

Investigating the resilience of kelp forests to harvest amid a rapidly changing ocean

**by
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Abstract

While kelp-related activities have become a major component of the global blue economy, the resilience of kelp forests to forest-scale harvest remains understudied. To determine how kelp harvest affects ecological and biophysical characteristics of an entire kelp forest, we conducted a seascape-scale harvest experiment of giant kelp (*Macrocystis pyrifera*). In collaboration with Indigenous kelp harvesters, knowledge holders, and leaders from the Kwakiutl First Nation, in addition to government and university scientists, we established harvested and unharvested control sections in three large kelp forests which ranged from 6.91 to 25.62 hectares. Harvesters then decided which kelp forest to harvest based on a 20% harvest quota, sea condition, kelp condition, and travel time. While harvesters consistently removed an average of 7100 +/- 325 kg of kelp from the top 5.81 +/- 2.17m of the forest canopy per harvest event, overall removing <10% of surface canopy over the season, the occurrence, timing, and magnitude of kelp harvest varied across each experimental site. Post-harvest, we detected a significant reduction in surface frond density at one of the three kelp forests that experienced early season and sequential press harvest effort. Moreover, we detected significant yet variable and ephemeral responses in benthic light intensity, seawater temperature, and flow to sequential harvest at two experimental kelp forests. Counter to our predictions, benthic light intensity within one kelp forest dropped following harvest likely due to the accumulation of kelp detritus. While we did not detect an effect of a single pulse harvest event on benthic light intensity or seawater flow, we did detect a significant cooling in seawater temperature at one of two harvested sections of kelp forest following sequential harvest. Bryozoan coverage was found to be significantly impacted by kelp harvest, however the seasonality and directionality of those impacts varied between kelp forests. Lastly, we did not detect an effect of harvest on individual kelp reproduction or new frond growth. Our results underscore the resilience, yet context-dependence, of kelp forests to harvest. More broadly, the co-design, co-production, and co-implementation of this experiment, conducted at ecologically and socially relevant scales, models an equitable way to inform a more resilient and just blue economy.

Keywords: kelp harvest; blue economy; *Macrocystis pyrifera*; ecological impacts; social-ecological systems

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List of Acronyms

MaPP	Marine Plan Partnership
SFU	Simon Fraser University
UAV	Unmanned Aerial Vehicle

Glossary

Kwak'wala

Kaladi

Kax̣ḳalis

Tsax̣is

Wádelkola

Wawadi

Wazulis

English (Latin)

Giant kelp patch

Giant kelp (*Macrocystis pyrifera*)

Fort Rupert

Bull kelp patch

Bull kelp (*Nereocystis luetkeana*)

Deer Island

Positionality

I am of European ancestry, specifically English and Ukrainian. My family settled on Turtle Island in the early 20th century. I grew up in Treaty 7 territory, which includes the traditional territory of the Blackfoot Confederacy, the Tsuut'ina Nation, and the Stoney Nakoda. It was in the surrounding mountains and rivers of my childhood that I first spent time building relationships to the land and water. I now live on the territories of the Lək'wəŋən and W̱SÁNEĆ peoples. As a non-Indigenous researcher, I have been guided by so many different people who all have generously gifted me with their time and expertise. I am immensely grateful to the Kwakiutl knowledge keepers who have taught me and for the lessons I've learned from the sea and her many inhabitants. When I use 'we' throughout this thesis I hope to illustrate that this work was shaped and guided by a collective that is much greater than myself. Gilakas'la (Thank you).

Introduction

The creation and scaling of ecologically resilient, socially just, and economically viable ocean-based industries has been proposed as a critical means by which global economies can transition towards sustainability. A major component of these ‘blue economy’ strategies includes the harvest and cultivation of seaweeds, in particular kelps (Choudhary et al., 2021). Kelps are marine primary producers that are fast growing, habitat forming, fix atmospheric carbon, and serve as a source of food, fuel, fertilizer, and pharmaceuticals (Buschmann et al., 2017). Moreover, they do so without the use of energetically costly fertilizers or freshwater, making their production relatively sustainable (Tiwari & Troy, 2015). The resilience of kelps to harvest however, remains less well known, particularly at large spatial scales and amid a swiftly warming ocean. Here, we conducted a seascape-level experiment to test the extent to which harvest may alter the ecological and biophysical characteristics of a kelp forest.

Kelps have been harvested for food, medicine, and materials by people along the world’s temperate coastlines for millennia (Kuhnlein & Turner, 1991; Dillehay et al., 2008). Today, kelps continue to be harvested at a diversity of scales for a diversity of objectives, from locally based food, social, and ceremonial use (Kobluk et al., 2021), to small-scale artisanal commercial fisheries (Thompson et al., 2010) and larger-scale industrial commercial operations (Buschmann et al., 2014; Steen et al., 2016). For many coastal communities, the rising demand for seaweed presents an economic opportunity to scale-up or commercialize what were previously subsistence-based kelp fisheries (Krumhansl et al., 2017). However, structural marginalization, economic barriers, and social-ecological trade-offs (Gutzmann, 2023) must be addressed to ensure that resource-dependent coastal communities are not negatively impacted by the scaling-up of kelp harvest activities (Bennett et al., 2021).

