature showed great variation throughout the sound (**Figure 4C**). Water temperature and wave energy were significantly negatively correlated (rho = -0.579, $p < 0.001$), however there were still some sites with high relative wave energy paired with fairly high temperature. Air temperature and wave energy were also significantly negatively correlated (rho=0.402, $p < 0.05$), although to a lesser extent. The correlogram in **Figure 5** displays the significant negative relationship between wave energy and both water and air temperature.

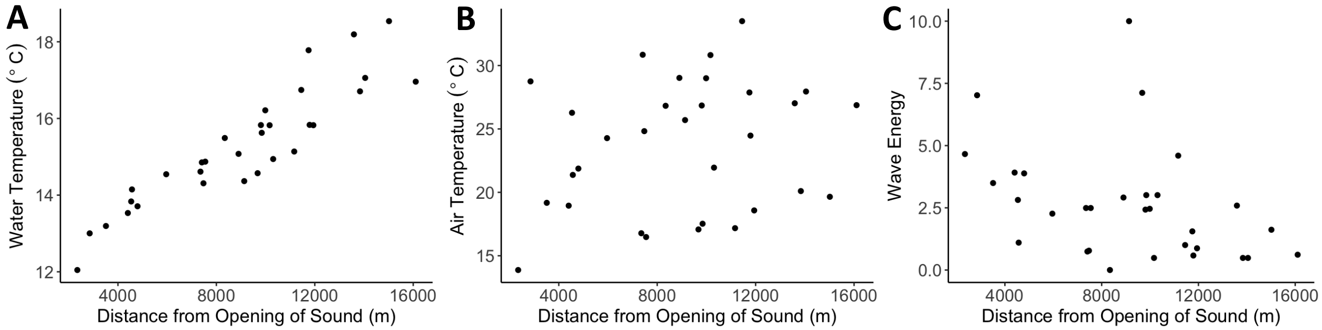

Figure 4. Plot of the A) average water temperature, B) average air temperature, and C) relative wave energy at each site with increasing distance from the opening of the sound, measured as the shortest distance across water to a transect line drawn from Cape Beale Lighthouse to Amphitrite Point Lighthouse.

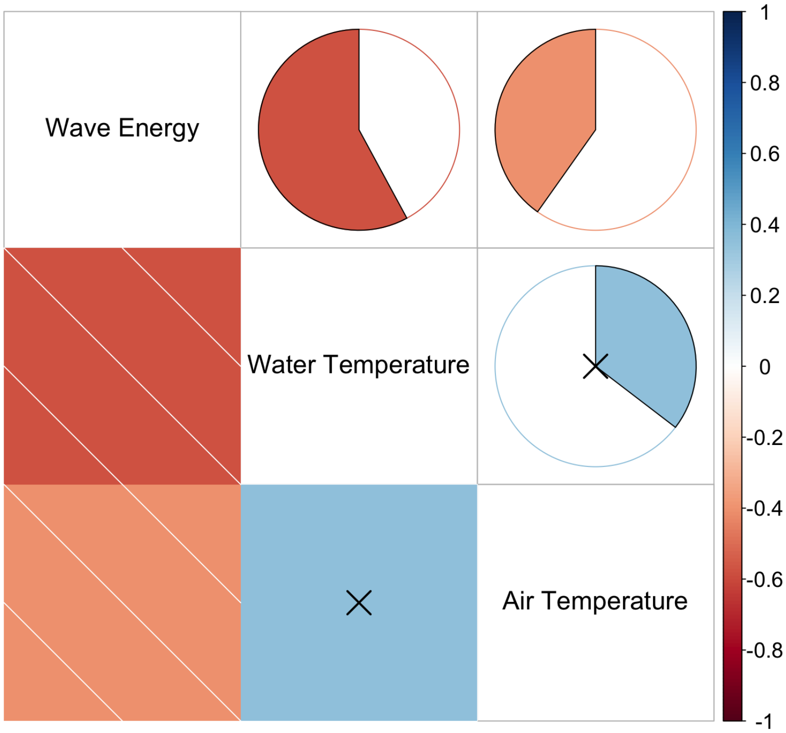

Figure 5. Correlogram of environmental variables with a scale bar indicating the strength and direction of the correlation. The 'X' indicates insignificant correlation (p-value < 0.05).

Kelp and Turf Cover

The percent cover of kelp visually decreased with increasing temperature, showed no visual trend with air temperature, and increased with increased wave energy (**Figure 6A-C**). Linear models confirmed these trends, as the best model based on AICc values included water temperature and wave energy (**Table 1**) and showed a significant negative effect of water temperature (p< 0.01), with sites below 15.8°C ranging from 0% to 85.6% kelp, and sites above 15.8°C having no kelp. Wave energy had a significant positive effect (p<0.001) on average percent kelp cover for each site (**Table 2**), with sites with a relative wave energy < 2.5 having less than 20% kelp. Sites with an average temperature of ~15°C or greater (e.g. S22, S21, S14, S9, S17) show great variation in percent cover of kelp (See Appendix **Figure A1** for site comparison with temperature and wave energy). This variation visually appears to be correlated by site differences in relative wave energy, in which sites with high relative wave energy (e.g.

S22) have higher percent cover than those with low wave energy (e.g. S9). Air temperature residuals were not normal with kelp cover according to the Shapiro-Wilk test. However, since there was visually no relationship between kelp and air temperature, the lack of significance of the result is likely robust to this slight deviation from normality.

