

# **Temperature, size, and harvest method drive recovery in an Indigenous kelp fishery**

**by**

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## Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

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## Abstract

Identifying how to harvest populations in a way that maintains ecological resilience is a fundamental issue in applied ecology. Fortunately, resources users around the world have gathered knowledge of these strategies over millennia. Today, within the context of new market opportunities and changing environmental conditions, communities are being faced with the conservation and management challenge of adapting traditional harvest systems within shifting social-ecological conditions. *Egregia menziesii*, an ecologically and culturally important intertidal kelp, has been harvested on the coast of British Columbia by the Hałtzaqv (Heiltsuk) First Nation for generations. In light of an emerging commercial opportunity for a small-scale harvest, we worked in collaboration with Heiltsuk managers to examine effects of a traditional *Egregia* harvest. Using Indigenous knowledge interviews and a harvest experiment, we found no detectable effect of harvest treatment (25% frond removal) on *Egregia* recovery, and that pre-harvest size, site-level seawater temperature and wave exposure were the most important drivers of kelp recovery from harvest. Additionally, we found parallel understandings of these drivers within Heiltsuk Indigenous knowledge. Overall, we found that traditional *Egregia* harvest practices reflect the ecological conditions that confer resilience, and specifically that harvest practices rooted in Indigenous knowledge promote recovery. Lastly, we provide an example of how successful co-produced research can produce locally legitimate and relevant research outcomes to inform resource management problems in a changing world.

**Keywords:** Kelp, harvest, Indigenous knowledge, *Egregia menziesii*, Knowledge co-production

*For my Grandmother,  
who taught me that the most beautiful and rewarding things in life  
take care, hard work, and a little bit of love*

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# Chapter 1.

## Introduction

Identifying what makes populations ecologically resilient to harvest is a fundamental question in applied ecology. Fortunately, knowledge of these conditions has been gathered over centuries, if not millennia, of experimentation, observation and learning by resource users around the world (eg. Ferguson et al. 1998, Olsson and Folke 2001, Mulyoutami et al. 2009, Jackley et al. 2016). Today, however, particularly along the world's shorelines, communities are being faced with changing climatic conditions (Hobbs et al. 2009) and new market opportunities (Campbell et al. 2016, Ehlers 2016). Consequently, coastal communities are increasingly being confronted with the management and conservation challenge of maintaining or adapting traditional small-scale harvest systems within new social-ecological conditions. Globally, this challenge is heightened among coastal indigenous communities, which experience disproportionate levels of poverty (UN 2009), growing food insecurity (Turner and Turner 2008, Kuhnlein et al. 2013), and constrained economic opportunities (Mackey and Strathdee 2015).

Coastal indigenous peoples' food security, livelihood, health and culture are intimately connected to and dependent on the ocean (Capistrano and Charles 2012, Cisneros-Montemayor et al. 2016, Islam and Berkes 2016, Mathews and Turner 2017). For people who rely heavily on seafood, it provides both an important source of protein and critical micronutrients (Golden et al. 2016) and coastal indigenous people consume 15x more protein from the sea per capita relative to non-indigenous communities (Cisneros-Montemayor et al. 2016). Additionally, maritime harvest activities are also a foundation of cultural identity and intergenerational knowledge transmission (Brown and Brown 2009, Turner et al. 2013). However, climate change and other human activities, such as over harvesting, are projected to impact both commercial and subsistence fisheries (Cheung et al. 2015, Savo et al. 2016, Weatherdon et al. 2016). For example, on the Pacific coast of North America the potential catch of Pacific herring (*Clupea pallasii*) is projected to decline up to 49% by 2050 under future climate change scenarios (Weatherdon et al. 2016). Presently, in the same area, 41% of Indigenous households

(on reserve) are food insecure (Chan et al. 2011), the depletion of culturally important species, such as abalone, by commercial fisheries has resulted in limited subsistence access for Indigenous communities (Turner et al. 2013), and the dietary transition away from traditional foods has led to negative health problems (Egeland et al. 2011, Kuhnlein et al. 2013). These interconnected problems of climate change and poverty threaten culture, health, and food security (Turner and Turner 2008, Turner et al. 2013, Cisneros-Montemayor et al. 2016). Consequently, a pressing need exists to devise new opportunities, and adapt existing ones, that provide economic benefit while maintaining culture and the productivity of the coastal ecosystems that communities and harvest systems rely on.

Among the world's coastal communities, seaweeds have been harvested for food, medicine, materials and trade for millennia (Turner 2001, Mac Monagail et al. 2017). From the Arctic to the tropics, seaweed is an important source of nutrition for maritime peoples (eg. Wein et al. 1996, Hart et al. 2014). Seaweed also has intrinsic social value as a trade item between communities (Turner 2001, 2003) and embedded cultural value associated with the act of harvesting (Turner and Turner 2008, Hart et al. 2014, Mac Monagail et al. 2017). The use of seaweed by coastal societies has been dated back 2,000 in European countries (Mac Monagail et al. 2017), and up to 14,000 years ago in Chile (Dillehay et al. 2008). It's even hypothesized that the peopling of North America may have occurred by sea, as people followed and made use of rich kelp forests along the fringe of the Pacific 16,000 years ago (Erlandson et al. 2007). In more recent years, there is an increasing global market for seaweed (Buschmann et al. 2014, Nayar and Bott 2014), and small-scale artisanal harvest of seaweed may provide a sustainable source of income for coastal communities (Rebours et al. 2014, Mac Monagail et al. 2017) building on cultural traditions of harvest that have sustained seaweed over time.

Kelps, seaweeds in the order Laminariales are found along temperate and arctic coastlines worldwide, are often targeted for harvest due to their fast growth rates (Mann 1973), high levels of biomass, and a strong capacity to recover from disturbances (Dayton et al. 1992). Consequently, kelp harvesting may provide a unique economic opportunity that doesn't compromise ecological integrity and other cultural uses. For example, recent research on *Lessonia nigrescens* in Chile showed no detectable effect of selective commercial harvest on kelp populations or macroinvertebrate richness after

6 years of continuous harvesting activity (Vásquez et al. 2012). On the coast of British Columbia, recent research on the harvest of *Macrocystis pyrifera* showed complete recovery (100-137% recovery) from partial canopy removal (30-70%) after three weeks with growth rates of 4-30 cm/d and no long-term effects on associated reef fish communities (Krumhansl et al. 2017). However, kelp harvest can also negatively affect kelp population dynamics by reducing reproduction potential (Reed 1987, Geange 2014) and recruitment (Thompson et al. 2010). Moreover, removal of kelp biomass can alter associated algal communities and affect dependent consumers through direct and indirect effects (Druehl and Breen 1986, Lorentson et al. 2010). Additionally, kelp provides important ecosystem services, such as habitat provisioning for commercially important fish (Smale et al. 2013, Vasquez et al 2014), and thus the removal of kelp biomass may pose trade-offs. Although there are examples of sustainable contemporary commercial harvest systems that confer ecological resilience, this may not be the case for all harvests. Other culturally important kelps have existing systems of harvest, such as *Egregia menziesii*, the feather boa kelp (hereafter '*Egregia*'), however these kelps are comparatively slower growing and thus may have lower potential to sustain a commercial harvest while retaining ecological resilience and balancing cultural uses.

*Egregia* is a culturally and ecologically important kelp species for Northwest Coast Indigenous peoples, including the Haítzaqv (Heiltsuk) people on British Columbia's central coast. *Egregia* is a perennial kelp found in wave swept rocky intertidal and shallow sub-tidal habitats along temperate reefs from northern Baja to south central Alaska (Abbott and Hollenberg 1976). As a foundation species, *Egregia* acts as a source of food and shapes intertidal community composition by scouring substrate while also providing habitat for some species (Hughes 2010). Culturally, yáka (yagia) refers to *Egregia* when it is layered with Pacific herring (*Clupea pallasii*) roe, an important gift, food and trading item for the Heiltsuk people (Fig 1). *Egregia* harvesting practices reflect traditional ecological knowledge; Heiltsuk harvesters partially harvest individual *Egregia* plants<sup>1</sup>, and cut fronds above the holdfast to ensure regeneration. *Egregia* is currently harvested for food, social and ceremonial purposes but there is opportunity to expand this harvest to a small-scale artisanal fishery. Heiltsuk resource managers are interested in informing *Egregia* harvest management that continues to

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<sup>1</sup> While *Egregia* is not a 'plant' taxonomically but a macroalga in the order Laminariales, plant is commonly used as a colloquial term to mean one individual macroalga

uphold cultural values and ecological integrity while potentially providing economic opportunity.

Here, in collaboration with the Heiltsuk First Nation, and driven by Heiltsuk research priorities, we examined individual *Egregia* recovery following harvest using a traditional harvest method. Specifically, we used Indigenous knowledge and a harvest experiment to ask: 1) how does traditional harvest practice affect *Egregia* biomass, frond elongation and new frond production; 2) what local environmental conditions most effect this recovery; and 3) what management and stewardship practices are currently being used in the harvest of *Egregia*? We predicted that harvested *Egregia* plants would have reduced growth compared to un-harvested control plants due to meristem removal (See Appendix A for description of *Egregia* growth). Moreover, we predicted four key environmental conditions would drive variation in recovery post harvest. Based on the intermediate disturbance hypothesis (Grime 1973, Connell 1978) and previous kelp specific research, we predicted that wave exposure and *Egregia* biomass recovery would have a dome shaped relationship, where optimal recovery would occur at intermediate magnitudes of wave exposure (Friedland and Denny 1995, Demes et al. 2013). Based on density dependent effects on *Egregia* growth (Black 1974), we predicted that ambient kelp density would have a negative effect on recovery. We also predicted that warmer seawater temperatures would have a negative effect on recovery (Gordon and De Wreede 1978, Krumhansl et al. 2017). Lastly, based on the relationship between *Egregia* size and grazer density (Black 1976), we predicted that higher grazer densities would reduce biomass recovery. Finally, we surmised that stewardship practices for *Egregia* would include selection of plants based on individual plant characteristics, population level characteristics, and fundamental sustainability practices of limited harvests and resilience principles of reciprocity and respect (Brown and Brown 2009, Artelle et al. 2018).

## Chapter 2. Methods

### 2.1. Study area

We experimentally harvested *Egregia* at five rocky intertidal sites along the central coast of British Columbia, Canada, in the traditional territory of the Heiltsuk Nation (Fig 1, Fig B1) during the spring growing season (April 2017). Sites were selected based on recommendations from Indigenous natural resource managers and harvesters as known areas of *Egregia* abundance and common harvesting areas. Specific study sites were chosen along a gradient of wave exposure, and are characterized by accessible sloping bedrock outcrops and contiguous stands of *Egregia* above mean low water mark.