Specific kelp species such as giant kelp (*Macrocystis pyrifera*) have become the focus of harvest due to their rapid recovery rates and consistent long-term yields (Vasquez, 1995). In Chile for example, large-scale giant kelp fisheries have had little detectable effect on plant morphology, reproduction, or associated kelp forest biodiversity (Vasquez et al., 2012). Similarly, further north in Baja California, the large-scale harvest of giant kelp was found to have minimal impacts on kelp recruitment,

survivorship, and community interactions (Barilotti & Zertuche-Gonzalez, 1990). However, increasing kelp harvest rates amid a rapidly warming ocean have triggered concerns regarding the long-term viability and resilience of giant kelp to harvest. Global kelp forest responses to climate impacts are highly variable across and within regions, with anthropogenic threats, including warming sea surface temperatures, driving site-specific trends in kelp densities (Krumhansl et al., 2016). Additionally, warming seawater temperatures resulting from human-induced climate change are likely to increase the sensitivity of kelp forests to cumulative impacts of disturbances caused through chronic and acute harvests (Krumhansl et al., 2017). Research assessing the effects of harvest on kelp forest ecosystems, therefore, needs to account for the duration and magnitude of kelp harvest while assessing the context-dependent responses of kelp forests at seascape-level scales.

Multiple factors are known to mediate the effects of harvest on kelp recovery rates. For example, while giant kelp can recover from one-off harvest levels of 30 – 70%, its resilience to harvest in temperate waters averaging 8-16°C has been shown to be highly temperature sensitive, with recovery rates slowing by 40% with less than a 1°C increase in sea water temperatures (Krumhansl et al., 2017). Similarly, results from a small-scale one-time experimental harvest of the intertidal feather boa kelp (*Egregia menziesii*) suggests that larger individual plant size, lower temperatures, and higher wave exposure facilitate faster kelp recovery rates post harvest (Kobluk et al., 2021). During a harvest season, kelp forests can experience impacts from both pulse harvest events, where harvesters harvest a kelp forest once then leave it to recover for a period of time, and repeated press harvest pressure, where forests are harvested multiple days in a row (Bender et al., 1984). While previous research has focused on impacts of one-time pulse harvests, the ecological impacts of repeat, press harvests at the kelp forest-scale remain understudied, as have these harvest effects on the ecological characteristics of the forests themselves.

Kelp harvest can affect biotic and abiotic processes that structure kelp forest habitat and ecosystem dynamics. For example, the reduction of surface kelp frond density via harvest could increase water flow, thereby reducing sea water temperature, increasing light, and thus altering the growing conditions for kelp and other components of kelp forests (Wood et al., 2017). Kelp harvest may also impose trade-offs between somatic growth and potential reproductive output, impacting the long-term population

characteristics of kelp forests and the viability of future harvest. Previous studies have demonstrated that following harvest, kelps downregulate reproduction, possibly in favour of using that energy to replenish somatic tissue lost to harvest (Geange et al., 2014). Reduced reproduction, if caused in a small number of plants, may not however influence kelp forest characteristics given giant kelp sporophytes display strong negative density dependence (Reed et al., 1991). In fact, high growth rates of giant kelp, with possible upregulation of this growth post harvest, may cause canopy sections to be quickly replaced, leading to initial harvest impacts that swiftly decrease following initial harvest.

Kelp density and the magnitude, occurrence and timing of harvest may also influence the prevalence of fouling organisms, such as epiphytic bryozoans. Density of giant kelp forests have been found to influence settlement and growth of bryozoan, with denser forests having higher bryozoan coverage (Denley et al., 2022). Reciprocally however, kelp encrusting bryozoans can negatively impact kelp by increasing susceptibility to erosion and breakage, reducing nutrient absorption, photosynthesis, and reproduction (Krumhansl et al., 2011; Hepburn et al., 2012). Highly colonized kelp fronds are avoided by kelp harvesters due to the inability of these fronds to be ground up and sold as fertilizer. These diverse and reciprocal interactions among kelp density, water flow, fouling organisms, temperature, light, kelp reproduction, and growth all influence long term kelp population dynamics.

The persistence of harvested kelp forests is not only influenced by environmental conditions but is also a function of the values and decisions of kelp harvesters. While environmental conditions impact growth and recovery of kelp forests through time, kelp harvest mediates these ecological relationships, which in turn affect harvest practices. For example, within kelp forests, kelp reproduction and growth are driven by interacting biotic and abiotic conditions, such as kelp density, light, and temperature. Surface harvest of the kelp canopy may reduce the density of canopy fronds, opening gaps in the canopy and increasing benthic light levels, thereby stimulating new frond production. Increases in new frond growth may increase subsequent harvest effort. However, abundance may not be the only metric used to determine when and where to harvest. Harvest effort and location may also be influenced by a harvesters' knowledge and values. Harvesters who strive to limit negative consequences on kelp forest persistence will make different decisions on when, where, and how much to harvest compared to purely profit driven harvesters. Selective harvest of kelp fronds and blades based on the

preferred characteristics of their use, local knowledge on kelp forest health, seasonal condition and recovery rates all influence the response and subsequent re-growth of kelp forests following harvest. Kelp harvest experiments at the forest-scale that wish to mimic real-world harvest conditions must acknowledge the value systems of harvesters, and the impact they will have on the outcomes of harvest. These social-ecological relationships between kelp harvesters and kelp forests have existed for millennia in the Pacific Northwest and shape the current coastal seascape of British Columbia. Commercial kelp harvest has the potential to maintain sustainable yields due to these longstanding social-ecological interactions, however overharvesting and warming ocean temperatures can quickly erode these relationships.

Here, in collaboration with the Kwakiutl First Nation of the northeastern Pacific coast, including Indigenous and non-Indigenous kelp harvesters, knowledge holders, and Leaders we asked: (1) how does kelp forest subsurface light intensity, sea water temperature, and water flow respond to both pulse and press seascape-scale kelp harvest, and (2) to what extent does kelp harvest drive changes in kelp forest frond density, frond growth, and bryozoan cover? To address these questions, we co-designed and co-implemented a collaborative kelp harvest experiment in which we established harvested and unharvested control sections at three large (0.05-0.26 km²) and dense (8.64 +/- 1.2 fronds/m²- 20.1 +/- 1.8 fronds/m²) kelp forests. We predicted that a reduction in kelp frond density within the harvested sections of the kelp forests would increase light levels, decrease seawater temperatures, increase water flow, and reduce kelp epiphytes at the scale of a kelp forest. Moreover, we hypothesized that at the individual kelp plant scale, reduced kelp frond density would lead to a decrease in potential reproductive output, and an increase in new frond growth.