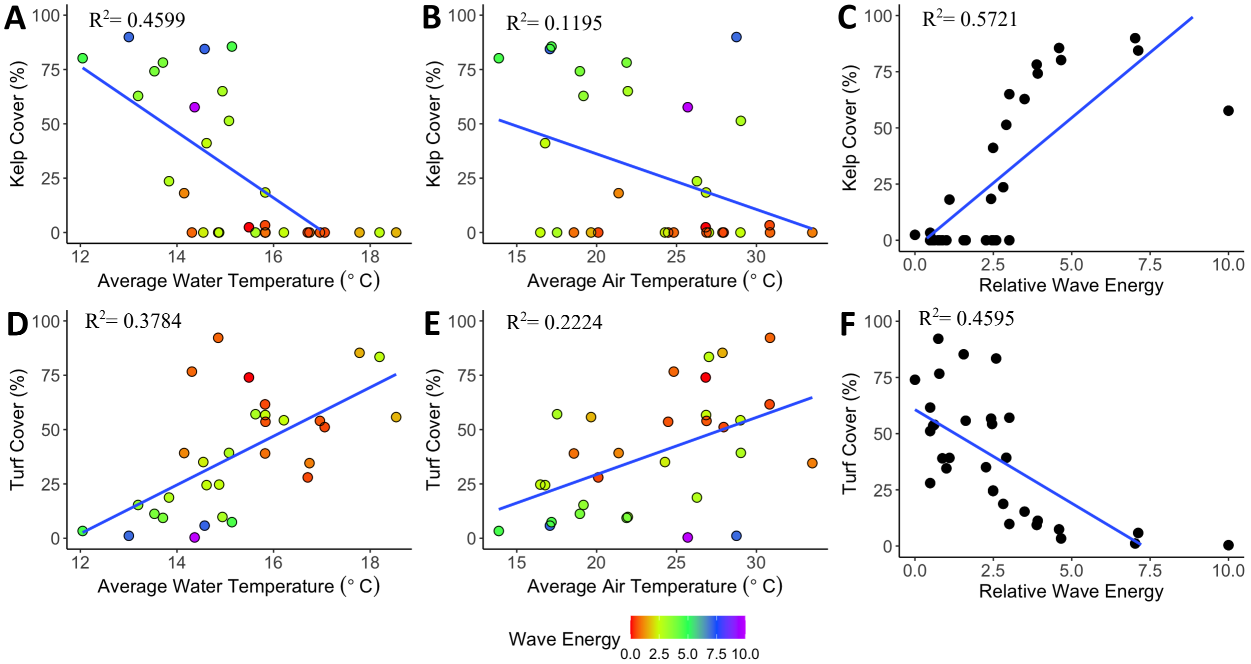

Figure 6. Average percent kelp (top row) and turf (bottom row) cover at each site in relation to environmental variables: A) and D) average water temperature, B) and E) average air temperature and C) and F) relative wave energy. Sites in the water and air temperature plots are colour coded by their relative wave energy. Blue lines indicate significant regressions ($p<0.05$) for the univariate linear models. R^2 is reported for each model.

Turf algae visually increased with increasing water and air temperature and decreased with increasing wave energy (**Figure 6A-F**). All three environmental variables combined best explained turf cover (**Table 1**). Water temperature and air temperature had a significant positive influence on percent cover ($p< 0.05$ for both), with a 2°C change in water temperature typically resulting in a 22% increase in turf cover, and a 5°C change in air temperature typically resulting in a 13% increase in turf cover (**Table 2**). Wave energy had a significant negative influence on percent cover ($p<0.01$), with sites above a relative wave energy of 4 having less than 16% turf cover, and sites below this level of wave energy having up to 92% turf cover (**Table 2**). Air temperature and wave energy residuals were not normal with turf cover. However, since log and square root transformations of both variables did not change the results, the regression is robust for departures from normality.

Table 1. AICc output from linear models examining the effects of water temperature, air temperature, and wave energy on the average proportional cover of kelp and turf algae. Models in bold had the lowest AICc value.

Response	Model	AICc	Δ AICc	df	R^2 (adj)
Kelp Cover	Water Temp	293.74	16.14	29	0.4599
	Wave Energy	285.48	7.88	29	0.5721
	Air Temp	307.85	30.25	29	0.1195
	Water Temp + Air Temp + Wave	279.22	1.62	27	0.6856
	Water Temp + Wave	277.6	0	28	0.6844
	Water Temp + Air Temp	294.85	17.25	28	0.4495
	Wave + Air Temp	285.21	7.61	28	0.5967
Turf Cover	Water Temp	282.85	11.5	29	0.3784
	Wave Energy	278.51	7.16	29	0.4595
	Air Temperature	289.78	18.43	29	0.2224
	Water Temp + Air Temp + Wave	271.35	0	27	0.6142
	Water Temp + Wave	273.71	2.36	28	0.5598
	Water Temp + Air Temp	280.5	9.15	28	0.452
	Wave + Air Temp	273.93	2.58	28	0.5566

Table 2. Estimate output for the best linear models of kelp and turf cover with water temperature, wave energy, and air temperature selected based on AICc values. Estimates significantly different are bolded. Asterisks indicate levels of significance (* $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$).

Response	Model	Predictor	Estimate	SE	t-value	p-value
Kelp Cover	Water Temp + Wave	Water Temp	**-8.859****	2.633	-3.364	0.00224
		Wave	**8.641*****	1.789	4.831	0.000044
Turf Cover	Water Temp + Wave + Air Temp	Water Temp	**5.4506***	2.3954	2.275	0.03103
		Wave	**-5.6549****	1.5823	-3.574	0.00135
		Air Temp	**1.4234***	0.6399	2.224	0.03468

The relationship between site-level turf and kelp cover was negative (**Figure 7**). This was validated by a significant Spearman's rank correlation rho of -0.742 ($p<0.001$), as well as a negative relationship between turf cover and kelp cover (Linear model: estimate = -11.457, SE =1.322, t-value = -9.731, adjusted $R^2 = 0.7149$, df=29, $p<0.001$).

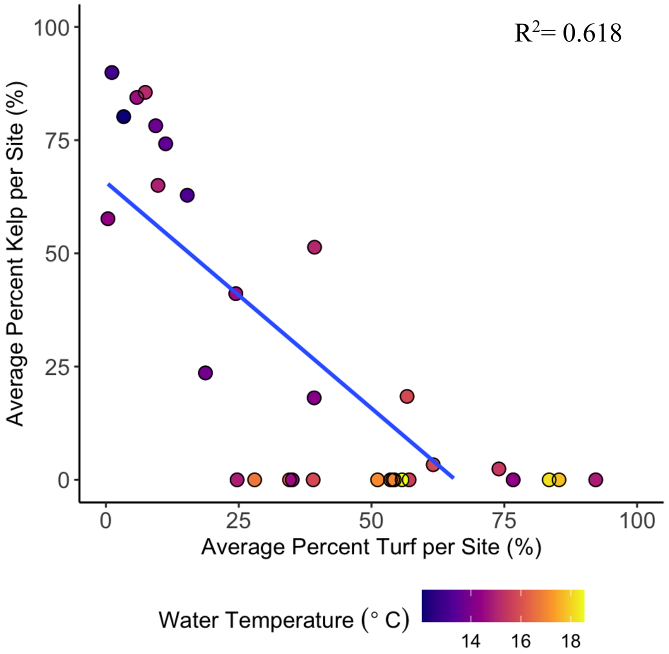

Figure 7. Relationship between site level average percent kelp cover and average percent turf algae cover. Linear regression of Kelp~Turf ($p<0.001$) is shown as a line with adjusted R^2 value. Average water temperature for each site is presented as a colour scale.

Kelp Diversity

Out of all eight kelp species observed, *Egregia menziesii* appeared in highest abundance across sites, and was the most frequently observed, appearing in 14 sites out of the 16 sites with any kelp cover (**Figure 8**). *Eisenia arboria* was the least abundant across sites and was observed in only two of the 16 possible sites. Kelp species were not found at any sites beyond an average water temperature of 15.83°C. *Alaria marginata* was found in highest abundance at the two coldest sites (<13°C), but was found in very low abundance at sites up to 15.8°C.