At each site, a 30 x 2 m horizontal belt transect was placed at approximately the same tidal height (~1m above chart datum) through the zone of densest *Egregia*. Within this belt transect we measured daily sea surface temperatures, estimated grazer and ambient kelp densities, and conducted a harvest experiment.

### 2.2. Harvest experiment

To test the effects of the traditional harvest practice, we randomly selected n=9-15 *Egregia* plants within our belt transect, tagged all the fronds of each plant at the holdfast and/or branch point using numbered tubing, and measured each plants' fronds from origin to distal end (1cm accuracy). We then randomly imposed a harvest treatment to n= 6-10 plants and left the remaining plants as un-harvested controls. For each harvested plant, we clipped 25% of the fronds, 45 cm above the holdfast mirroring a recommended 'sustainable' harvesting levels for *Egregia* (L. Druehl pers. comm. 2017). The clipped ends of fronds were then measured (max length) and weighed (grams wet weight) to establish length-weight regressions used later to estimate biomass. To measure *Egregia* recovery rates post harvest, we re-measured the length of all tagged and new untagged fronds 99-114 days later (July 2017).

We calculated six plant level recovery metrics. 1) Net biomass production was calculated based on the following length-weight regression ( $y_i = 0.29462x_i^{1.28818}$ ; *pseudo*

$R^2 = 0.84$ ;  $n = 219$  fronds) and adding all frond biomass during the sampling interval ( $g_{\text{final}} - g_{\text{initial}} \cdot \text{day}^{-1}$ ). 2) Relative biomass production was calculated as the rate of change in biomass between sampling intervals divided by initial biomass ( $(g_{\text{final}} - g_{\text{initial}}) / g_{\text{initial}} \cdot \text{day}^{-1}$ ). 3) Frond production was calculated as the rate of new fronds sprouted between sampling intervals, not accounting for lost fronds ( $\text{fronds}_{\text{final}} - \text{fronds}_{\text{initial}} \cdot \text{day}^{-1}$ ). 4) Relative frond production was calculated as the rate of change in number of fronds between sampling intervals divided by initial number of fronds ( $(\text{fronds}_{\text{final}} - \text{fronds}_{\text{initial}}) / \text{fronds}_{\text{initial}} \cdot \text{day}^{-1}$ ). 5) Frond elongation was calculated as the difference in length during the sampling interval, not including negative measures (similar to Blanchette et al 2002), and adding all frond lengths ( $cm_{\text{final}} - cm_{\text{initial}} \cdot \text{day}^{-1}$ ). 6) Relative frond elongation was calculated as the rate of change in length of all fronds between sampling intervals divided by initial length ( $(cm_{\text{final}} - cm_{\text{initial}}) / cm_{\text{initial}} \cdot \text{day}^{-1}$ ). As these measures are based on net difference between sampling intervals, we do not account for tissue loss experienced during the study period and estimates of frond elongation and biomass production are likely underestimates.

## **2.3. Environmental drivers**

### **2.3.1. Temperature**

At each site, we measured ambient intertidal temperature every 5 minutes for the duration of the study period using HOBO tidbit loggers affixed to the rock at either end of the transect approximately 1m above chart datum. We divided temperature data into exposed air temperature and sub-tidal seawater temperature based on our estimate of when transects were submerged using the nearest observed tidal heights available from Canadian Hydrographic Service. We took the average of all sub-tidal temperature readings for the duration of the study to create mean seawater temperature. We ran models to investigate the relative effect of seawater temperature and air temperature on biomass recovery. The effect of seawater temperature had more empirical evidence, and thus was included in global environmental models over air temperature.



### 2.3.2. Wave Exposure

We used the following model of fetch distance, and wind speed and wind frequency to calculate a relative exposure index (REI) for each site over the study period (from Krumhansl and Scheibling 2011):

$$REI = \sum_{i=1}^{16} (V_i \times W_i \times F_i)$$

where  $V_i$  is average monthly wind speed (km h<sup>-1</sup>),  $W_i$  is wind frequency and  $F_i$  is fetch (km), from the  $i$ th direction (north, north northeast, northeast, east northeast, etc., in 16 increments of 22.5°). Wind data were accessed from Environment Canada's National Climate Data and Information Archive.

### 2.3.3. Grazer & Ambient Kelp densities

To estimate the densities of dominant herbivores and kelps at each site, we counted all visible grazers (*Katharina tunicata*, *Strongylocentrotus droebachiensis*, *S. purpuratus*, *Mesocentrotus franciscanus*) and kelp stipes (*Alaria marginata*, *Macrocystis pyrifera*, *Saccharina sessilis*, *Saccharina groenlandica*, *Costeria costata*, *Egregia menziesii*) in  $n = 8$ , 1m<sup>2</sup> plots randomly stratified within our 30 x 2 m belt transect.

## 2.4. Indigenous Knowledge Interviews

We interviewed *Egregia* experts (resource users, knowledge holders and managers) in the nearby Heiltsuk community of Bella Bella in May 2018 (Fig B1). Experts were selected through recommendations from the local stewardship office and through chain-referral (Huntington 2010). We conducted a quantitative survey combined with semi-directed interviews. Survey questions were used to quantify expert knowledge, and semi-directed questions allowed experts to share knowledge beyond the scope of the survey. We asked questions about *Egregia* harvest rates, variables that influenced recovery post harvest, observed changes over time, and subsistence harvest and stewardship practices. We recorded and later transcribed interviews.

To quantify the magnitude and variation on reported subsistence harvest rates we asked harvesters to identify the amount they typically harvest to the closest percent

using a diagram (Fig B2). To quantify local observations on the environmental factors that influence *Egregia* recovery rates we asked harvesters to rank the relative importance of environmental variables using a Likert scale (1-7), where respondents select a ranking from 1 (not important) to 7 (extremely important). These rankings were relativized for ease of comparison among ecological models. We first asked harvesters to identify environmental variables, and then we presented them with a standardized list of variables analogous to those measured in our ecological experiment to be ranked. For open-ended questions about harvest practices, similar responses were categorized into dominant themes. Because not all participants answered each question, sample sizes varied per question.

## 2.5. Statistical Analysis

### Model Selection

To determine the strength of evidence for an effect of harvest on *Egregia* recovery across our five sites, we took an information theoretic approach. We compared multiple candidate models that included treatment (harvest, control), site and their interaction as fixed effects for a total of 5 candidate models including an intercept null model of no effect. Site was used as a fixed effect (as opposed to a random effect) in order to quantify and compare its relative effect on recovery with the effect of treatment. To determine effects of site and treatment we used proportional measures of growth because on average harvest treatment plants were larger due to sampling effort and by using proportional measures we removed the effect of size in driving model outcomes. We built generalized linear models (GLM) using a Gaussian error distribution for models of relative biomass recovery, and a Gamma error distribution for models of relative frond production and relative frond elongation. For models looking at the effect of harvest on relative frond production we removed one outlier that didn't conform to the error distribution. Models were fit using maximum likelihood and alternative candidate models were compared using small-sample corrected Akaike information criterion (AIC<sub>c</sub>) standardized to the most parsimonious model to produce  $\Delta\text{AIC}_c$  and normalized Akaike weights ( $w_i$ ) (Burnham and Anderson 2002). Empirical support for a model was taken to be when the next most parsimonious model had a  $\Delta\text{AIC}_c$  value  $>2$ .

To assess the strength of evidence of various environmental drivers (i.e. initial plant size, seawater temperature, wave exposure, grazer density, and ambient kelp density) influencing growth and recovery of harvested *Egregia* plants we built a series of generalized linear models (GLM). We selected individual predictors based on *a priori* hypotheses about *Egregia* growth (Burnham and Anderson 2002) and used a Gaussian error distribution for models of biomass and relative biomass recovery, and a Gamma error distribution for models of frond production, relative frond production, frond elongation and relative frond elongation. Models were fit using maximum likelihood and alternative candidate models were compared using small-sample corrected Akaike information criterion (AIC<sub>c</sub>) standardized to most parsimonious model to produce  $\Delta\text{AIC}_c$  and normalized Akaike weights ( $w_i$ ) (Burnham and Anderson 2002). Empirical support for a model was taken to be when the next most parsimonious model had a  $\Delta\text{AIC}_c$  value >2.

We compared all model subsets, and model averaged a set of (“top”) candidate models ( $\Delta\text{AIC}_c < 4$ ) using the MuMIn package in R (Bartoń 2018). We selected this threshold ( $\Delta\text{AIC}_c < 4$ ) to facilitate comparison of all fixed effects across models and knowledge types, while still selecting for models with some empirical support ( $w_i > 0$ ). Regression coefficients were calculated using conditional averages and relative variable importance (RVI) using sum of Akaike weights ( $w_i$ ) (Burnham and Anderson 2002). Predictors were assessed for co-linearity using correlations coefficients ( $<|0.5|$ ) and variance inflation factors (VIFs) ( $<10$ , Quinn and Keough 2002) (Fig B3). Predictors were centered and scaled (by one standard deviation) to facilitate comparison between fixed effects (Schielzeth, 2010). Residuals were inspected to ensure data met assumptions of normality and homoscedasticity. We tested for normality with the Shapiro Wilk test. For *Egregia* biomass recovery, we completed analyses with and without two outliers and found no difference in our results. Moreover field notes indicated that these outliers were within *Egregia*'s natural range of variation. Consequently, outliers were kept for all subsequent analyses. All of the statics above were conducted in R (R Core Team 2017).

## Chapter 3. Results

### 3.1. Effect of Harvest

Relative biomass production over the duration of our experiment was most strongly influenced by site ( $\Delta AIC_c = 0.0$ ,  $w_i = 0.80$ , Table 1a), and ranged from 0.8 %·day<sup>-1</sup> (Cape Mark) to 3.9 %·day<sup>-1</sup> (Spider) (Fig 2a). This resulted in a 5-fold difference in relative biomass production between sites. Net biomass production also varied widely across sites, ranging from 6.92 g·day<sup>-1</sup> (Cape Mark) to 42.56 g·day<sup>-1</sup> (Simonds), a difference in net biomass production of 6.2 times.

Across all sites, harvested and un-harvested control plants produced comparable kelp biomass (of 3.1 %·day<sup>-1</sup>). There was little support for an effect of harvest treatment on relative biomass recovery in statistical models, with all models including harvest treatment having a  $\Delta AIC_c > 2$  and low model weights (Table 1a). We also found no evidence for an interaction between site and harvest treatment ( $w_i = 0.0$ , Table 1a).