Methods

Knowledge Co-Design, Co-Production, and Co-Implementation

This research was designed and conducted in partnership with the Kwakiutl Nation, one of several Kwakwaka'wakw tribes of the Northeastern Pacific Coast. Based on previously established relationships, we held three initial meetings to discuss research priorities and information needs of the Kwakiutl Nation in the fall of 2021. These included initial informal conversations with the Kwakiutl Nation Fisheries department and Kwakiutl kelp harvesters. Initial discussions were then followed by a more formal meeting seeking research consent and guidance from the Kwakiutl Head Hereditary Chief, *walas* 'Namugwis David Mungo Knox, the contemporary rights holder and descendant of the original, deep time leaders responsible for managing the relationships between people, lands, and waters prior to the incursion of settler-colonial laws. During these meetings, we honed research questions guided by both Indigenous and western knowledge of the local ecology, with the goal of informing future kelp management in Kwakiutl territory. In the spring of 2022, we sought consent for our collaborative research proposal by the elected Kwakiutl band council. Field work began only once approval and consent were given.

Results were shared back to the Kwakiutl Nation Fisheries department after each stage of the work and reviewed following Kwakiutl protocol. Additionally, we followed ethics and data protocols laid out by the First Nations Information Governance Centre's (2023) principles of data sovereignty Ownership, Control, Access, and Possession; OCAP®. By upholding ancestral Indigenous governance principles, protocols, and authority, this approach modeled a more equitable way to co-produce policy-relevant science. It also supports Nation-to-Nation environmental governance and equitable research and knowledge transfer processes that align with the United Nations Declaration on the Rights of Indigenous People (UNDRIP) and the British Columbia Declaration on the Rights of Indigenous Peoples Act (DRIPA).

Study Area and Socio-Cultural Context

Kelp Forest Ecology, Biology, and Harvest

We established 3 kelp forest sites off the east coast of the northern tip of Vancouver Island, British Columbia, Canada. Here, kelp forest canopies are primarily comprised of *ḵaxḵḵalis* giant kelp, *Macrocystis pyrifera*, along with fringing wawadi bull kelp, *Nereocystis luetkeana*, and a diversity of understory laminarian species. The kelp forests themselves are relatively large for British Columbia, extending upwards of 25.62 hectares or 0.26 square kilometers, owing in large part to substantial, shallow (average 5 m, max 10 m below chart datum) subtidal benches composed of boulders interspersed with sediment. The largest giant kelp forests in the province of British Columbia range from 0.13 to 32.70 hectares, with average frond densities of 4.45 fronds/m² (Sutherland, 2008).

Giant kelp has one of the fastest growth rates of any organism on earth (Mann, 1973). Each giant kelp is made up of multiple fronds, which originate from a basal meristem. Fronds elongate from an apical meristem, also called a scimitar. The placement of these meristems means that when a frond is harvested from the surface of the water, the growing end (i.e. the scimitar) is removed. That frond will no longer grow, sinking to the bottom and decaying over time. However, the kelp plant may still produce new fronds, growing up from the basal meristem. Specialized blades at the base of the kelp called sporophylls produce spore packed patches called sori which tear away from the blade, dispersing spores in the process.

Kwakiutl Cultural Traditions and Brief History

Stretching from the northern tip of Vancouver Island, up into Knight Inlet and down the Johnston Strait lies the sacred geography of the Kwakiutl people. This land has been occupied, stewarded, and cared for by Kwakiutl people for millennia. Prior to European contact, the land sustained complex traditional economies, including subsistence, trade, ceremonial, and spiritual use of marine and terrestrial resources, such as kelps (Turner & Bell, 1973; Pasco & Compton, 1998; Kwakiutl First Nation, 2018; Kwaxsistalla Wathl'thla et al., 2022). Colonial dispossession of the land and sea deeply impacted the ability of Kwakiutl people to access marine resources, and systemic

barriers continue to create challenges for Kwakiutl people today, including the harvest and use of seaweeds (Mustonen et al., 2021; Hunt, 2023). Nonetheless, the Kwakiutl people remain deeply connected to their lands and waters and continue to assert their rights and responsibilities by revitalizing stewardship practices of harvesting, gathering, tending, and managing resources in their territory (Everson, 2021). The variety of ecological and cultural stewardship practices enacted by Kwakiutl people are not only maintaining but restoring the productivity of local terrestrial and marine ecosystems (Everson, 2021).

Commercial Kelp Fishery

A Kwakiutl-led commercial kelp harvest operation, called Confidence Fishing Company, started in Kwakiutl territory 25 years ago. Today it is the largest commercial kelp harvest in the province of British Columbia. This operation hand harvests giant kelp 5 days a week from May till October using two small boats (max length 9m) filled with sixteen 3.5 x 4 x 3m totes that carry kelp to be processed. During harvest, the boats drift into the forests, relying on the wind or small motorized adjustments to push themselves through the kelp forests. The harvesters on board use gaff hooks to pull bundles of kelp fronds taut to the kelp forest benthos, then cut the top 5.81 m (+/- 2.17m) (Appendix A) of fronds on average and pull them aboard and into the totes. The harvesters continue to pull and cut until all their totes onboard are full, averaging 3550 kg of kelp per skiff per day (total 7100 kg of kelp removed per day +/- 325) (Appendix A). The harvesters alternate which forests they harvest from, depending on sea condition, kelp condition, travel time, and quotas set by the provincial government.