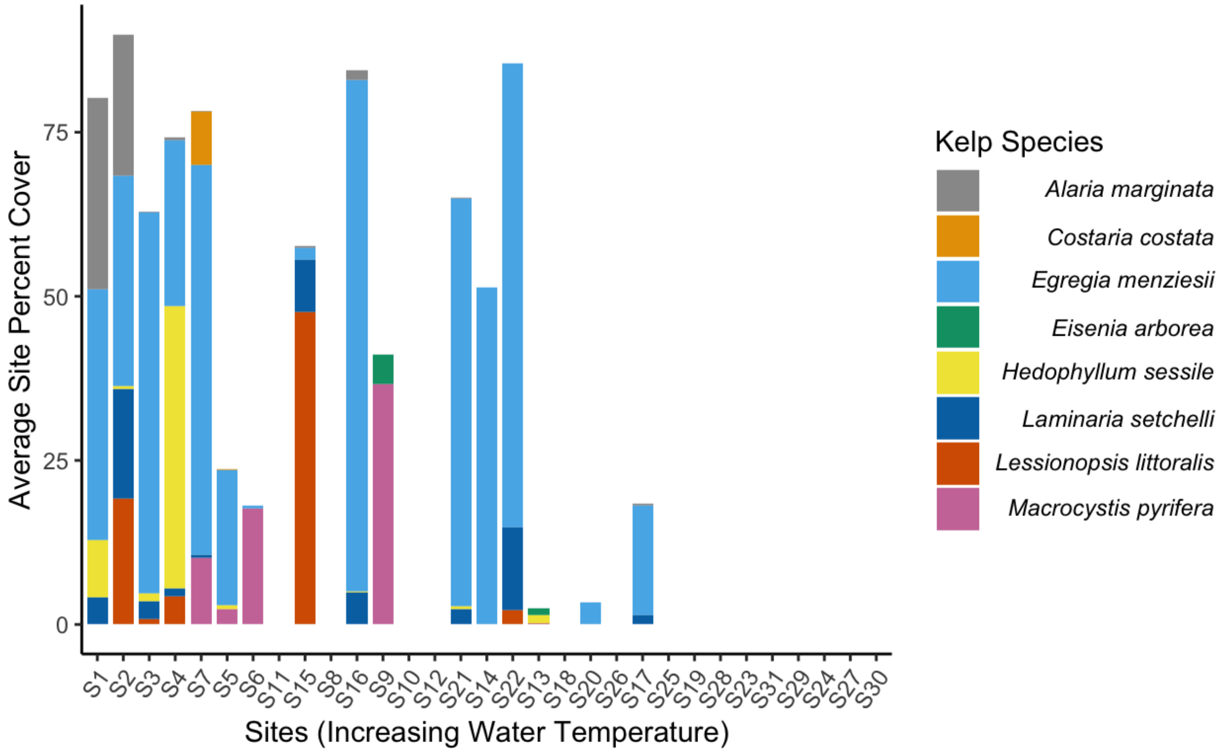

Figure 8. Average percent cover for each of the eight kelp species at each site, plotted in order of increasing average site water temperature. Legend displays genus and species of the kelp found in the region.

Much like kelp percent cover, all diversity metrics of kelp species were negatively related to temperature, while wave energy had an opposing effect. Trends for richness and Simpson Diversity are reported in **Figure 9**. Shannon Diversity Index appeared visually the same as Simpson Diversity Index. According to AICc values, the best generalized linear model of kelp species richness included wave energy and water temperature (**Table 3**), which had a significantly positive ($p<0.001$) and significantly negative ($p<0.05$) influence on richness, respectively (**Table 4**). The best linear model for both Shannon Diversity and Simpson Diversity included water temperature and wave energy (**Table 5**), in which water temperature had a significantly negative influence for both metrics (Shannon $p< 0.01$, Simpson $p<0.01$) and wave energy had a significantly positive influence for Shannon Diversity only (Shannon $p< 0.05$) (**Table 6**). Air temperature and wave energy residuals were not normal for Simpson Diversity and species richness, and air temperature was not normal with Shannon Diversity. Transformations of non-normalities were not effective, likely due to the small number of species analyzed.

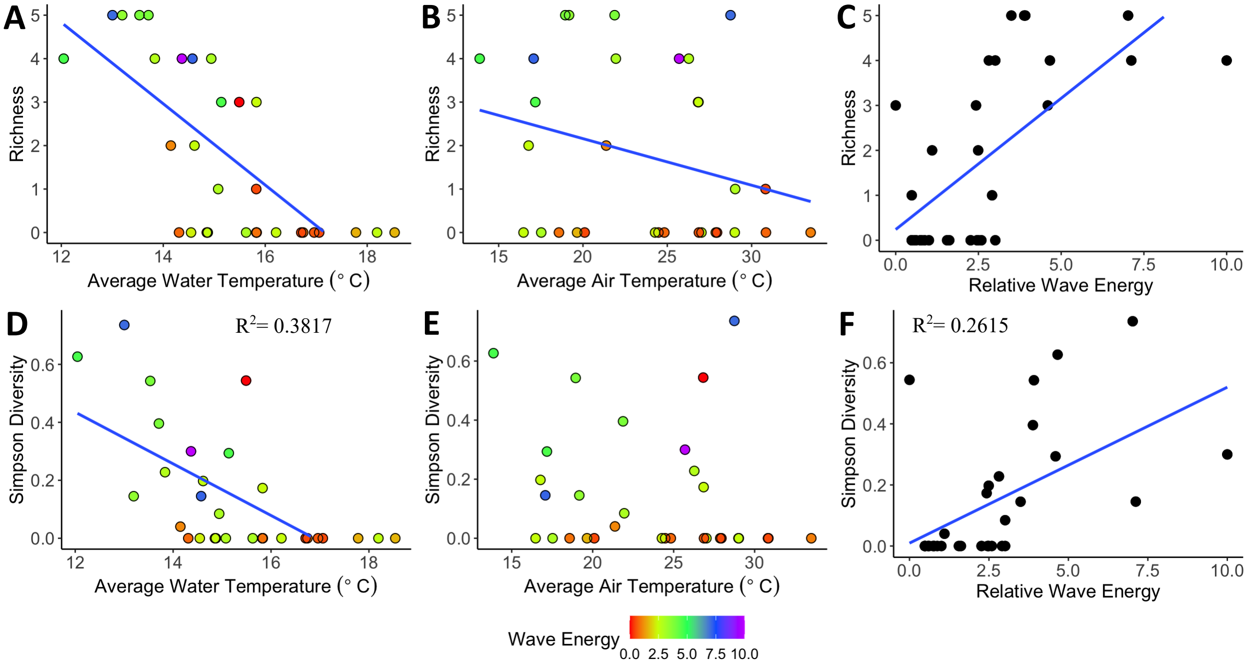

Figure 9. Kelp species richness (top row) and Simpson Diversity Index (bottom row) for each site with environmental variables: A) and D) average site water temperature, B) and E) average site air temperature and C) and F) relative wave energy. Sites in the water and air temperature plots are colour coded by their relative wave energy. Lines indicate significant linear regression ($p<0.05$) for the univariate generalized linear model (species richness) or univariate linear model (Simpson Diversity) with the x-axis as the predictor and the y-axis as the dependent variable. Since species richness is analyzed as a GLM, R^2 is not reported.