We found similar results across all 3 metrics of *Egregia* growth (relative biomass production, relative frond production, relative frond elongation), with strong evidence for an effect of site on relative frond elongation ( $w_i = 0.79$ ,  $\Delta AIC_c = 2.65$ ), and relative frond production ( $w_i = 0.89$ ) (Fig B4, Tbl B1). We found evidence for an effect of treatment on frond production but it was relatively weak compared the effect of site ( $w_i = 0.48$ , SI Fig 4).

The level of frond removal we used for our experimental harvest treatment (median = 0.24) was within the range of variation of natural loss experienced by un-harvested control plants (0 – 0.50, median = 0.17) but 2 times lower than realized subsistence harvest levels reported by harvesters (median = 0.49) (Fig 2B).

### 3.2. Environmental Drivers of Kelp Recovery

Initial biomass, seawater temperature and wave exposure explained 69% of the variation in net kelp biomass recovery post-harvest (Table 1B). Across all measures of kelp growth, including biomass production, new frond production and frond elongation,

initial measures of plant size, specifically plant biomass, number of fronds and frond length, were the most important variables influencing kelp recovery alongside seawater temperature. Once initial size was accounted for in our relative measures of growth, seawater temperature was the most important variable influencing all measures of kelp recovery followed by wave exposure and grazer density.

### **3.2.1. Initial Size**

We found strong evidence that initial size of harvested individuals had a precise, positive effect on net biomass recovery, frond elongation, and frond production post-harvest (RVI = 1, Table 1B; Fig 3A). The amount of biomass recovered increased with initial biomass, (Fig 4A), and frond production increased with higher numbers of initial fronds. Experts ranked pre-harvest size as the lowest driver of kelp recovery rate post harvest (median ranking = 0.57; Fig 3B).

### **3.2.2. Seawater Temperature**

We found strong evidence that seawater temperature had a precise, negative effect on recovery in ecological models of multiple growth metrics; net biomass recovery (RVI = 1, Table 1B, Fig 3A), relative biomass recovery (RVI = 1, Table 1b, Fig B5), frond production (RVI = 0.8, Table 1B, Fig B5) and elongation rate (RVI = 1, Table 1B, Fig B5). Additionally, experts ranked seawater temperature as the most important environmental driver of kelp recovery after harvest method (median rank = 0.86, Fig 3B). Across our five sites, seawater temperature ranged from 11.52 °C (+/- 1.78) to 12.53 °C (+/- 3.10 sd). We observed a 7.41 times greater median biomass recovery and 3.44 times greater median relative biomass recovery, at coolest compared to warmest sites (Fig 4B,D).

### **3.2.3. Grazer Density**

For relative biomass production we found that grazer density had a relatively strong positive effect on recovery post-harvest (RVI = 0.84, Table 1B, Figure 4C). Mean grazer density estimates ranged from 0 to 7.75 /m<sup>2</sup> (+/- 2.21 se). We observed a similar effect of grazer density on relative frond elongation (RVI = 0.87, Fig B5). Grazer had a relatively weaker and variable effect on relative frond production (RVI = 0.36, Fig B5). Experts ranked grazer density as one of the least important drivers, only more important

than pre-harvest size, but still relatively high (median rank = 0.71, Fig 3B). Conversely for models of biomass production, and frond production that included size as a fixed effect, there was relatively little evidence for an effect of grazer density, and the effect was variable (RVI = 0.11; RVI = 0.25, Fig 3A, Fig B5, respectively).

### **3.2.4. Wave Exposure**

We found a relatively important negative effect of wave exposure on biomass recovery ( $w_i = 0.71$ , Fig 3A, Table 1B), relative biomass recovery ( $w_i = 0.66$ , Fig B5, Table 1B), and relative frond elongation (RVI = 0.87, SI Fig 5). The effect of wave exposure on frond production was less important than initial number of fronds and seawater temperature, and this effect was variable (RVI = 0.43, Fig B5). Experts ranked wave exposure as an important driver of kelp biomass recovery, wave exposure was ranked similar to seawater temperature but less important than harvest method (median rank = 0.86, Fig 3B).

### **3.2.5. Ambient Kelp Density**

We found relatively little strength of evidence for an effect of ambient kelp density on growth post-harvest across metrics of growth (RVI = 0.19 for biomass recovery, Fig 3A; RVI = 0.4 for relative biomass recovery, Fig B5; RVI = 0.19 for frond production, Fig B5; Table 1B). Kelp stipe densities at experimental sites ranged from 7.38 +/- 1.59 se to 52.25 +/- 18.45 se stipes•m<sup>-2</sup>. Experts ranked ambient kelp density to be somewhat important for recovery post harvest (median rank = 0.75), ranking above grazer density and pre-harvest size (Fig 3B).

In interviews, kelp harvest experts also identified sunlight, air temperature, “seeding” (new growth emerging from discarded ends of harvested *Egregia*), sea otters, and weather/storms as important environmental drivers of recovery post-harvest (not included in figure as the rankings for these factors came from < 9% of respondents).

## **3.3. Stewardship Practices**

In total 22 people took part in quantitative surveys and semi-structured interviews. In general participants ranked their knowledge of Heiltsuk food fisheries,

harvest and stewardship practices at 4.57 (+/- 0.13 SE) out of 5, and at 4.05 (+/- 0.18 SE) out of 5 for yáka harvest and stewardship practices specifically. We interviewed 18/26 (69%) recommended people as well as an additional 4/12 (33%) of names received through chain referral for a total of 22/38 (58%) people. Of all (n = 22) participants 91% were male and 9% were female. Participants ranged from 36 to 88 years old with an average age of 60. Some respondents had more knowledge of processing (specifically women respondents) or broader knowledge of stewardship practices in general (elders), whereas current harvesters could speak more to modern day practices and trends.

### **3.3.1. Harvest Method**

Harvest method was ranked (by experts/harvesters) as the most-important driver of recovery post-harvest relative to all ecological drivers (median = 1).

### **3.3.2. Amount Harvested**

On average, harvesters (n = 17) remove 50% (median) of individual *Egregia* (Fig 2B) (ranging from 20% to 65%) and expressed that the amount they harvest per plant varies with weather conditions, and associated ease of harvesting, as well as the age/length of the plant.

### **3.3.3. Plant Characteristics**

Harvesters are selectively harvesting for large plant size (68%, n = 19), good health (47%), good quality and amount of blades (42%), and/or the health of a particular 'patch' of *Egregia* (11%) (Fig 5A). Experts that identified 'long fronds' (grouped with large size) as a characteristic of choice expressed that 'long' meant a range from 1.5 to 6 feet (mean 4.19', median of 4.5'). Experts also selected for *Egregia* that had many, long blades.

### **3.3.4. Harvesting Practices**

Nearly all harvesters (91%, n = 22) advocate leaving the holdfast of *Egregia* during harvest to ensure sustainable use. Other practices include taking only what you

need/leaving some behind (41%), assessing the patch size (and harvesting accordingly) (23%), cutting fronds instead of ripping them (23%), and leaving small fronds for regeneration (9%) (Fig. 5B).

### **3.3.5. Harvest Location**

When selecting a location to harvest 68% (n = 19) of harvesters typically return to the same general area every year, and 21% go to different areas every year. People conditionally change where they harvest depending on the proximity to *M. pyrifera* kelp beds (another kelp of harvest interest) and/or the herring spawn (37%), weather and tide conditions (26%), and/or the health of *Egregia* in a certain area (26%) (Fig 5C).

### **3.3.6. Changes Over Time**

Participants that observed changes in *Egregia* abundance over time (74%, n = 19) hypothesized that observed decreases (16%) were due to improper harvesting or environmental changes, and observed increases (26%) were due to harvesting/seeding practices, weather and/or the return of otters. Observed fluctuations in abundance (32%) were due to (improper) harvesting and/or environmental changes/weather. Some participants (26%) observed no changes in abundance over time.

### **3.3.7. Change in Number of Harvesters**

People hypothesized that increases in the number of people harvesting was because more people were participating in the commercial herring spawn on kelp fishery and harvesting *Egregia* simultaneously for subsistence (29%). People also hypothesized that observed increases in the number of people harvesting was due to more people and more boats (24%), and *yáka* gaining popularity as a food source (10%).

### **3.3.8. *Yáka* Uses**

Participants most often harvest *yáka* to give to family or others in the community (64%, n=22), for personal consumption (50%), for trading (36%), for cultural events (14%), and one participant harvests commercially (5%)(Fig 1).



## Chapter 4. Discussion

Our results reveal kelp harvesting practices, rooted in Indigenous knowledge, that enable the recovery of harvested individuals and likely confer resilience in this social-ecological system. Specifically, we found that Indigenous *Egregia* harvest practices mimicked natural levels of loss (Fig 2B). Moreover, we found parallel knowledge of the drivers of recovery among local experts (Fig 3). Plant production was site specific, such that variation in plant size and site-level seawater temperature, and wave exposure influenced *Egregia* recovery (Fig 3, Table 1b). Indigenous stewardship practices reflect these ecological relationships, for instance the complimentary practice of selecting large plants from healthy patches of *Egregia* (Fig 4a, 5a). Here, we used an ecological experiment and field surveys alongside Indigenous knowledge to create an enriched picture of kelp harvesting, and better inform future harvests and local management.

### Kelp Harvest Within Range of Natural Loss

A management challenge for small-scale kelp harvest is determining what level of biomass removal allows for recovery. Counter to our predictions, we found no detectable effect of our harvest treatment (25% frond removal designed to mimic traditional practices), on kelp biomass production (Fig. 2a, Table 1a). This moderate level of harvest was within the natural range of frond loss we observed over the same period (Fig. 2b), and therefore the lack of detectable effect is attributable to these similar rates of loss. Both the level of natural frond loss we observed (median 17% frond loss) as well as our level of harvest (25% frond removal) are within recorded rates of frond loss for *Egregia* (Demes et al. 2013), potentially indicating we could expect a comparable effect of a similar level of harvest elsewhere. However natural levels of loss in kelp vary temporally and spatially, and natural tissue erosion rates can exceed production leading to biomass loss over time (Krumhansl and Scheibling 2011). Thus, mimicking natural levels of loss may not necessarily provide a benchmark practice for sustainable kelp harvest. Additionally, harvested plants are also exposed to natural loss in addition to harvest, which could potentially magnify cumulative levels of loss and affect the ability of kelp to recover. The effect of harvest, or the detection thereof, may

therefore change depending on the ambient levels of frond loss experienced by kelp at a particular harvest site, and the intensity of frond loss relative to growth at that site.