Decisions by kelp harvesters on when and where to harvest are based on local ecological knowledge and influenced by fuel costs and weather conditions. At the beginning of the season kelp harvesters in British Columbia apply for permits granted by the provincial government which dictate a harvest quota based on an estimate of kelp biomass per kelp forest. This estimate is based on the area and depth of a kelp forest. A maximum of 20% of a kelp forest is allowed to be harvested over the course of the season, with harvesters typically applying to harvest multiple kelp forests. Beyond this quota harvesters define when and where they harvest, with harvesters using local knowledge and observation of kelp forest health and harvestability across the harvest season to decide where to harvest. Environmental assessments of previous and current

annual temperature trends also inform decisions on when to harvest and when to leave forests to recover. External factors such as market forces, supply chains, weather, culture, governance, and management also play a role in these harvest decisions. This study maintained the autonomy of harvesters to rely on this social ecological decision space to determine when and where to harvest, allowing for harvest results to assess recovery rates and harvest impacts of current harvest regimes.

Experiment Design

To assess how kelp harvest affects the physical and biological characteristics of kelp forests, we conducted a large-scale, seascape-level kelp harvest experiment from May 23 to August 1, 2022. Three kelp forests in Kwakiutl territory were chosen based on their contemporary harvest history, ease of access, and the knowledge and experience of Kwakiutl kelp harvesters (Figure 1). At each kelp forest, we designated an active harvest section, where kelp harvesters would harvest kelp using their established methodologies, and a control section where no kelp would be harvested. Constrained only by a 20% harvest quota, harvesters had autonomy over decisions on when, where, and how much to harvest within each harvest section, creating variability in the magnitude and frequency of harvest at each of the three experimental kelp forests through time.

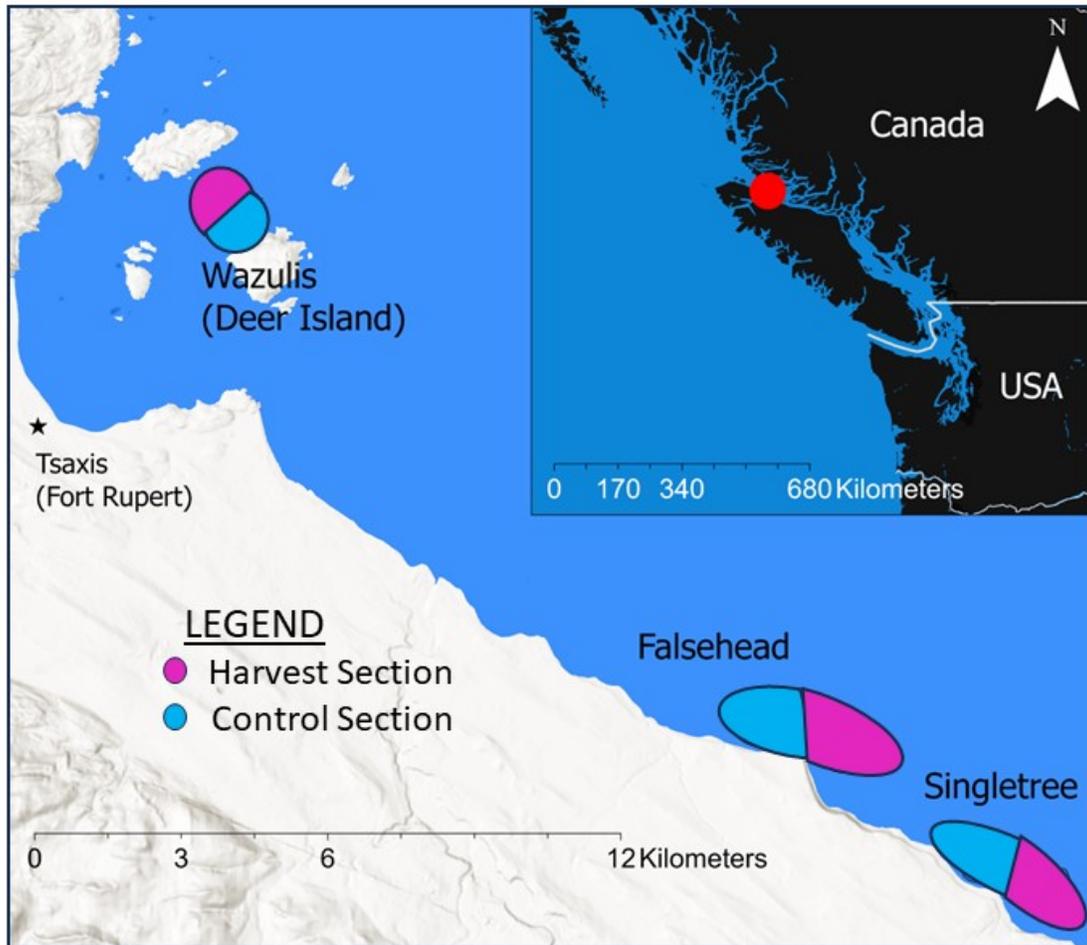


Figure 1: Three experimental kelp forests were established in Kwakiutl territory, nearby Tsaxis (Fort Rupert), on the north coast of Vancouver Island, Canada; Deer Island (Wazulis), Falsehead, and Singletree. Harvesters cut surface fronds of *Macrocystis pyrifera* in delineated harvest sections of the forest (pink polygon), leaving control sections (blue polygon) unharvested.

Harvest Assessments

Daily records of kelp biomass (wet weight) and harvest location were recorded and shared by harvesters. Quantity of kelp fronds harvested per tote was assessed through two repeat harvests at Falsehead performed by the kelp research team where number and length of fronds needed to fill the totes were recorded and averaged ($n=2$ totes). Frond length and weight harvested was assessed during a subset of repeat

harvests at each kelp forest, measurements were taken for all harvested fronds every 3 weeks from May to August and averaged for each forest (Appendix A).