Table 3. AICc output from generalized linear models examining the effects of water temperature, air temperature, and wave energy on kelp species richness. The lowest AICc model is bolded.

Response	Model	AICc	Δ AICc	df	Fisher Scoring
Richness	Water Temp	97.50409	2.49087	29	5
	Wave Energy	112.5479	17.53468	29	6
	Air Temp	129.7726	34.75938	29	6
	Water Temp + Wave + Air Temp	97.66276	2.64954	27	5
	Water Temp + Wave	95.01322	0	28	5
	Water Temp + Air Temp	99.82726	4.81404	28	5
	Wave + Air Temp	112.2923	17.27908	28	6

Table 4. Estimate output for the best generalized linear model of kelp species richness with water temperature, wave energy, and air temperature selected based on AICc values. Estimates significantly different are bolded. Asterisks indicate levels of significance (* $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$).

Response	Model	Predictor	Estimate	SE	z-value	p-value
Richness	Water + Wave	Water	**-0.49035*** **	0.11219	-4.371	0.0000124
		Wave	**0.13059***	0.05511	2.37	0.0178

Table 5. AICc output from linear models examining the effects of water temperature, air temperature, and wave energy on kelp species richness, Shannon Diversity Index, and Simpson Diversity Index. Models in bold had the lowest AICc value.

Response	Model	AICc	Δ AICc	df	R^2 (adj)
Shannon Diversity	Water Temp	16.84154	2.33222	29	0.4202
	Wave Energy	22.17592	7.6666	29	0.3113
	Air Temp	33.29372	18.7844	29	0.01427
	Water Temp + Wave + Air Temp	17.24316	2.73384	27	0.4719
	Water Temp + Wave	14.50932	0	28	0.4886
	Water Temp + Air Temp	19.48313	4.97381	28	0.3997
	Wave + Air Temp	24.60462	10.0953	28	0.2918
Simpson Diversity	Water Temp	-17.33638	0.92022	29	0.3817
	Wave Energy	-11.82789	6.42871	29	0.2615
	Air Temp	-2.769926	15.48667	29	0.0109
	Water Temp + Wave + Air Temp	-15.47988	2.77672	27	0.4098
	Water Temp + Wave	-18.2566	0	28	0.4293
	Water Temp + Air Temp	-14.69161	3.56499	28	0.3598
	Wave + Air Temp	-9.407611	8.84899	28	0.2408

Table 6. Estimate output for the best linear models of kelp diversity metrics with water temperature, wave energy, and air temperature selected based on AICc values. Estimates significantly different are bolded. Asterisks indicate levels of significance (* $P < 0.05$, ** P <0.01, ***$P < 0.001$).

Response	Model	Predictor	Estimate	SE	t-value	p-value
Shannon Diversity	Water Temp + Wave	Water	**-0.1257****	0.03781	-3.325	0.00248
		Wave	**0.05674***	0.02568	2.209	0.0355
Simpson Diversity	Water Temp + Wave	Water	**-0.06879****	0.02229	-3.087	0.00453
		Wave	0.02799	0.01514	1.849	0.0751

Total Biotic Community Composition

More than 95% of the substrate across sites was biotic, and aside from two sites (S15, S12), most sites contained >87% seaweed species. Kelp cover decreased with increasing distance into Barkley Sound, while turf was more abundant further into the sound (**Figure 10**). Both red and non-kelp brown canopy-forming algae appeared in similar sites as turf algae. Site S15 showed a notably high percent cover of invertebrates, which was comprised mostly of mussels. Only two sites had notable seagrass cover (>15%), S12 and S19, both of which were dominated by turf algae and had no kelp.

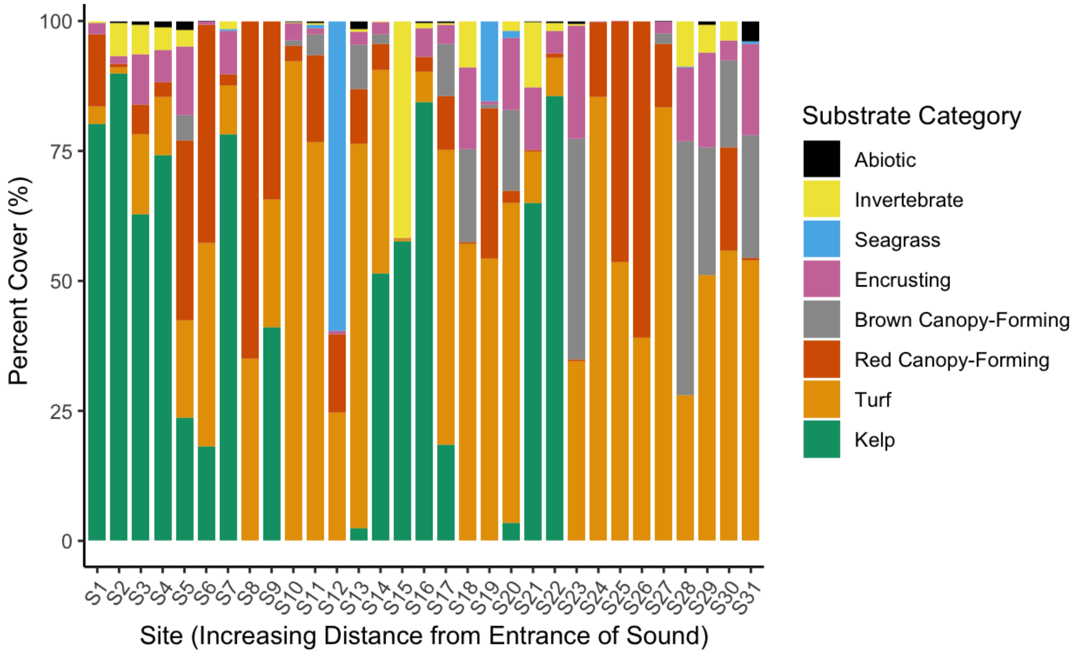

Figure 10. Percent cover of all possible substrate categories at each site sampled, ordered in terms of increasing distance from the entrance of Barkley Sound.

The community-wide Principal Coordinate Analysis (PCoA) revealed three distinct clusters of similar sites based on their species composition, with intermediate sites scattered between each cluster (**Figure 11**). Principal coordinate axis 1 explained 32.65% of the variance and appears to represent dissimilarity between kelp dominated sites (>50% kelp) (left side) and 'turf' dominated sites (>50% turf, red canopy-forming, or brown canopy-forming) (right side) according to the colour gradient of kelp cover displayed in the legend. Principal coordinate axis 2 explained 28.72% of the variance and appears to capture variation in community composition between 'turf' dominated sites, which have formed two visually distinct clusters of similarity in ordination space. Site differences between these two groups are likely due to differences in the distribution of red-canopy forming and brown canopy-forming algae such that the top right cluster appears to represent sites with up to 60% cover of red canopy-forming algae (*Mazzaella splendens* and *Chondracanthus sp.*), and the bottom right represents sites with up to 40% cover of brown canopy-forming algae (*Sargassum muticum* and *Fucus distichus*) (**Figure A2**). Arrows of environmental variables show wave energy as a positive driver of 'kelp-dominated' sites, and temperature as a positive driver for 'turf-dominated' sites. Air temperature and water temperature appear to have a stronger positive impact on the lower cluster of sites represented by brown canopy-forming algae presence (**Figure A2**).