The method with which kelp is harvested can affect its ability to recover (Levitt et al. 2002, Rothman et al. 2006, Thompson et al. 2010, Borrás-Chavez et al. 2012). Research on *M. pyrifera* demonstrated the ability of multi-frond kelp to generate new fronds and recover from partial harvest methods (Borrás-Chavez et al. 2012, Krumhansl et al. 2017). Contrary to our original predictions, we observed that *Egregia* recovered to and exceeded pre-harvest biomass after being partially harvested. This is because, similar to *M. pyrifera*, *Egregia* is a multi-frond kelp and after harvest sprouted new fronds from the remaining stipes (see Appendix A for more detailed description of growth). It was this unexpected, prolific growth of new fronds that led to complete recovery from harvest, suggesting this kelp is resilient to moderate harvest methods.

Harvesting of kelp biomass at rates higher than annual or seasonal renewal can cause over-exploitation (Mac Monagail et al. 2017), and negatively impact kelp population dynamics and surrounding ecosystems (eg. Lorentsen et al. 2010, Geange 2014). Additionally, higher intensity of harvest can reduce the capacity of kelp to recover (eg. Borrás-Chavez et al. 2012). We found reported subsistence harvest of *Egregia* to be highly variable and on average double the amount that we removed experimentally (Fig 2b). This level of harvest could have negative implications for kelp recovery. Additionally, even when individual kelp plants recover, impacts can occur over the long-term and at the population level. For example, despite recovery of vegetative biomass after removal of *M. pyrifera* surface canopies, research showed that the generation of reproductive blade was reduced by 68% (Geange 2014). The removal of biomass from the ecosystem can also impact dependent ecological communities, whereby the majority (80%) of kelp production enters marine (and terrestrial) food chains as detritus (Krumhansl and Scheibling 2012). Although we observed no detectable effect of harvest (Table 1a), we specifically looked at recovery of biomass after 25% frond removal, and not at the effects on reproductive capacity nor did we quantify ecosystem effects. We find that individual *Egregia* plants are resilient to this harvest method, including amount, but further work would be required to examine effects of increased intensity of harvest, and potential population and ecosystem level effects.

## Plant Size and Seawater Temperature Influence Kelp Recovery

The size of an individual within a population has been shown to influence growth, and resistance to disturbance (eg. Duggins et al. 1989, Claessen et al. 2000, Audzijonyte et al. 2015). Similar to previous work on kelps (Rothman et al. 2006) including *Egregia* (Black 1974) that showed larger plants grow faster, we found that larger plants recovered more biomass (Fig. 4a). This could be due to greater photosynthetic capacity of larger fronds. Alternatively, Black (1974) observed crowded plants grew slower and consequently larger plants may have escaped effects of crowding and shading. However, we did not find support for an effect of ambient kelp density in our models (likely because densities were too low over the range measured to have an effect on recovery), which would have added further support to this hypothesis.

Paradoxically, initial plant size did not emerge as an important driver of recovery from expert knowledge (Fig 3b) yet experts did describe the deliberate use of size selective harvesting practices (Fig 5A). The experiential nature of expert knowledge means that here knowledge is likely based primarily, if not entirely, on larger plants targeted by harvest. So while we found an important effect of plant size on recovery rates based on our ecological models, the findings from our ecological experiment are based on randomly selected plants that represent a range of plant sizes. Thus, this paradox may be due to the respective sample populations upon which Indigenous knowledge and ecological observations were made. As traditional harvesting practices already reflect this relationship with size (by selecting for large plants), this experimental finding corroborates existing practice. Furthermore, the environmental conditions we detected that most promote *Egregia* recovery post harvest were reflected, in the same order of importance, in Heiltsuk Indigenous knowledge.

Temperature, one of the main factors influencing kelps (Dayton 1985, Dayton et al. 1999), is known to drive kelp geographic distribution and abundance (Lüning 1990, Dayton et al. 1992). For example, seawater temperature regulates physiological processes, whereby increasing temperatures above species thermal optimum, can negatively affect reproduction and growth (Harley et al. 2012, Eggert 2012). As predicted we observed a negative effect of seawater temperature on biomass recovery. However, average temperatures in our study are lower than recorded temperatures in the southern part of *Egregia*'s range (Blanchette et al. 2002), and therefore do not exceed its thermal

tolerance across the range. Kelp species can become locally adapted to their environment, altering individual responses to temperature changes throughout a species' latitudinal range (Blanchette et al. 2002, Buschmann et al. 2004, Moring et al. 2014). Within BC, growth and photosynthesis was observed to be limited in *Egregia* at temperatures higher than 10°C, with detrimental impacts to survival at 15°C (Gordon and De Wreede 1978), possibly indicating that the negative effect of temperature observed here was because temperatures were exceeding thermal optimum of locally adapted populations.

Seawater temperature is also tightly coupled with nutrient availability and seawater temperature is often used as a proxy for examining the effect of nutrients on kelp growth (Zimmerman and Kremer 1984, Dayton et al. 1999, Parnell et al. 2010). Cooler water is more nutrient rich and drives higher density, growth, and recruitment of kelp (Dayton et al. 1999, Parnell et al. 2010, Bell et al. 2015, Pérez-Matus et al. 2017). We observed higher growth at cooler temperatures, over a small range (Fig.4b, d). Multiple studies have shown a threshold temperature of around 10°C above which nitrate concentration drops off rapidly and approaches zero at 15 °C (Dayton et al. 1999, Parnell et al. 2010). This range that encompasses the average seawater temperatures we observed and therefore the effect of temperature we observed might be a signal of an effect of tightly coupled factors such as nitrate concentration. However, our data does not allow us to disentangle these effects. In addition to effects on growth, warmer temperatures and low nutrients can also lead to tissue degradation (Rothäusler et al. 2009, Krumhansl and Scheibling 2011) and thus may be important considerations for both harvested kelp biomass and quality.

## **Waves and Grazers 'Prune' Kelp**

Kelps are exposed to dynamic wave forces that can alter production, size, or morphology of individuals over a range of wave exposure (Gaylord et al. 1994, Hurd 2000, Bell et al. 2015, Starko and Martone 2016). Increased wave exposure can negatively affect kelp biomass through tissue erosion and dislodgement (Cavanaugh et al. 2011, Krumhansl and Scheibling 2011, Bell et al. 2015), but it also supports rapid recovery and increased production compared to more sheltered sites (Graham et al. 1997, Pedersen et al. 2012). This suggests a non-linear relationship between kelp size and wave exposure. *Egregia*, for one, is known for its adaptations to survive in wave-

disturbed environments, including robust holdfasts and 'self-pruning' at high wave exposures (Demes et al. 2013, Friedland and Denny 1995). Given this, we hypothesize highest net biomass production in *Egregia* may occur at wave exposures lower than the upper range of tolerance, and that the negative relationship we observed (Fig 3a) may only be capturing part of a non-linear, hump shaped relationship. As traditional harvest practices target larger plants, consideration of wave exposure is important, as indicated by the relatively high ranking of wave exposure by local experts (Fig3b).

The ability of grazers to alter kelp ecosystems is well-documented (Foreman 1977, Duggins 1980). For instance, in temperate kelp forests, in the absence of keystone predators, high densities of urchins can reduce kelp forests down to barrens (Duggins 1980, Byrnes et al. 2013). However, grazers can also have positive effects on plant growth. For instance, intermediate grazing by *Littorina littorea* has been shown to increase algal diversity in tide pools (Lubchenco 1978). Here, contrary to our hypothesis, we observed a positive relationship between grazer density and proportional growth (Fig 4c). Although grazed fronds are more likely to break (Haggerty et al. 2018), once broken, more branches grow from the main frond or holdfast (Black 1976). By grazing below frond meristems, grazers are stimulating growth of new fronds, similar to 'pruning' of land plants. However, we did not observe an effect of grazers on non-relative measures of *Egregia* production, confirming our original hypothesis that grazer presence would reduce size and ultimately amount of biomass. As plants at highly grazed sites were smaller overall, we hypothesize these individuals have a greater capacity to increase proportionally.

Lastly, the factors driving kelp forest ecology are never independent (Dayton 1985, Dayton et al. 1999) and interactive effects on kelp production can affect kelp differently than on their own (eg. Wernberg et al. 2010, Filbee-Dexter et al. 2016). Although we did not find any evidence for an interaction between site and harvest, we found an effect of local stressors like temperature over small scales. Even within the context of large-scale global change, local scale-stressors dominate as important drivers of kelp dynamics (Krumhansl et al. 2016) and together this highlights the possibility for localized conditions, and other stressors, to influence resilience to harvest, as well as underscoring the importance of local management.

## Indigenous Harvest Practices Reflect Resource Stewardship

Emerging ethnographic and archaeological evidence suggests that many Indigenous harvesting practices work in concert with natural processes to maintain or enhance production, and sustain use of resources over time (Turner and Peacock 2005, Ford and Nigh 2009, Mulyoutami et al. 2009, Groesbeck et al. 2014). The suite of kelp harvesting practices described here, emergent from Indigenous knowledge, reflect multiple conditions for kelp recovery. As described above, harvesters primarily select for kelp size when harvesting (Fig 5a), which is complimentary with our finding that larger plants recover more biomass post-harvest (Fig 4a). Therefore, harvesters are, whether intentionally or not, selecting for plants that are more resilient to harvest. Additionally, partial harvest and the technique of leaving the plant's holdfast attached to the rock (Fig 5b) likely allows for regeneration based on observed branching abilities of *Egregia* (Black 1976, Appendix A). Lastly, returning to the same area every year (Fig 5c) suggests the ability to monitor perennial patches of kelp, such as *Egregia*, for harvest effects.

Restricting harvests of marine species to specific areas is common practice among coastal First Nations along the north-eastern Pacific (Trospen 2003, Powell 2012). For example, family ownership of herring spawns, allowed for limited access and monitoring of harvest, and contingent proprietorship meant harvesters were held accountable for sustained harvest over time (Powell 2012). Similar concepts are reflected in contemporary Chilean Territorial Use Rights Fisheries (TURFs) where fisher co-operatives collectively manage fishing areas, incentivizing stewardship of the resources (Gelcich et al. 2010). Visiting the same area every year for kelp harvesting does not imply proprietorship per se, but may reflect similar longer term resource stewardship principles.