Environmental Variables

To create the space for multiple ways of knowing to inform our research, our hypotheses were based on lived experience on the water, Indigenous knowledge, and western science. We monitored environmental response variables hypothesized to be impacted by kelp harvest based on peer reviewed literature and conversations with collaborators.

Temperature and Light

To test for an effect of harvest on temperature and light levels within each experimental kelp forest (n=3), we deployed temperature and light sensors on four mooring lines, two in the harvest section and two in the control section (Figure 2). Mooring lines in the harvest section of the kelp forest were placed in areas frequently targeted by the harvesters, as determined through observation and conversation with the harvesters. All mooring lines were placed a minimum of 10 meters into the kelp forest, as evaluated during a tidal height of less than 2 meters chart datum, to prevent edge effects.

Affixed to each mooring line were two HOBO pendant temperature and light loggers. The top logger was placed ~1m below the ocean surface and the bottom logger was placed ~1 meter above the benthos. Quantity of light and seawater temperature measurements were taken every two minutes for the duration of May 24 until July 31. For both the top and bottom light loggers, light intensity (lumen/m²) measured during daylight hours was averaged daily during tidal heights over 2 meters chart datum. Similarly, for both the top and bottom temperature loggers, daily average temperature (°C) was calculated during tidal heights over 2 meters chart datum. Tidal height minimums for measurements were established to minimize erroneous spikes correlated with kelp and mooring entanglement during low tides.

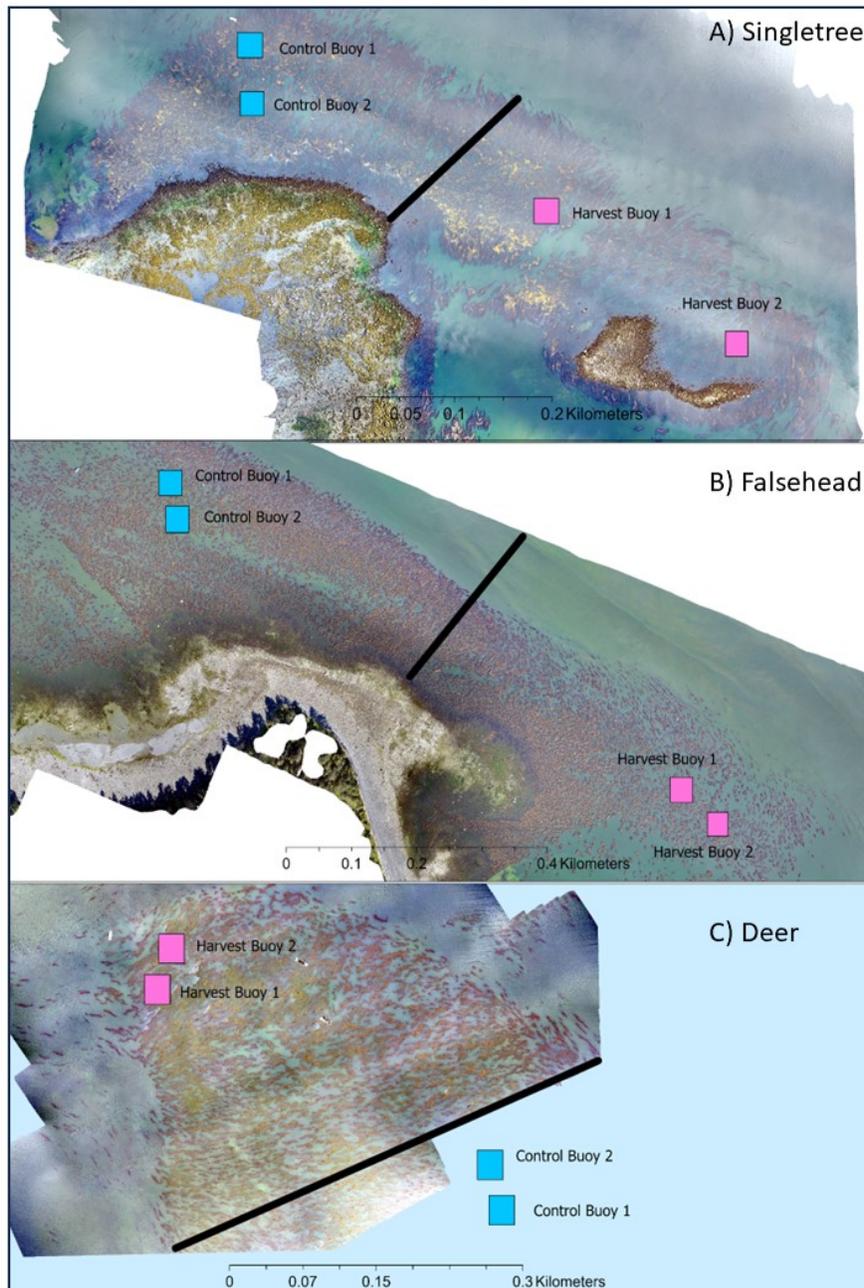


Figure 2: Drone imagery of A) Singletree, B) Falsehead, and C) Deer Island experimental kelp forests. At each experimental kelp forest light, temperature and flow loggers were attached to two moorings (blue and pink polygons) in both the harvest and control (unharvested) section of the forest. The black line breaks the kelp forest into the harvest section, pink polygons, and unharvested control section, blue polygons. The control section of Deer Island was unable to be photographed due to proximity to the Port Hardy airport.