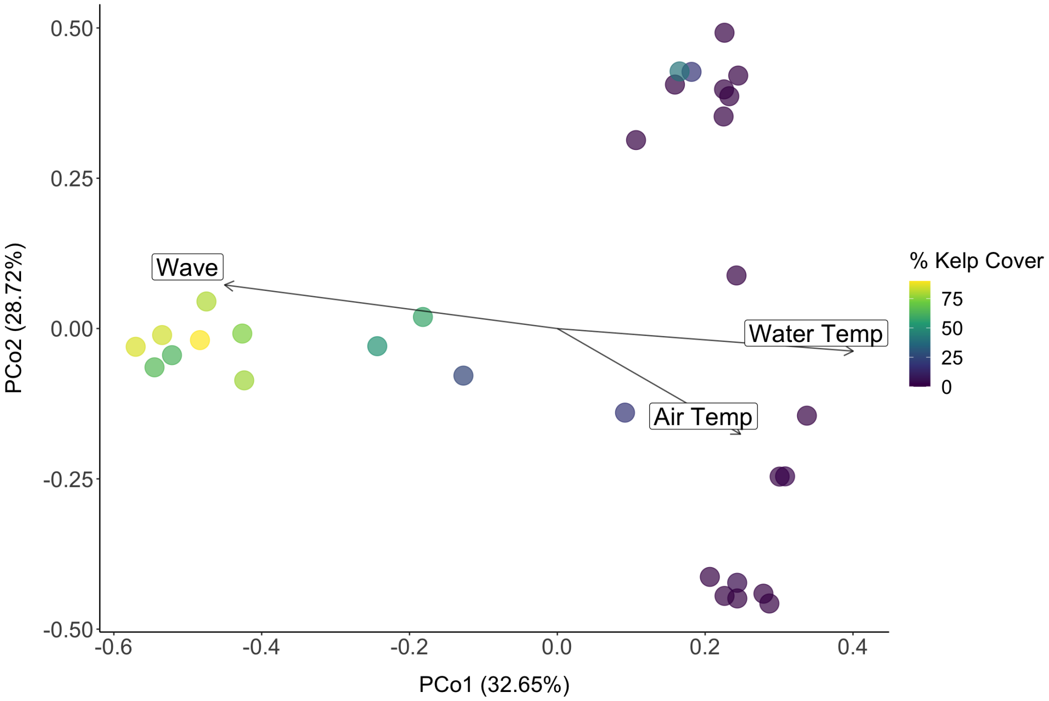

Figure 11. Principle coordinate analysis (PCoA) biplot of community composition, quantified using Bray-Curtis dissimilarity. Percent cover of each biotic species category at each site was used to calculate dissimilarity matrix. Average percent kelp cover for each site is represented as a colour gradient. Arrows represent each of the environmental variables examined as drivers for community composition.

Discussion

Overall, in this study I found evidence that water temperature and wave energy have opposing influences on kelp and turf prevalence in a temperate intertidal community. Specifically, kelp cover and diversity increased as water temperature decreased. Kelp cover and diversity also increased as relative site wave energy increased, in some cases despite high average site temperatures. In contrast, turf prevalence was best explained by a combination of air temperature, water temperature, and wave energy, such that air and water temperature had significantly positive effects, and wave energy had a significantly negative effect. A PCoA based on Bray-Curtis dissimilarity of species composition across the sound also verified the opposing manner in which kelp and turf respond to these environmental drivers. These results could further imply that increasing local temperatures result in a decline in habitat structural complexity due to the prevalence of turf over kelp, an effect which may be ameliorated at the site level by high relative wave energy.

Responses of Kelp Cover to the Temperature Gradient

Historically within Barkley Sound, kelp cover has significantly declined over time following decadal-scale gradual warming, in addition to a 2013-2016 marine heatwave in the Northeast Pacific, reaching the coast of Vancouver Island (Starko *et al.*, 2019). However just south of the island in Washington State, kelp populations have been observed to remain at historical levels despite long-term warming (Pfister *et al.*, 2018). The findings in this study complement those of Starko *et al.,* 2019, such that changes in temperature have been shown to influence distribution and presence of kelp species in Barkley Sound on a spatial gradient of temperature in addition to the previously observed temporal changes.

In the summer of 2021 in Barkley Sound, percent cover significantly declined with increasing temperature, and was not observed at any sites higher than an average water temperature of 15.8°C, which is likely attributable to the negative physiological impacts of temperature on kelp tissue and growth (Simonson *et al.*, 2015; Mabin *et al.*, 2019; Nepper-Davidsen *et al.*, 2019; Hollarsmith *et al.*, 2020). Significant sublethal tissue loss has been observed in experiments on kelps from the coast of Nova Scotia (*Saccharina latissima, Agarum clathratum, Laminaria digitata*) chronically exposed to water temperatures above 18°C (Simonson *et al.*, 2015). Growth rates in *Macrocystis pyrifera* kelp sporelings from Tasmania, Australia were observed to decline with experimental water temperatures above 12°C (Mabin *et al.*, 2019). Similar patterns of negative growth rate with increasing chronic temperature conditions have been observed in experiments with temperatures ranging 18-21°C in *Saccharina* *latissima* kelp from Northern Europe (Nepper-Davidsen *et al.*, 2019). If the rate of tissue loss exceeds growth rate in kelp for a sufficient time, such conditions can lead to kelp mortality (Simonson *et al.*, 2015). Additionally, developmental failure in egg and sporophyte stages among *M. pyrifera* populations has been detected under temperature conditions increasing from 12.7 to 19.8°C (Hollarsmith *et al.*, 2020). The risk of reduced long-term establishment and survivability of kelp posed by warmer waters could explain we observed a steady decline in kelp abundance with the increasing temperature gradient along Barkley Sound (Simonson *et al.*, 2015; Mabin *et al.*, 2019; Nepper-Davidsen *et al.*, 2019; Hollarsmith *et al.*, 2020)..

Average maximum air temperature was not shown to have a significant impact on the prevalence of kelp cover throughout Barkley Sound, despite the possible threat of desiccation and temperature stress (Hargrave *et al.*, 2017). Some sites were shade-exposed during the morning and midday low tides, while others were fully exposed to the sun throughout the day, leading to variation in air temperature that was independent of water temperature. Despite the insignificant effect of air temperature on kelp cover and diversity, air temperature has been shown to impose desiccation stress on kelp when coupled with low wave energy during low tides over long time-scales (Thomsen *et al.*, 2019). It is possible that due to the small number of dates across which air temperature was measured, the times at which maximum air temperature was measured did not effectively capture the dynamics of acute stress occurring during low tide, leading to insignificant relationships of kelp cover and diversity with air temperature.