Overall we find that *Egregia* harvest reflects the ecological conditions that confer resilience to this form of disturbance, and specifically, that harvest practices rooted in Indigenous knowledge promote recovery. Based on our data we cannot know with certainty the intentionality of these practices, however the nature of traditional ecological knowledge (see Turner and Berkes 2006), suggest that these kelp harvest practices may have evolved over time through processes of learning, observation, and experimentation specifically so as to sustain natural systems upon which societies depended. On the

central coast of BC, harvesting practices are informed by Heiltsuk *Gvi'ilas* (customary law and knowledge) that, for millennia and to this day, have guided relationship to place, and promoted reciprocity, responsibility and respect towards the natural world (Housty et al. 2014). So, while we show how a particular harvesting practice might confer resilience, it is important to contextualize practice within the broader system of values within which it is embedded, and recognize the role that values play in sustaining and healthy environments and societies over time (Artelle et al. 2018).

Over time, Indigenous knowledge and practices have been co-evolving and changing with the dynamic ecosystems within which they are embedded (Berkes et al. 2000, Brown and Brown 2009). Current social-ecological changes, such as high costs of going out harvesting (E. Newman interview May 2018), environmental changes, and ease of access of non-traditional foods (Hilitis P. Waterfall interview May 2018), in addition to continuing effects of colonialism (Turner and Turner 2008) can contribute to intergenerational knowledge loss. We hypothesize this may be catalyzing some of the changes observed in this harvesting system, such as perceptions that some people are improperly harvesting *Egregia* (R. Johnson, R. Carpenter Jr. Interview May 2018) and potentially why reported subsistence harvest is higher than the level of harvest used to inform our experiment (Fig 2b). These reported harvest rates may also be higher due to implementation error, or survey bias. Despite these challenges, cultural practices, such as salmon weirs, are now being adapted to monitor effects of climate change (Atlas et al. 2017), continuing to evolve Indigenous practice in a changing world.

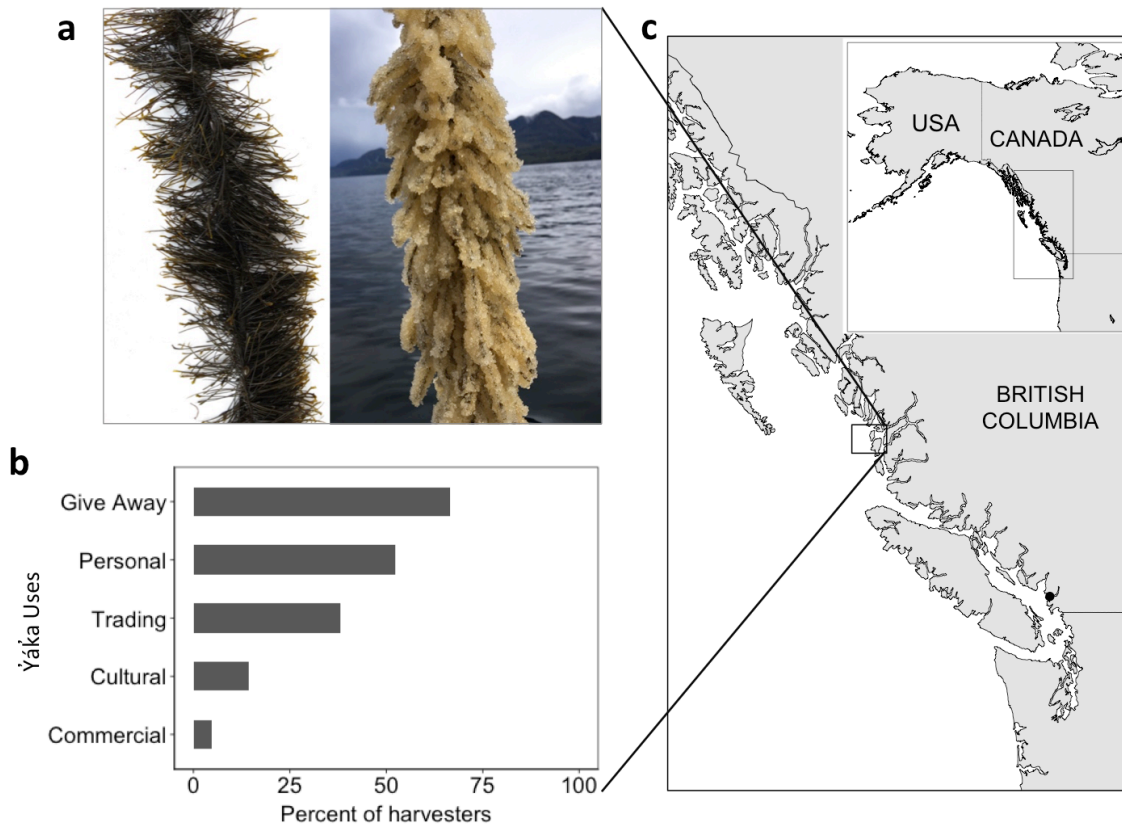
## **Knowledge Co-production to Inform Better Management and Conservation**

Knowledge co-production can contribute to resilient socio-ecological systems by providing a diversity of knowledge systems (Folke 2004, Salomon et al. 2018) and by closing the science-policy gap (Bennett 2018). Additionally, drawing from multiple knowledge forms can lead to innovative solutions in the face of complex problems (Mistry and Berardi 2016, Tengö et al. 2017) such as the complex problem of maintaining and adapting traditional harvests systems within shifting social-ecological conditions. Here, we provide a successful example of knowledge co-production, and show how rooting our research questions in local practice and management priorities, and co-designing the research with local managers, can enhance the legitimacy

(Pinkerton and John 2008) and relevance of research outcomes (Adams et al. 2014, Tengö et al. 2014). Further we show the strengths of including multiple ways of knowing, and the importance of considering both the social and ecological dimensions within resource management problems. Most importantly, this co-developed knowledge is available for local decision makers, and empowers them to make informed management decisions, govern marine resources, and foster resilient communities.

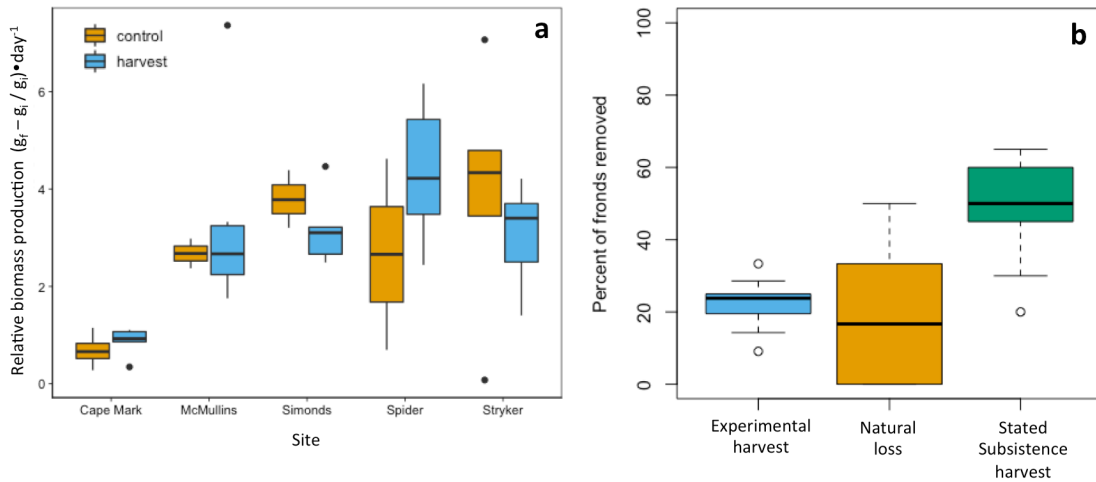


# Figures

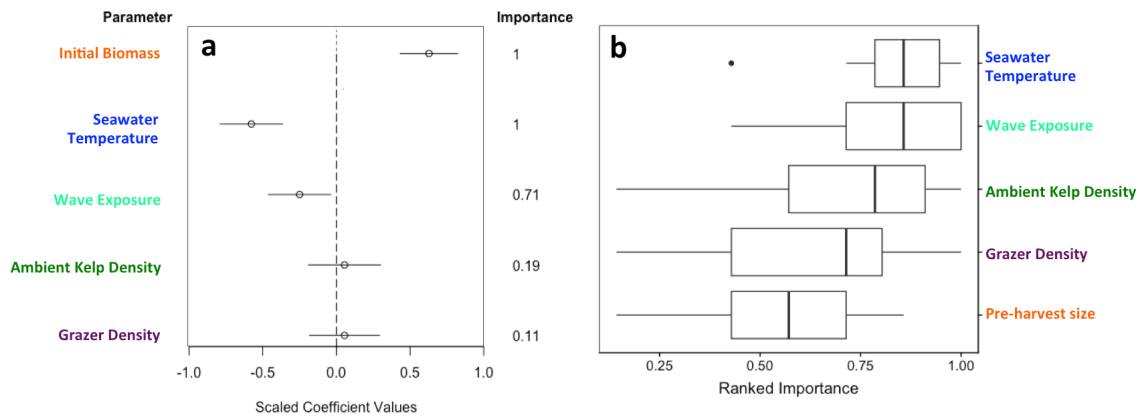


**Figure 1** Study context (a) *Egregia menziesii*, and yáka, *Egregia* coated in herring roe, (b) most prevalent uses of yáka in Heiltsuk community, and (c) geographic location on the central coast of British Columbia.