Water Flow

We estimated the effect of harvest on surface water flow using gypsum cement 'clods' (McClanahan et al., 2011; Hart et al., 2002). The dissolution rate of each clod was used to approximate water motion within each section of the kelp forest. Clods were created by pouring gypsum cement into ice cube trays, attaching an eye bolt within each clod, followed by drying and weighing (g) before deployment. In the field, two clods were attached to each mooring line, both ~1 meter below the surface. Clods were retrieved within 24 hours with the retrieval time noted and factored into each loss rate calculation. Each clod was dried in an oven for 24 hours then re-weighed. To determine dissolution rate (g/hr), weight post deployment was subtracted from weight pre deployment divided by time elapsed during deployment.

Surface Surveys of Kelp Fronds and Bryozoan Cover

To assess the effect of harvest on kelp surface density and kelp epiphyte presence across sites and season, we conducted repeat surface surveys following methods implemented by the Marine Planned Partnership (MaPP), with minor modifications (Thompson, 2021). Modifications included increasing tidal windows for surveys from below 1.5 m chart datum to 2m to allow for additional time to assess all three kelp forests and randomly stratified surveys replacing transects. Specifically, we counted the number of fronds in 60 1 x 1m quadrats randomly stratified across the harvest and control section of each experimental kelp forest. Surveys were conducted at each experimental kelp forest during tide windows below 2 meters chart datum every 3 weeks from May 24 until July 31. The total number and percent cover of kelp fronds within each quadrat was recorded, as was the percent cover of bryozoan covering the kelp. Bryozoan cover was assessed as the percent of the kelp canopy present in each quadrat that was covered by bryozoan.

SCUBA Surveys of Kelp Frond Growth, Elongation and Reproductive Output

To measure the effect of harvest on the production and elongation of new fronds, we tagged and measured (n=8) individual kelp plants in the harvest and control sections of each experimental kelp forest using SCUBA (n=48 kelp plants total). All tagged kelps

were within 10 meters of the mooring buoys. The number and length of all kelp fronds for each kelp were counted and recorded in June and July. We did not tag individual fronds, instead we assessed the number and size of fronds per kelp, which was assessed through repeat measurements twice during the harvest season. In the harvest section of each experimental kelp forest, all fronds over 3m of the tagged kelps were cut by divers beginning on June 15 following counts, guaranteeing harvest on the individual kelp level on June 15 and July 9/10. To test the effect of harvest on the potential reproductive output of kelp, we counted the number of sporophylls and sori patches on each tagged kelp plant.

Drone Surveys of Kelp Canopy Area

To quantify the effect of harvest on total surface kelp canopy area through time we took drone images of the experimental kelp forests at three time points across the harvest season, and once a year later. UAV images of each forest's control and harvest sections were collected during tides of less than 2 meters chart datum from a height of 60-120m. Orthomosaics were processed through Kelp-O-Matic (v0.6.1) (Denouden & Reshitnyk, 2023) to detect surface kelp present in the drone imagery. We quantified total kelp canopy area (m²) for each forest and each section through time using methodologies recommended for Kelp-O-Matic outputs in ArcGIS. Images of the control section of Deer were unobtainable due to the proximity to the Port Hardy airport.

Statistical Analyses

Temperature and Light

To analyze the effect of harvest on temperature and light, we used a progressive change before-after control-impact paired series (progressive change BACIPS: Thiault et al., 2017) analysis. Traditional BACIPS analyses distinguish between natural spatial and temporal variability from variability caused by an intervention using paired sampling at control and impacted sites. Traditional BACIPS analyses assume perturbations impact response variables immediately and that changes to the system are consistent after an impact. However complex ecological interactions impacting temperature and light levels following kelp harvest are likely not constant nor linear. In fact, *Macrocystis pyrifera* can grow in favourable conditions up to 35cm per day (O'Clair & Lindstrom, 2021) potentially,

quickly obscuring the effects of a surface harvest. Any quantifiable impacts hypothesized to not be constant through time, violate the assumptions of traditional step-change BACIPS analysis.

The Progressive-Change BACIPS we deployed can discern impacts, and the timescales over which they operate, by fitting alternative recovery models, allowing data to dictate the response model form instead of the inverse. Understanding and quantifying the shape of the response following harvest is as important to understand as detecting the presence of a response, rendering the progressive change BACIPS a more accurate method of interpreting the complex ecological impacts triggered by kelp harvest.