Responses of Kelp Diversity to the Temperature Gradient

All three metrics of diversity showed a decline in kelp diversity with increasing water temperature, indicating that temperature negatively influences both kelp species richness and evenness. The observed decline in the number of kelp species with increasing temperature may reflect a decline in the number of heat-sensitive species of kelp at each site with increasing temperature, along with persistence of heat-resistant species, though trends did not follow previous knowledge of thermal tolerances precisely. The maximum summer isotherm for *Costaria costata, Hedophyllum sessile, Alaria marginata,* and *Laminaria setchelli* in Vancouver Island have been reported to be 10°C, 10°C, 12°C and 13°C respectively (Lüning and Freshwater, 1988). However, each of these species were found at temperatures higher than their maximum summer isotherm. This could be due to other factors influencing the species-specific differences, such as relative wave energy (Fernández *et al.*, 2020).

Egregia menziesii was by far the most common and abundant kelp species across the sound, closely matching previous observations of its thermal tolerance (**Figure 9**) (Gordon and Wreede, 1978). Survival of *E. menziesii* in British Columbia reportedly has a higher upper thermal tolerance relative to other kelp species, limited by temperatures greater than 15°C (Gordon and Wreede, 1978), which is comparable to the observed threshold of 15.8°C in this study. Unlike other species in Barkley Sound, this species has not been observed to significantly decline since 1993, despite a 2013-2016 marine heatwave in the region (Starko *et al.*, 2019). This could suggest that the prevalence of *E. menziesii* in the thermal range limit for kelp in Barkley Sound is a function of the species' high heat tolerance.

Responses of Kelp Cover and Diversity to Wave Energy

Relative wave energy was shown to have a significant positive influence on kelp cover, species richness, and Shannon diversity, which is likely explained by the dynamics of nutrient uptake mediated by wave energy (Hurd, 2017; Millar *et al.*, 2020). While local mixing from waves tends to cool the surface water, and splashing during low tides cools the exposed shore, making the environment more favourable for kelp growth (Hurd, 2017), the positive response of kelp to wave energy is also supported by studies on the physiological effects of wave energy on kelp nutrient uptake and subsequent growth (Hurd, 2017; Millar *et al.*, 2020). Wave energy provides greater access to nutrients via mixing and upwelling (Huisman and Weissing, 1995). It also influences the rate of nutrient delivery and uptake by kelp by altering the diffusion boundary layer thickness, resulting in significantly higher rates of tissue growth under high water motion conditions (Millar *et al.,* 2020).

The positive effects of wave energy on kelp persistence may have further implications for wave energy as a form of amelioration from heat stress. Variation in kelp cover at sites with a similar average water temperature appeared to visually correlate with the substantial differences in wave energy (**Figure A1**). For example, in **Figure A1**, although Site 22 and Site 14 had the same average water temperature of 15.1°C, Site 22 showed higher percent kelp cover than Site 14, possibly due to the higher relative wave energy at Site 22 (4.6) compared to Site 14 (2.6). This positive influence of wave energy on kelp cover in sites with average temperatures approaching the threshold for kelp species survival could be explained by the positive effects of efficient accumulation of nitrogen on the resistance of kelp to heat stress, as sufficient nitrogen supply in kelp tissue has been shown to have a key role in regulating cellular processes that modulate physiological responses to high temperatures (Gerard, 1997; Fernández *et al.*, 2020). Thus wave energy, which controls supply and uptake of nitrogen in kelp (Millar *et al.*, 2020), acts to ameliorate the negative impacts of temperature on growth and photosynthesis. Variation in environmental nitrogen, mediated by wave energy, could therefore be an important factor in the local distribution of kelp in Barkley Sound, particularly in regions where high water temperature would otherwise prevent the presence of kelp.

The site with the highest relative wave energy did not have the highest percent cover of kelp (Site 14), as it contained ~40% invertebrates, which were primarily mussels (**Figure 10**). This could suggest a limiting level of wave energy for kelp cover, at which point mussel beds exhibit greater competitive ability. However, this contrasts previous studies on kelp recruitment outcompeting mussel recruitment in high wave energy conditions, thus this may represent an outlier in the dataset (Witman, 1987).

Turf Cover and Temperature Tolerance

Turf algae responded in a contrasting manner to kelp cover and diversity for all three environmental variables. The prevalence of turf algae in high temperature sites is likely due to the higher heat tolerance described of these opportunistic species (Connell *et al.*, 2014; Filbee-Dexter and Wernberg, 2018). A few turf species observed and quantified in this study have been previously observed in the Northeast Pacific to have higher isotherms and higher temperature thresholds of survival than the species of kelp observed in this region, including *Mastocarpus sp., Neorhodomela sp., Odonthalia sp., Prionitis sp.,* and *Ulva sp.*, which were all observed to have temperature survival ranges up to 25°C or greater (Lüning and Freshwater, 1988).

The prevalence of turf at many sites in Barkley Sound could have further implications for the structural complexity of the community, which has been observed to influence prevalence of fish inhabiting seaweed communities (O'Brien *et al.*, 2018; Dijkstra *et al.*, 2019). Some studies have shown species-specific impacts of reduction the of seaweed structural complexity due to shifts from kelp to turf ecosystems on temporal scales. For example, cunner fish that use the tall subtidal kelp canopy for refuge and foraging lose this means of protection from predators when kelp ecosystems shift to turf algae, though the significance of protection offered by turf algae remains unclear (O'Brien *et al.*, 2018). In the wave-exposed intertidal, the holdfasts of kelp are ecologically important sources of shelter for marine invertebrates, which may become compromised should kelp in then intertidal shift towards turf-dominated ecosystems (Teagle *et al.,* 2017).

Correlation Between Kelp and Turf Cover

The significant negative correlation of kelp and turf is likely due to the lack of optimal conditions for kelp growth and diversity rather than due to competition with turf. This is because environmental factors, rather than competition, have been determined to be the major drivers for kelp presence (Pfister *et al.*, 2018). Turf algae responded significantly differently than kelp to wave energy, despite the fact that high nitrogen levels have been observed to positively influence the growth of turf algae (Gorgula and Connell, 2004). From this, it could be inferred that at conditions that favor kelp growth such as low temperatures, kelp may be outcompeting turf algae for space on the rocky intertidal, but once conditions become unfavorable for kelp, turf algae are able to dominate the substrate.