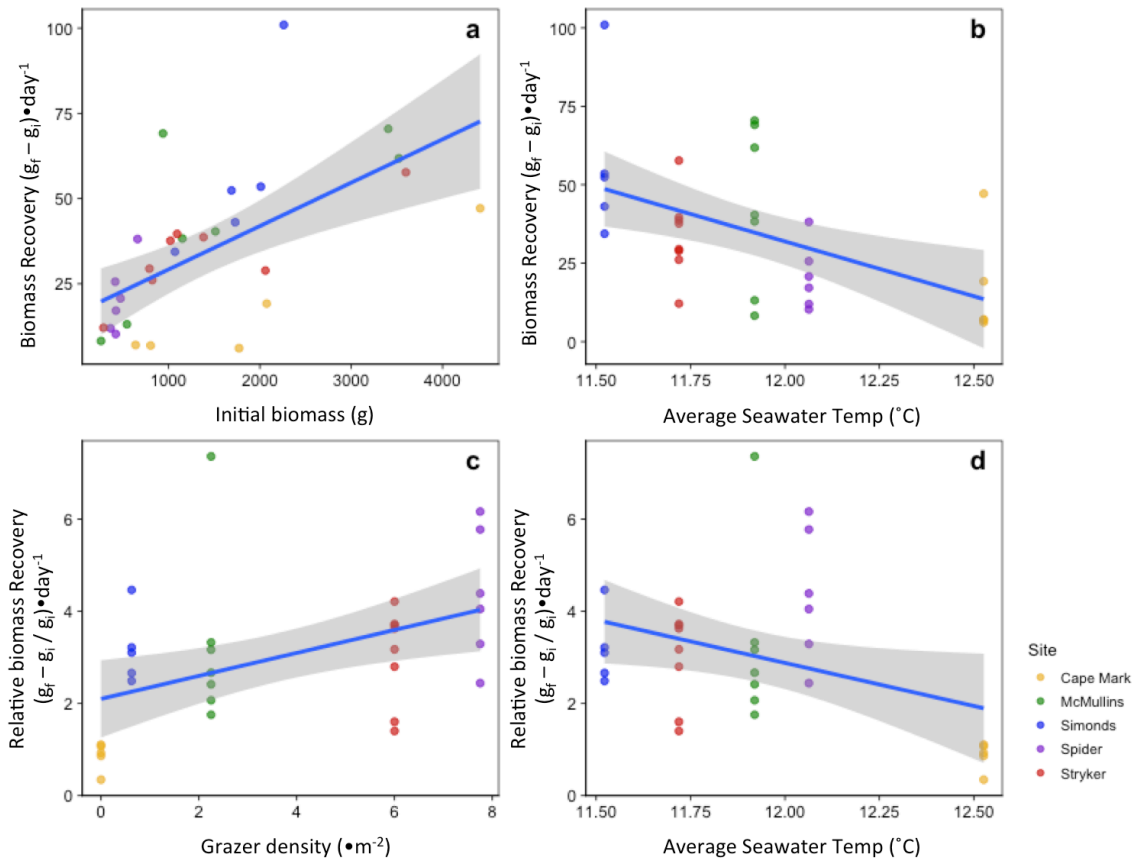
Left photo: Jenn Burt



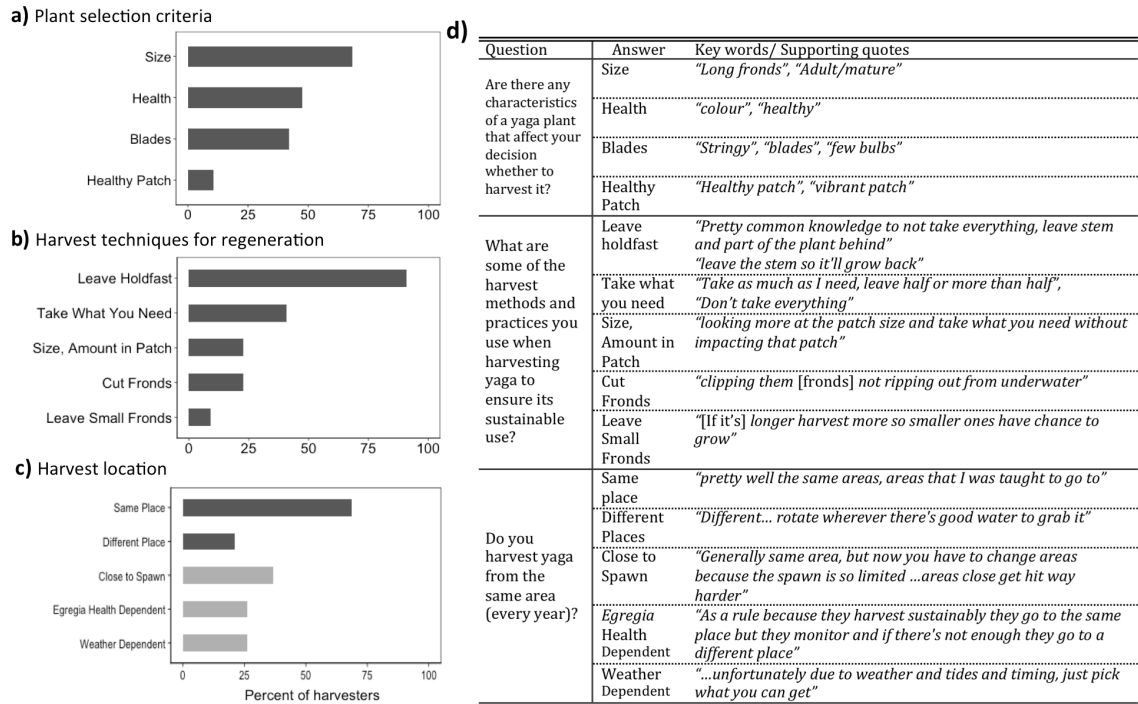
**Figure 2** The effect of experimental harvest on *E.menziesii* (a) relative biomass production as a function of harvest and site, and (b) frond removal of experimental harvest in relation to other sources of removal, experimental harvest and natural loss are from ecological experiment data, and stated subsistence harvest from Indigenous knowledge



**Figure 3** Relative importance of environmental, and social factors, in driving *E. menziesii* growth post-harvest from (a) generalized linear models of biomass recovery and (b) ranked importance by local experts. Parameter estimates and relative variable importances (a) calculated from Aikaike's information criteria corrected for sample size ( $AIC_c$ ) weights of top ( $\Delta AIC_c < 4$ ) models. Boxes (b) represent third and first quartiles, and median ranking denoted by line. Note different axes for importance.



**Figure 4** Plots showing biomass recovery and relative biomass recovery after harvest as a function of their most important predictor variables selected using  $\Delta\text{AIC}_c$  and model weights: biomass recovery as a function of (a) initial biomass, (b) average seawater temperature, relative biomass recovery as a function of (c) grazer density ( $\bullet \text{m}^{-2}$ ), and (d) average seawater temperature. Fitted linear regression lines in blue with 95% confidence intervals indicated in gray shading.



**Figure 5** Prevalence of local harvesting and stewardship practices of *E. menziesii* including; (a) selection criteria of individual *E. menziesii*, (b) harvesting techniques employed to ensure sustainable use, (c) location of harvest, and (d) supporting information for harvesting and stewardship practices from IK interviews with local experts (n = 19,22,19).

# Tables

**Table 1** Strength of evidence for alternative models predicting the effect of (A) harvest treatment and site (n = 5) on relative change in biomass of *Egregia* (n = 47), and (B) environmental variables (mean seawater temperature (Temperature °C), wave exposure, grazer density •(m<sup>-2</sup>), kelp density •(m<sup>-2</sup>)) on biomass recovery and relative biomass recovery of *Egregia* plants (n = 31).

Model <i>Response variable – Distribution (link)</i>	K	n	LL	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	W <sub>i</sub>	R <sup>2</sup> <sub>adj</sub>
<b>(A)</b>							
Relative biomass production – Gaussian (identity)							
Site	6	47	-80.59	175.3	0.00	0.80	0.40
Treatment + Site	7	47	-80.59	178.0	2.77	0.20	0.40
Treatment + Site + Treatment*Site	11	47	-78.22	186.0	10.71	0.00	0.46
Intercept	2	47	-92.20	188.7	13.40	0.00	0.00
Treatment	3	47	-92.11	190.8	15.50	0.00	0.00
<b>(B)</b>							
<b>Biomass recovery – Gaussian (identity)</b>							
Initial size + Temperature + Exposure	5	31	-122.07	256.5	0.00	0.47	0.69
Initial size + Temperature	4	31	-124.39	258.3	1.78	0.19	0.64
Initial size + Temperature + Exposure + Grazer density	6	31	-121.98	259.5	2.92	0.11	0.69
Initial size + Temperature + Exposure + Kelp density	6	31	-122.07	259.6	3.10	0.10	0.69
Initial size + Temperature + Kelp density	5	31	-123.85	260.1	3.57	0.08	0.65
<b>Relative biomass recovery – Gaussian (identity)</b>							
Grazer density + Temperature + Exposure	5	31	-48.94	110.3	0.00	0.50	0.45
Temperature + Kelp density	4	31	-51.58	112.7	2.42	0.15	0.35
Grazer density + Temperature + Exposure + Kelp density	6	31	-48.68	112.9	2.58	0.14	0.46
Grazer density + Temperature + Kelp density	5	31	-50.54	113.5	3.20	0.10	0.39
Grazer density + Temperature	4	31	-52.30	114.1	3.86	0.07	0.31
<b>FronD production – Gamma (log)</b>							
Initial fronds + Temperature	4	31	14.92	-20.3	0.00	0.31	0.42*
Initial fronds + Temperature + Exposure	5	31	16.22	-20.0	0.27	0.27	0.47*
Initial fronds	3	31	12.68	-18.5	1.83	0.12	0.33*
Initial fronds + Temperature + Kelp density	5	31	15.37	-18.3	1.97	0.12	0.44*
Initial fronds + Temperature + Grazer density + Exposure	6	31	16.82	-18.1	2.15	0.11	0.49*
<b>FronD elongation – Gamma (log)</b>							
Initial size + Temperature	4	31	-107.42	224.4	0.00	0.30	0.69
Initial size + Temperature + Exposure	5	31	-106.27	224.9	0.56	0.22	0.71
Initial size + Temperature + Kelp density	5	31	-106.43	225.3	0.88	0.19	0.71

Initial size + Temperature+ Grazer density + Exposure	6	31	-105.19	225.9	1.51	0.14	0.73
Initial size + Temperature+ Grazer density	5	31	-107.26	226.9	2.54	0.08	0.69

Notes: Models with varying numbers of parameters ( $K$ ) were compared using log – likelihood (LL), small-sample bias corrected Akaike’s Information Criterion ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta AIC_c$ ), normalized Akaike weights ( $W_i$ ) and adjusted R-squared ( $R_{adj}^2$ ), \* denotes R squared value ( $R^2$ ). All models for model set (a) shown, top 5 models for model sets (b) shown.

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## Appendix A.

### *Egregia menziesii* growth

Individual fronds grow out of a robust hold fast from an intercalary meristem near the frond's terminal end. Fronds were thought to senesce once the meristem is detached (Black 1976), however more recent work found the meristem to be more diffuse across the end of the frond, with some growth still occurring after meristems were removed (Fulton-Bennett 2016). However, re-growth mainly occurs through the generation and growth of new fronds that sprout from the holdfast (Black 1974).