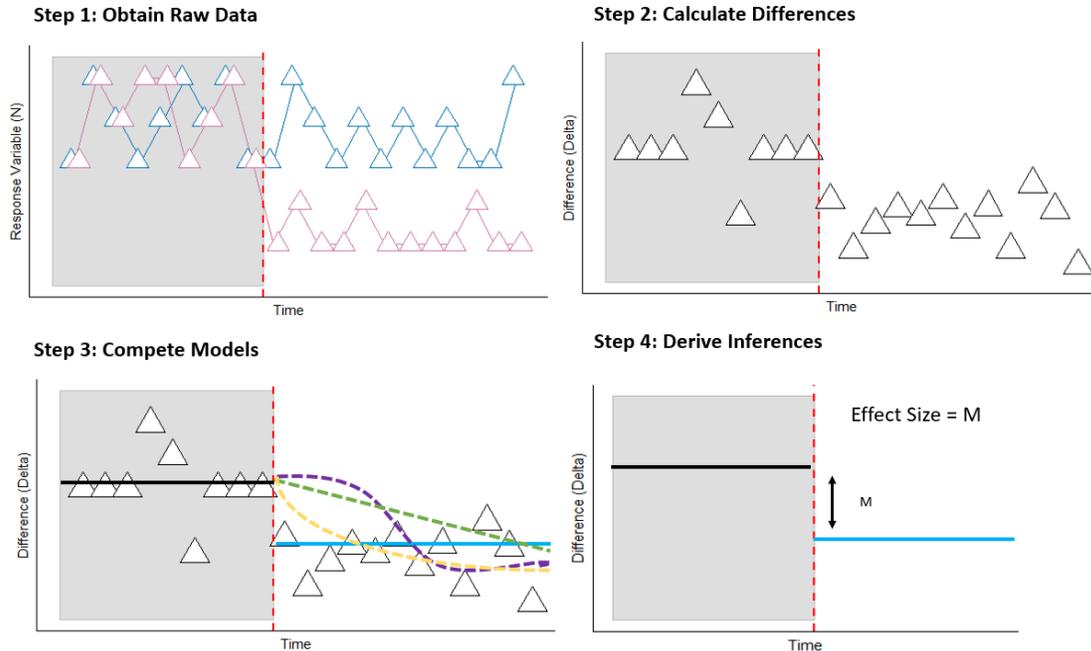


Figure 3: Methodology of the progressive change BACIPS, adapted from Thiault et al., 2017 (Figure 1) using hypothetical data. Step 1: A response variable is measured at harvested (pink) and control (blue) sites several times before (grey background) and after (white background) an experimental harvest (AKA: treatment) is imposed (red line). Step 2: Differences (Δ) between the harvested and control sections are calculated for each time step (white triangles). Step 3: Four candidate models (Step change (blue), linear (green), asymptotic (yellow) and sigmoidal (purple)) are fitted to the differences and compared using model selection criteria. Step 4: The best fitting model is used as the explanatory model to draw inferences about the effect of the impact, in this case, of kelp harvest.

To assess the impact of a single kelp harvest event on temperature and light at the beginning of the growing season (June), we assessed changes in these response variables over a 13–14-day period pre and post harvest at two kelp forests; Falsehead and Singletree (see Figure 4). To assess the impact of a 10–12-day sequential harvest of kelp on temperature and light, we assessed changes in these response variables, pre and post harvest, at the Deer Island and Falsehead kelp forests (see Figure 5).

We calculated daily differences in temperature and light (Δ) by subtracting control from harvest section values. Using before/during harvest and after harvest daily differences, four candidate models were fit to the data post harvest. Step change models fit an immediate and constant change in the difference between sections

following harvest. Linear models describe a continuous change in the magnitude of difference between harvest and control sections that accrues at a constant rate. Asymptotic models describe a continuous change in the magnitude of difference between harvest and control sections where the difference changes at a declining rate and approaches an asymptote. Lastly, sigmoidal models describe a continuous change in the magnitude of difference between the sections where the difference changes from initially accelerating to decelerating, leading to an asymptote.

All analyses were implemented using the R statistical software version 3.0.1 (R Core Team 2022). 'MINPACK.LM' (Elzhov et al., 2013) and 'NSL2' (Grothendieck, 2013) packages were used to perform nonlinear regressions and the 'AICCMODAVG' package (Mazerolle, 2016) was used to evaluate second order Akaike Information Criterion (AICc). We used the AICc of each model as a measure of their relative likelihood and number of parameters to discern the most parsimonious and best fit model. Adjusted R^2 was reported to assess the fit of linear, sigmoidal and asymptotic models whereas partial ETA^2 was reported to assess the fit of step-change models. To assess the magnitude of harvest effect for nonlinear models (step-change, asymptotic and sigmoid) we used the difference between the difference before the intervention and the eventual asymptote after the intervention, hence effect = M. For linear models, the magnitude of the harvest effect was measured as the slope of the differences after the intervention. The parameter estimates of the best fit model were used to estimate the probability of an effect of harvest, given the difference between harvest and control values and the time since harvest, and reported as p-values.

Water Flow

To test for an effect of harvest on water flow during time periods specified in the BACIPS analysis, we ran T-tests on those specific sites and periods. Where the t-tests returned a significant p value, we ran a repeat measures analysis of variance to determine seasonality of differences and post-hoc pairwise comparisons. We used the R packages 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017), and 'multcomp' (Hothorn et al., 2023) for ANOVAs and Tukeys HSD tests.

Surface Surveys of Kelp Fronds and Bryozoan Cover

To test for an effect of harvest on the number of surface fronds and percent cover of bryozoan post harvest, we ran a repeated measures ANOVA. To assess bryozoan coverage, we removed any quadrats which did not contain kelp due to bryozoan coverage being a function of kelp coverage. For both bryozoan and kelp frond analysis we removed any surveys where harvest had not occurred yet. Where tests returned a significant p value, we used a Tukey's honestly significant difference (HSD) post-hoc test. We used the R packages 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017), and 'multcomp' (Hothorn et al., 2023) for ANOVAs and Tukeys HSD tests.

SCUBA Surveys of Kelp Frond Growth, Elongation and Reproductive Output

To test for an effect of harvest and kelp forest site on the production of new fronds, total alive fronds, dead fronds, and number of sori patches observed on sporophylls, we ran a repeated measures ANOVA on each response variable. Where tests returned a significant p value, we used a Tukey's honestly significant difference (HSD) post-hoc test. We used the R packages 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017), and 'multcomp' (Hothorn et al., 2023) for ANOVAs and Tukeys HSD tests.

Assumptions and Limitations

Our experimental kelp forests, including harvest and control sections, differed in characteristics other than the presence or absence of harvest. Although we aimed to minimize differences in environmental factors among kelp forests such as wave exposure, water flow, substratum, species assemblages, turbidity, sedimentation, and proximity to each forest, no two kelp forests ever experience the same abiotic and biotic conditions, and no kelp forest is ubiquitous throughout. It was important to us to select kelp harvest experiment sites that would be most useful for our research partners, which lead to large distances (13km) between sites with somewhat different oceanographic influences. Those factors may have influenced the kelp forests and individual kelp plants

responses to harvest. Moreover, the magnitude, occurrence, and timing of harvest itself also varied among our experimental kelp forests.