Implications of Historical Climate Change Events

The results of this study pose an interesting query - how might the seaweed community of Barkley Sound have historically responded to temporal increases in temperature, and how might it respond to such changes in the future? Temperature-induced phase shifts to turf reefs from kelp have not been reported in the Northeast Pacific, where shifts away from kelp-dominated ecosystems have been largely observed as a result of urchin barrens in the subtidal zone (Feehan and Scheibling, 2014; Ling *et al.*, 2015; Filbee-Dexter and Wernberg, 2018). However, for this study, sea urchins are not primarily present in the intertidal zone of the region, likely not impacting the intertidal kelp to the same extent as subtidal kelp species (Starko *et al.*, 2019). Given that kelp abundance has been observed to decline in Barkley Sound since 1993 as sea surface temperatures rose (Starko *et al.*, 2019), and given the observed abundances of kelp and turf algae across Barkley Sound in this study, it is likely that turf algae has replaced kelp in high temperature, low wave energy regions.

Environmental Conditions of Barkley Sound

The striking 6°C water temperature gradient in Barkley Sound in the summer of 2021 was a novel observation relative to 2019 measurements of 3-4°C (Starko *et al.* In press.), which may be linked to a combination of outer sites being colder than in 2019 and atmospheric heatwaves that occurred in the early summer of 2021. In general, water temperature and wave energy were negatively correlated, such that higher wave energy typically resulted in lower temperatures (**Figure 5**). This result is likely due to the proximity of wave-exposed sites to the opening of the sound, which is cooler due to greater exposure to the cool, mixed water of the open ocean. Air temperature was also significantly negatively correlated with wave energy, possibly due to the effects of wave splash, which would cool the substrate within the splash zone when the tide is below the temperature logger (Harley and Helmuth, 2003).

Future Directions

The hypothesis that turf algae has been replacing kelp loss in Barkley Sound could be substantiated by comparing data in this study with historical seaweed distributions and environmental data, to understand whether turf algal presence is significantly negatively correlated with kelp over time in addition to space. This could have implications for whether shifts to less structurally complex turf reefs may be occurring in the Northeast Pacific intertidal, which would be a novel discovery for this region. Such an investigation could provide a greater understanding of the influences of climate change on the species composition, and further the structural complexity, of seaweed in this region.

Further metrics could have been measured in addition to abundance and diversity to evaluate ecosystem function in response to environmental changes. For example, a study on Australasian kelps by Wernberg *et al.* (2010) demonstrated that while metabolic adjustment allowed kelps to persist in warmer waters on a latitudinal temperature gradient, kelps in warmer waters had reduced physiological responsiveness to disturbances, and reduced ecological performance of kelp recruits, supressing canopy recovery post-disturbance (Wernberg *et al.*, 2010). Thus, measures of physiological responses to spatial variation in temperature could be also included in future studies to predict the possible resistance to disturbance of kelp in the warmer regions of the ecosystem.

Finally, other environmental factors that were not measured could be quantified in the future to investigate additional interacting effects on kelp communities and distribution. For example, UV radiation has been shown to antagonistically interact with the impacts of temperature on germination and cell growth of *Alaria marginata* and *Fucus gardneri* (Hoffman *et al.*, 2003). While this was not measured directly, air temperature could act as a proxy for sun exposure in this study, since air temperature is largely influenced by the aspect of the site in relation to the sun. However, air temperature did not have a significant influence on kelp cover or diversity, thus may not be a significant indicator of UV radiation. Another variable that could be considered for sampling in the future includes nutrients, which were not measured in this study. Nutrient availability influences productivity and thermal tolerance of kelp species, thus could have interacted with measured environmental variables to influence the observed distribution of kelp and turf species (Carnell and Keough, 2014). Future studies including measurements of site-level nutrient concentrations would be beneficial to resolving these interactions. Salinity was also not measured in this study, although the Sarita River expels into the innermost region of Barkley Sound, possibly contributing to local differences in salinity. However, estuarine flow was determined to be far enough from the study sites to not cause a significant effect on site-level salinity (> 4 km).

Conclusions

In this study, I quantified the influence of variation in air temperature, water temperature, and wave energy on kelp cover, kelp diversity and turf cover in Barkley Sound, Vancouver Island. I found that water temperature and wave energy were significant predictors of kelp cover, which was negatively influenced by water temperature and positively influenced by wave energy, and that turf algae responded in a significantly opposing manner. The results indicate that kelp growth and survival in Barkley Sound is predicted by the natural temperature gradient as well as variation in wave energy, and that high relative wave energy may act to ameliorate the negative influence of heat stress, allowing kelp to proliferate in higher temperature sites. It is also likely that, given the observed decline in kelp due to a local marine heatwave, and the observed dominance of turf algae in high temperature sites with low wave energy, turf may be replacing kelp that has been lost in the intertidal of Barkley Sound. This could have negative repercussions on the structural complexity of the seaweed community as whole, and further, the marine life that inhabit the intertidal kelp ecosystems.

Appendix

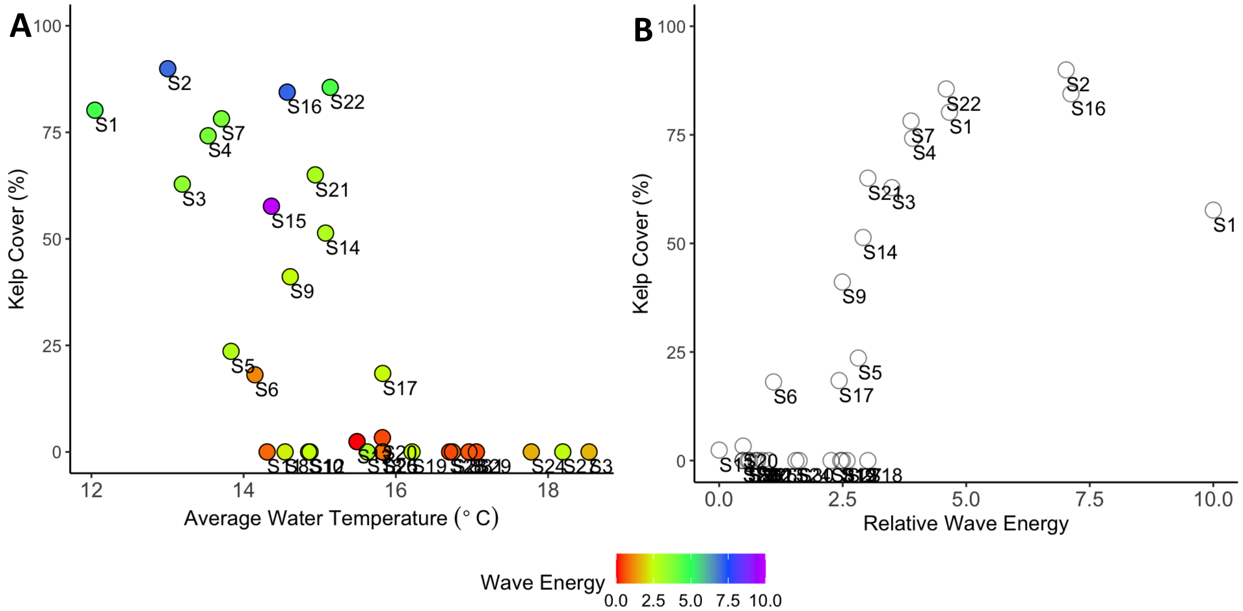

Figure A1. Average percent kelp cover at each site in relation to environmental variables: A) average water temperature, and B) relative wave energy. Wave energy is displayed as a color gradient for the water temperature plot. Site codes are shown for each site.