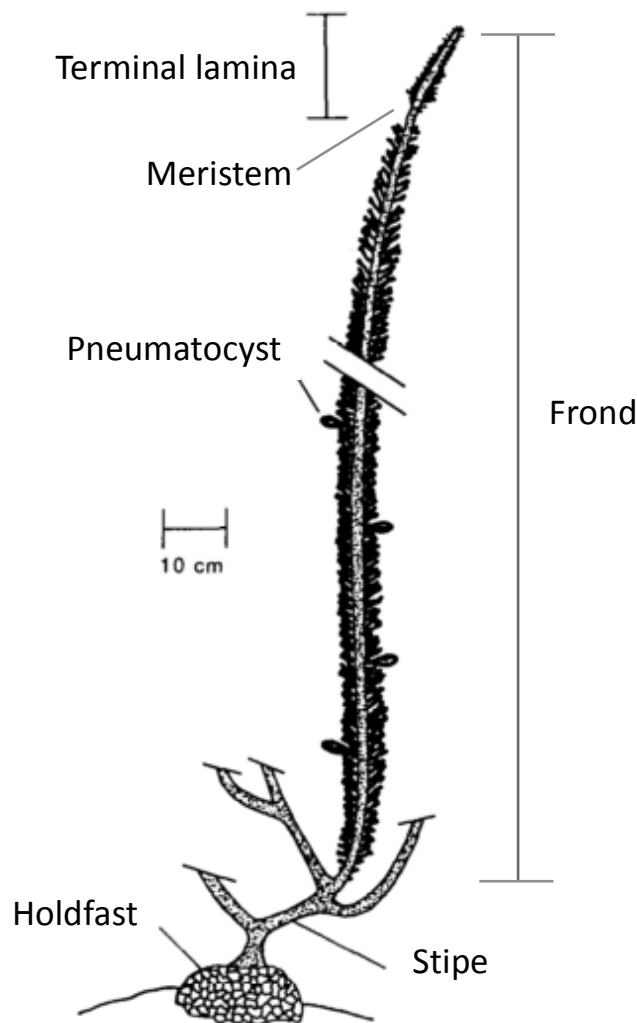
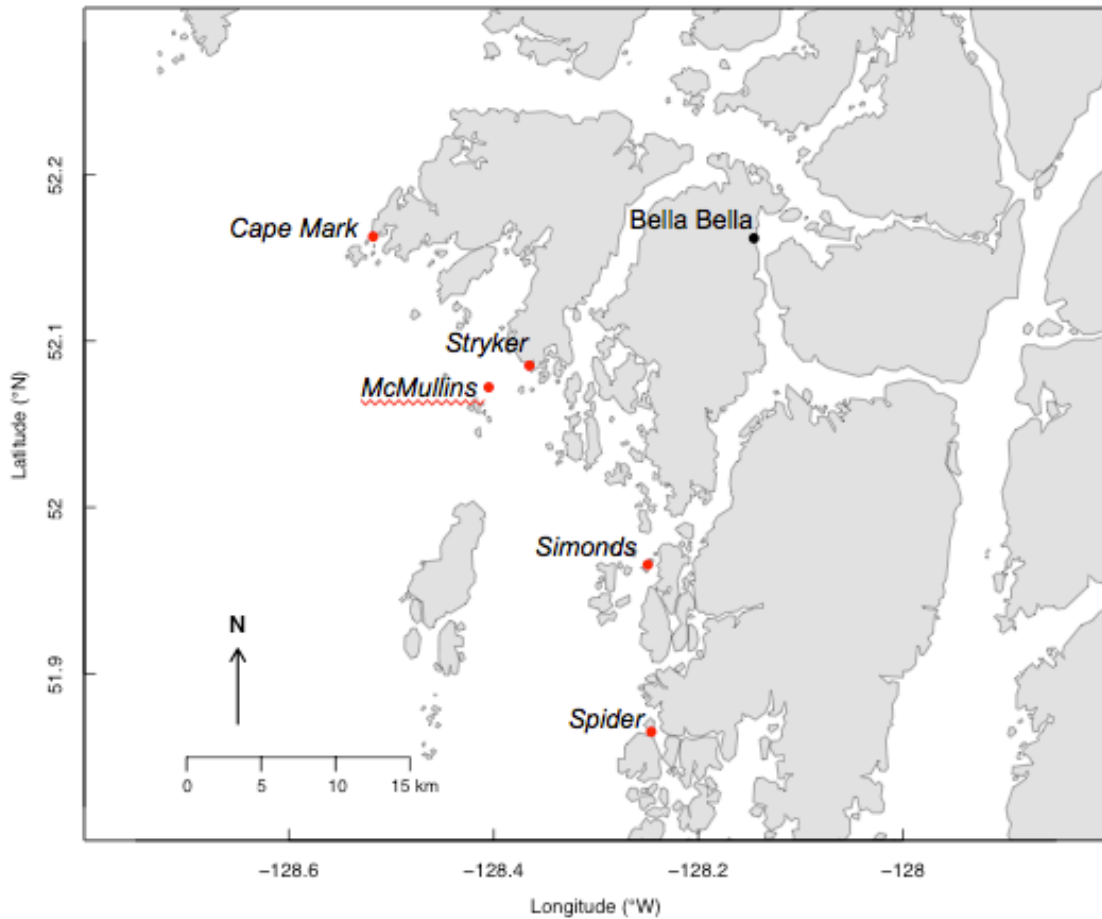


Figure A 1 *Egregia menziesii* morphology adapted from Friedland and Denny 1995

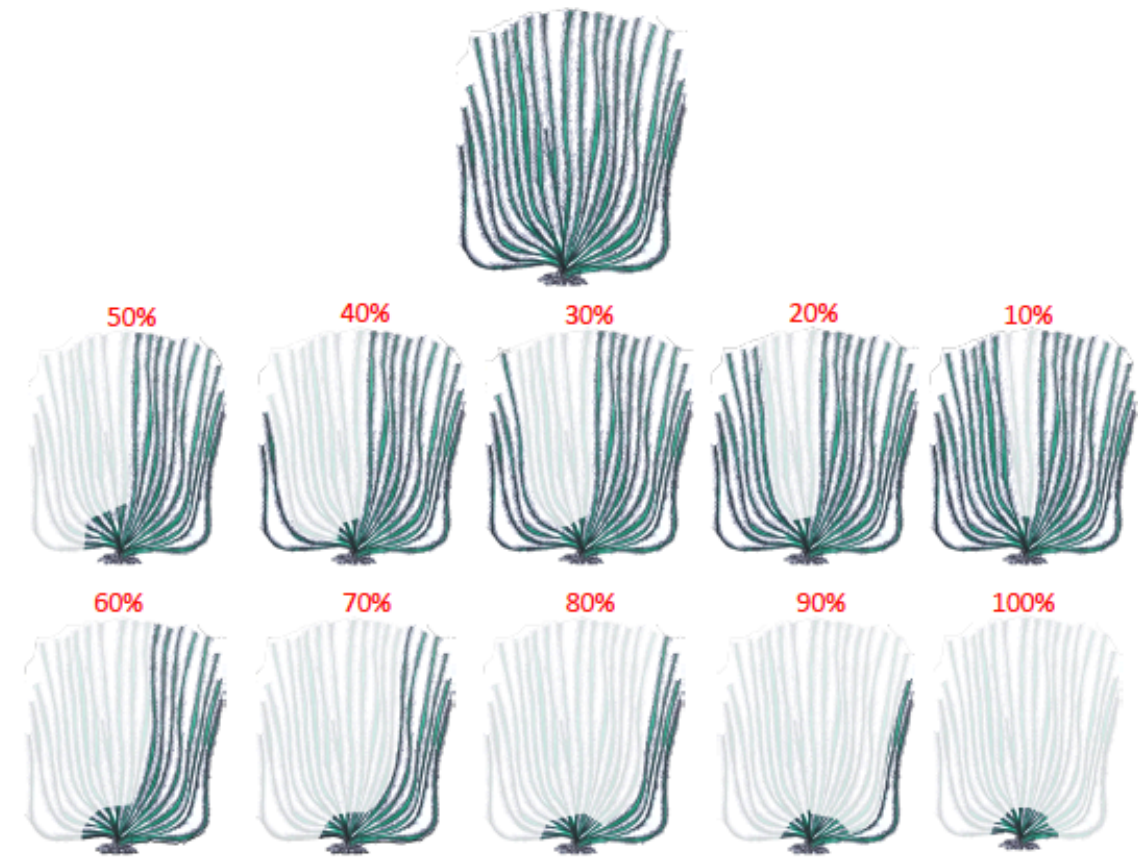


## Appendix B

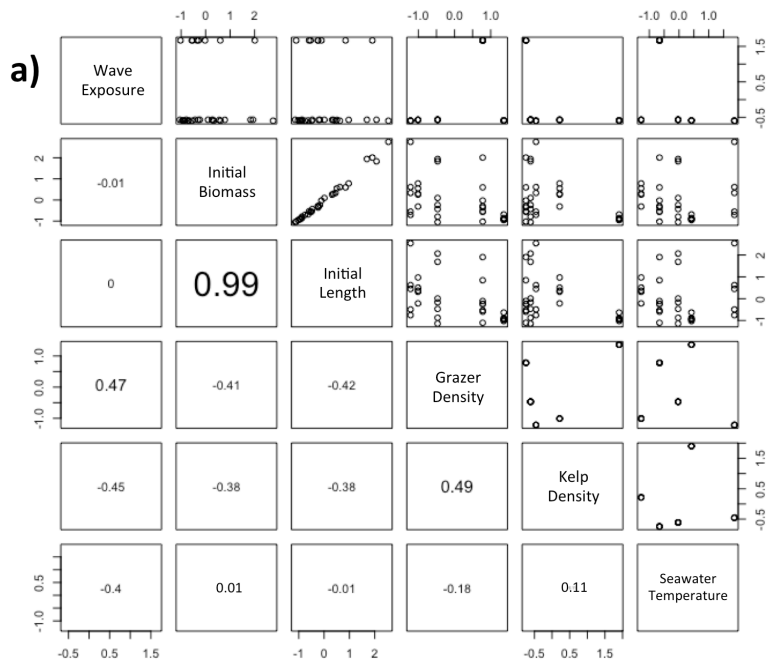
### Supplemental Figures and Tables



**Figure B 1** Map of study sites. Experimental harvest was implemented at Cape Mark, Stryker, McMullins, Simonds and Spider. Indigenous knowledge interviews were conducted in Bella Bella, home of the Heiltsuk people.