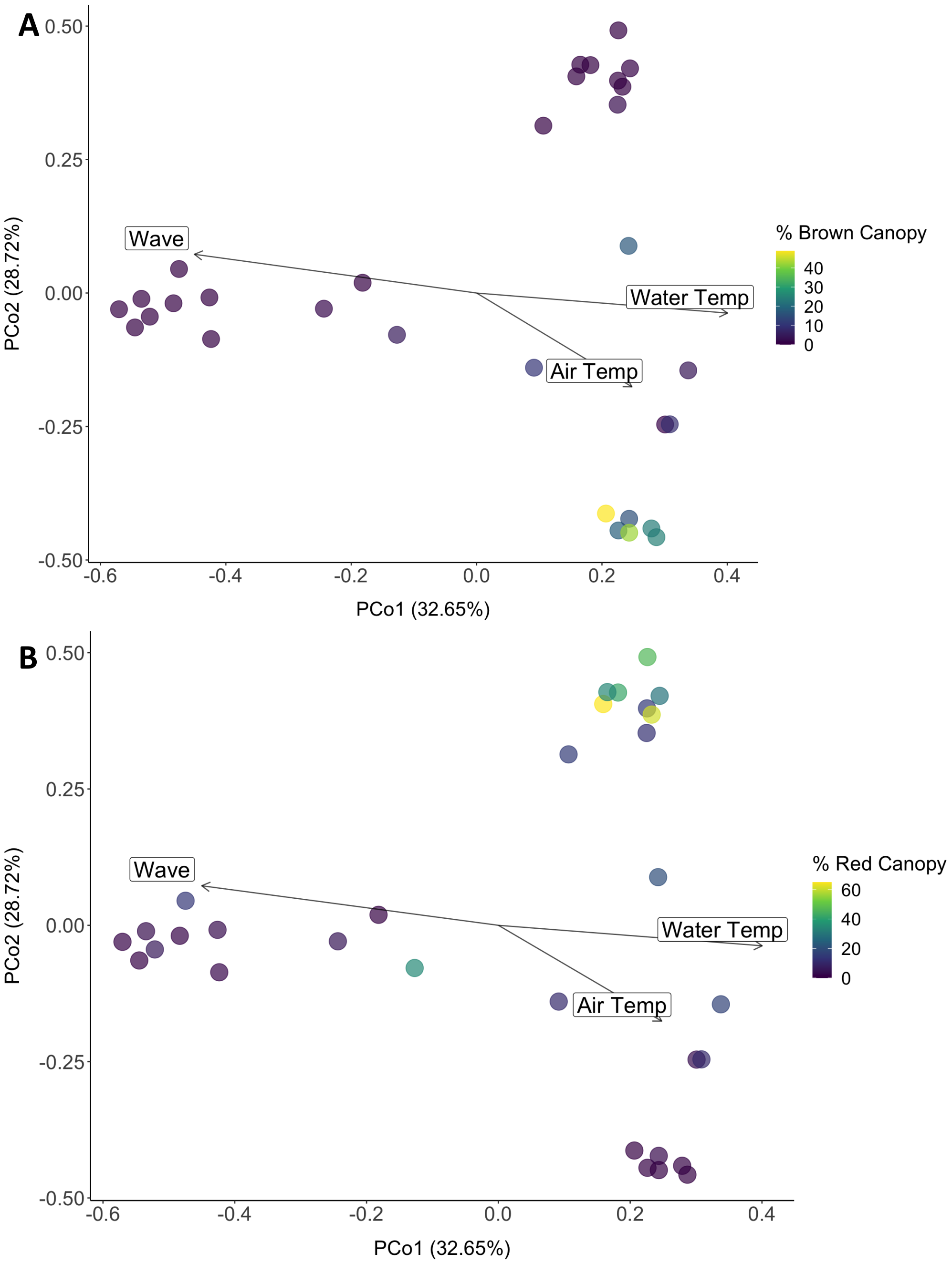

Figure A2. Principle coordinate analysis (PCoA) biplot of community composition, quantified using Bray-Curtis dissimilarity. Percent cover of each biotic species category at each site was used to calculate dissimilarity matrix. Average percent A) brown canopy-forming algal cover and B) red canopy-forming algal cover for each site is represented as a colour gradient. Arrows represent each of the environmental variables examined as drivers for community composition.

Table A1. Species included in each substrate category used to classify benthic cover. Brown algae, red algae, and green algae are classified as the class Phaeophyceae, the phylum Rhodophyta, and the phylum Chlorophyta respectively.

Substrate category	**Definition**	**Lowest possible taxonomic identification**	**Red, Brown or Green Algae**
Kelp	Seaweed species in the order Laminariales	*Alaria marginata* *Costaria costata* *Egregia menziesii* *Eisenia arboarea* *Hedophyllum sessile* *Laminaria setchelli* *Lessionoposis littoralis* *Macrocystis pyrifera*	Brown algae
Turf	Bushy, coarse, and filamentous seaweed species with >1 aggregated thalli and short blades (<15cm)	*Acrosiphonia sp.* *Ahnfeltiopsis sp.* *Cryptopleura sp.* OR *Hymenema sp.* OR *Polyneura sp.* *Gelidium sp.* *Grateloupia sp.* *Halosaccion glandiforme,* *Mastocarpus sp.* *Mazzaella affinis* *Microcladia sp.* *Nemalion helminthoides* *Neogastroclonium subarticulatum* *Neorhodomela sp.* *Odonthalia sp.* *Prionitis sp.* *Pyropia sp.* Articulated coralline algae Filamentous red algae Unidentifiable red turf algae	Red algae
		Ulva sp.	Green algae
		Leathesia marina *Colpomenia sp.*	Red algae
Red Canopy-Forming Algae	Red algae with long blades (>15cm)	*Mazaella sp.* *Chondracanthus sp.*	Red algae
Brown Canopy-Forming Algae	Brown algae with long blades (>15cm)	*Fucus distichus* *Sargassum muticum*	Brown algae
Encrusting Algae	A concretion of algae encrusted to the substrate	Crustose coralline algae Fleshy red encrusting algae (Encrusting *Mastocarpus* OR	Red algae

Substrate category	**Definition**	**Lowest possible taxonomic identification**	**Red, Brown or Green Algae**
		Hildenbrandia sp. OR unidentified red encrusting algae)	
Seagrass	Seagrass	*Phyllospadix sp.*	NA
Invertebrates	Animals classified as invertebrates	Anemone Bryozoan Chiton Seastar Barnacle (Non-stalked) Stalked barnacle (*Pollicipes sp.*) Mussel Sponge Tunicate	NA
Abiotic	Abiotic substrates	Rock	NA

References

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