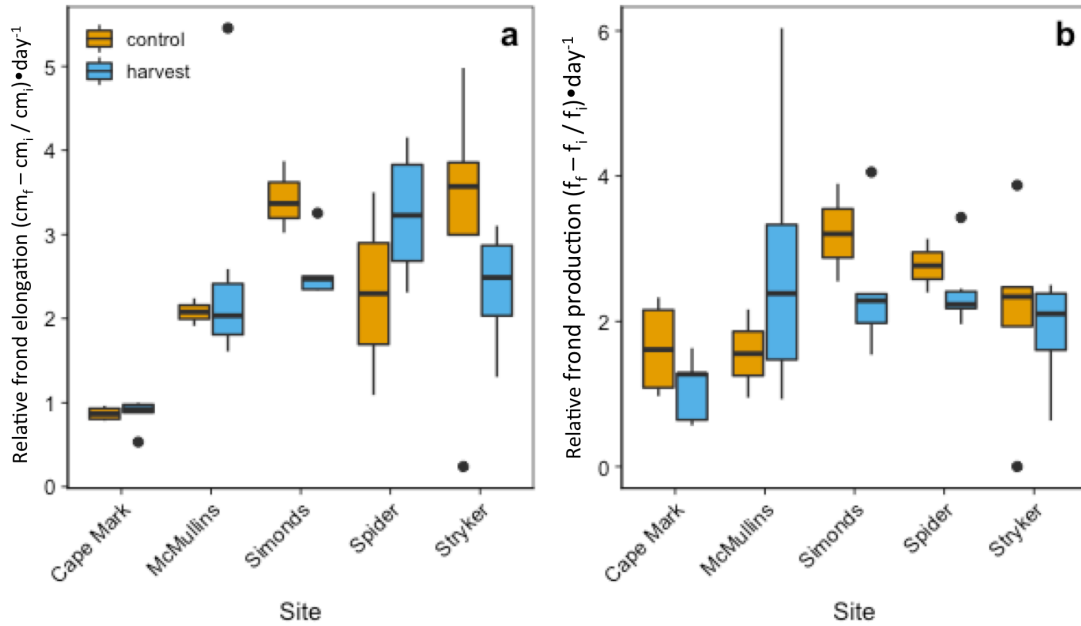
**Figure B 2** Harvest diagram used in Indigenous knowledge interviews to determine actualized subsistence harvest amount



b)	Response (model)					
	Δ Biomass	Relative Δ biomass	Frond production	Relative frond production	Growth rate	Relative growth rate
Exposure	6.105	6.085	6.408	6.085	6.129	7.189
Grazer	6.005	5.785	6.370	5.785	6.086	8.030
Kelp	5.735	5.716	5.825	5.716	5.722	4.149
SST	1.240	1.240	1.243	1.240	1.240	1.914
Initial size	1.276	-	1.208	-	1.297	-

**Figure B 3 Assessment for co-linearity between predictor variables using (a) Pearson’s correlation coefficients and (b) Variance inflation factors (VIFs) of global model for each considered metric of growth/response variable.**

Note: Initial biomass is a derivative of initial length, and both are used as response variables.

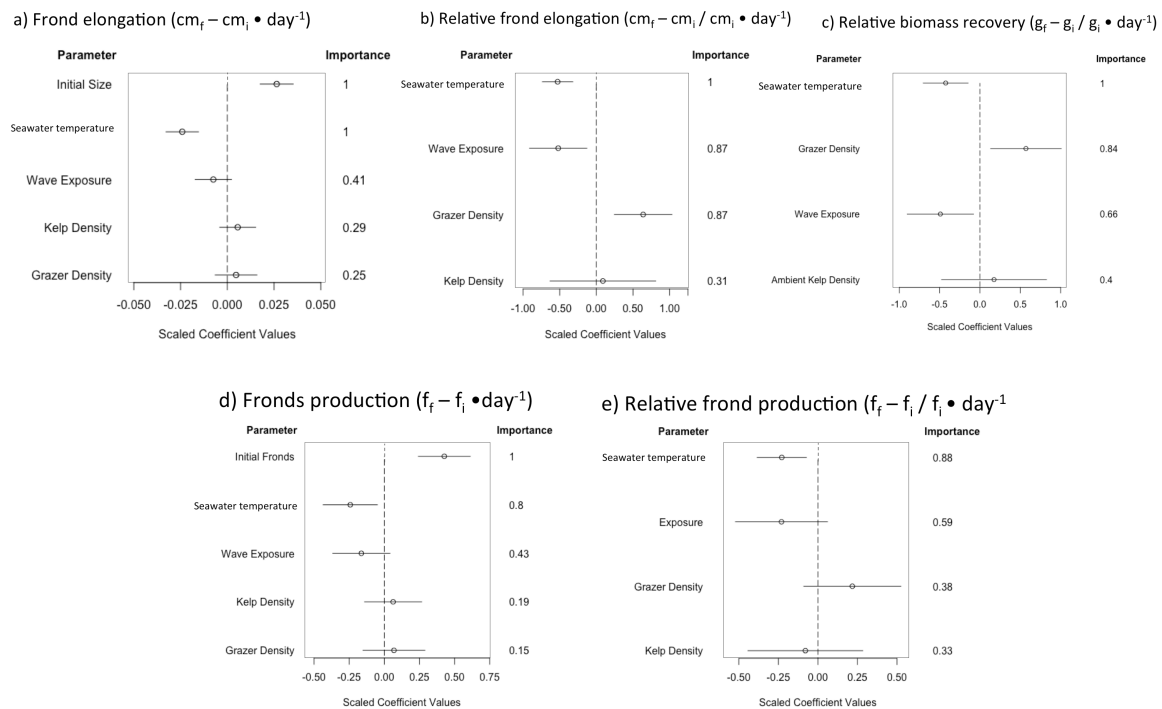


**Figure B 4** Effect of harvest (25% frond removal) and site on (a) relative frond elongation, and (b) relative frond production, of *Egreigia* (all measures relative to starting size)

**Table B 1** Model output table for showing strength of evidence for alternative models predicting the effect of harvest treatment and site (n = 5) on relative frond production, and relative frond elongation of *Egreigia* plants (n = 47), all measures relative to initial size.

Model	K	n	LL	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	W <sub>i</sub>	R <sup>2</sup> <sub>adj</sub>
<b>Response variable – Distribution (link)</b>							
<b>Relative frond production– Gamma (identity)</b>							
Treatment + Site	7	46	155.72	-294.5	0.00	0.50	0.30*
Site	6	46	154.11	-294.1	0.43	0.40	0.25*
Intercept	2	46	147.41	-290.5	3.96	0.07	0.00*
Treatment	3	46	147.56	-288.5	5.94	0.03	0.01*
Treatment + Site + Treatment*Site	11	46	158.01	-286.2	8.24	0.01	0.37*
<b>Relative frond elongation – Gamma (identity)</b>							
Site	6	47	-56.97	128.0	0.00	0.79	0.54
Treatment + Site	7	47	-56.91	130.7	2.65	0.21	0.55
Treatment + Site + Treatment*Site	11	47	-54.87	139.3	11.24	0.00	0.59
Intercept	2	47	-74.28	152.8	24.78	0.00	0.00
Treatment	3	47	-74.28	155.1	27.07	0.00	0.00

Note: Models with varying numbers of parameters (K) were compared using log – likelihood (LL), small-sample bias corrected Akaike's Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> differences (ΔAIC<sub>c</sub>), normalized Akaike weights (W<sub>i</sub>) and adjusted R-squared (R<sup>2</sup><sub>adj</sub>). \* denotes R squared value (R<sup>2</sup>). All models for each model set shown.



**Figure B 5** Parameter estimates and relative variable importances calculated from Aikaike's information criteria corrected for sample size ( $AIC_c$ ) weights of top ( $\Delta AIC_c < 4$ ) models of (a) frond elongation, (b) relative frond elongation, (c) relative biomass recovery, (d) frond production, and (e) relative frond production

**Table B 2** Strength of evidence for alternative models predicting the effect of environmental variables (average seawater temperature (temperature °C), wave exposure, grazer density  $\cdot (m^{-2})$ , kelp density  $\cdot (m^{-2})$ ) on frond production, relative frond production, frond elongation, and relative frond elongation of *Egregia* plants (n = 31).

Model <i>Response variable – Distribution (link)</i>	K	n	LL	$AIC_c$	$\Delta AIC_c$	$W_i$	$R^2$
<b>Frond production – Gamma (log)</b>							
Initial fronds + Temperature	4	31	14.92	-20.3	0.00	0.31	0.42*
Initial fronds + Temperature + Exposure	5	31	16.22	-20.0	0.27	0.27	0.47*
Initial fronds	3	31	12.68	-18.5	1.83	0.12	0.33*
Initial fronds + Temperature + Kelp density	5	31	15.37	-18.3	1.97	0.12	0.44*
Initial fronds + Temperature + Grazer density + Exposure	6	31	16.82	-18.1	2.15	0.11	0.49*
<b>Relative frond production – Gamma (log)</b>							
Temperature + Grazer density + Exposure	5	31	103.69	-195.0	0.00	0.17	0.28
Temperature + Grazer density + Exposure + Kelp density	6	31	105.22	-194.9	0.03	0.17	0.35
Temperature + Exposure	4	31	102.06	-194.6	0.40	0.14	0.20

Temperature	3	31	100.70	-194.5	0.47	0.14	0.13
Temperature + Kelp density	4	31	101.62	-193.7	1.27	0.09	0.18

**Fronnd elongation – Gamma (log)**

Initial size + Temperature	4	31	-107.42	224.4	0.00	0.30	0.69
Initial size + Temperature + Exposure	5	31	-106.27	224.9	0.56	0.22	0.71
Initial size + Temperature + Kelp density	5	31	-106.43	225.3	0.88	0.19	0.71
Initial size + Temperature+ Grazer density + Exposure	6	31	-105.19	225.9	1.51	0.14	0.73
Initial size + Temperature+ Grazer density	5	31	-107.26	226.9	2.54	0.08	0.69

**Relative frond elongation – Gamma (identity)**

Temperature + Exposure + Grazer density	5	31	-28.51	69.6	0.00	0.60	0.68
Temperature + Exposure + Grazer density + Kelp density	6	31	-28.36	72.2	2.67	0.16	0.69
Temperature + Kelp density	4	31	-31.66	72.8	3.29	0.12	0.60
Temperature + Kelp density + Grazer density	5	31	-31.08	74.6	5.00	0.05	0.62
Temperature + Grazer density	4	31	-32.67	74.9	5.31	0.04	0.57

Notes: Models with varying numbers of parameters ( $K$ ) were compared using log – likelihood (LL), small-sample bias corrected Akaike’s Information Criterion ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta AIC_c$ ), normalized Akaike weights ( $w_i$ ) and adjusted R-squared ( $R^2_{adj}$ ). \* denotes R squared value ( $R^2$ ) Top 5 models for each model set shown.