While our study gained relevance and legitimacy by working directly with kelp harvesters to impose the experimental harvest itself, our experimental design became unbalanced in its replication because we did not direct when or where the harvest happened. Our initial experimental design was based on 3 replicate kelp forests with control and harvest treatments. However, variability in the occurrence, harvest effort (i.e., number of boats), and timing of harvest across each kelp forest resulted in variability in the magnitude and duration of the harvest treatment effect. While we used this unexpected spatial and temporal distribution of harvest effort to our advantage by exploring the effects of both pulse and press harvest disturbances, experienced in most fisheries, we lost the power of a balanced and replicated Before, After, Control and Impact (BACI) design. Therefore, we analyzed the effects of kelp harvest on our BACIPS time-series responses (i.e., benthic light intensity and sea water temperature) as a separate, un-replicated time series. In contrast, harvest effects on post harvest, one time-step, harvested and control response variables (i.e., water flow, frond density, bryozoan cover, new frond growth, and potential reproductive output) were analysed with kelp forest and sample unit (i.e., quadrat or individual plant) as replicates, despite variability in harvest effort among kelp forests.

Results

Seasonal Trends in Kelp Forest Temperature and Light

Throughout the growing season from the end of May to the end of July, all three kelp forests experienced remarkable similarity in their overall trend and variability in sea water temperature. Sea water temperatures were at their lowest at the beginning of our time series, at the end of May, ranging from 9-11°C, and peaked near the end of July, with temperatures ranging from 14.5-15.5°C. While temperatures tended to be consistent between control and harvested sections of the kelp forests at Falsehead and Deer Island, the harvested section of the kelp forest at Singletree consistently experienced cooler sea water temperatures than the control site, especially when temperatures were relatively high during the end of June and July.

Across all three kelp forests, subsurface light intensity was highly variable both daily and throughout the growing season, ranging on average between 1 and 2166 lumens/m² with extreme values ranging as high as 187,379 lumens/m² (Figure 5). Light intensity was most variable at the Deer Island kelp forest, which also experienced the greatest magnitude and frequency of harvest early in the growing season (Figure 5).

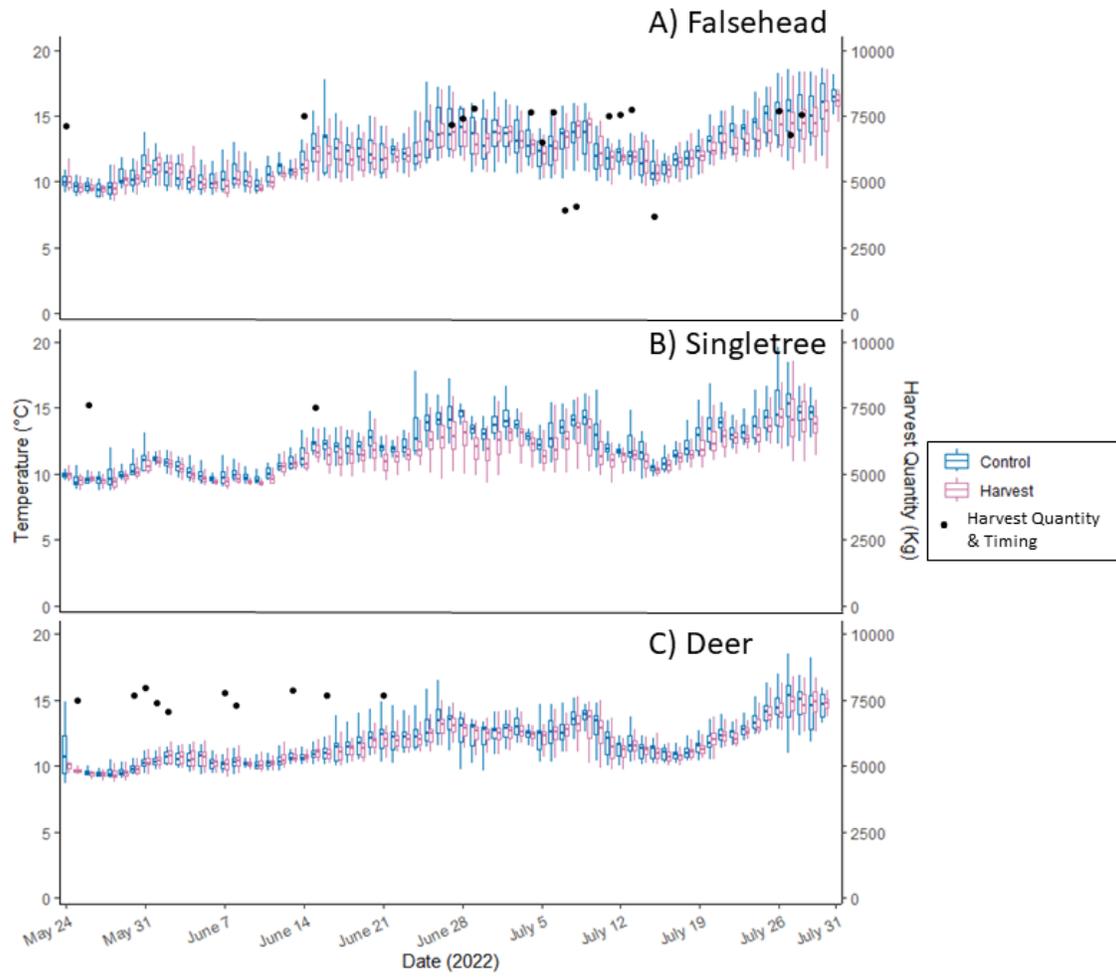


Figure 4: Daily temperatures (°C) recorded by top and bottom loggers at 3 experimental kelp forests; A) Falsehead B) Singletree and C) Deer Island in control (blue) and harvested (pink) sections of the forest. Black dots denote when and how much harvest occurred (Kg).

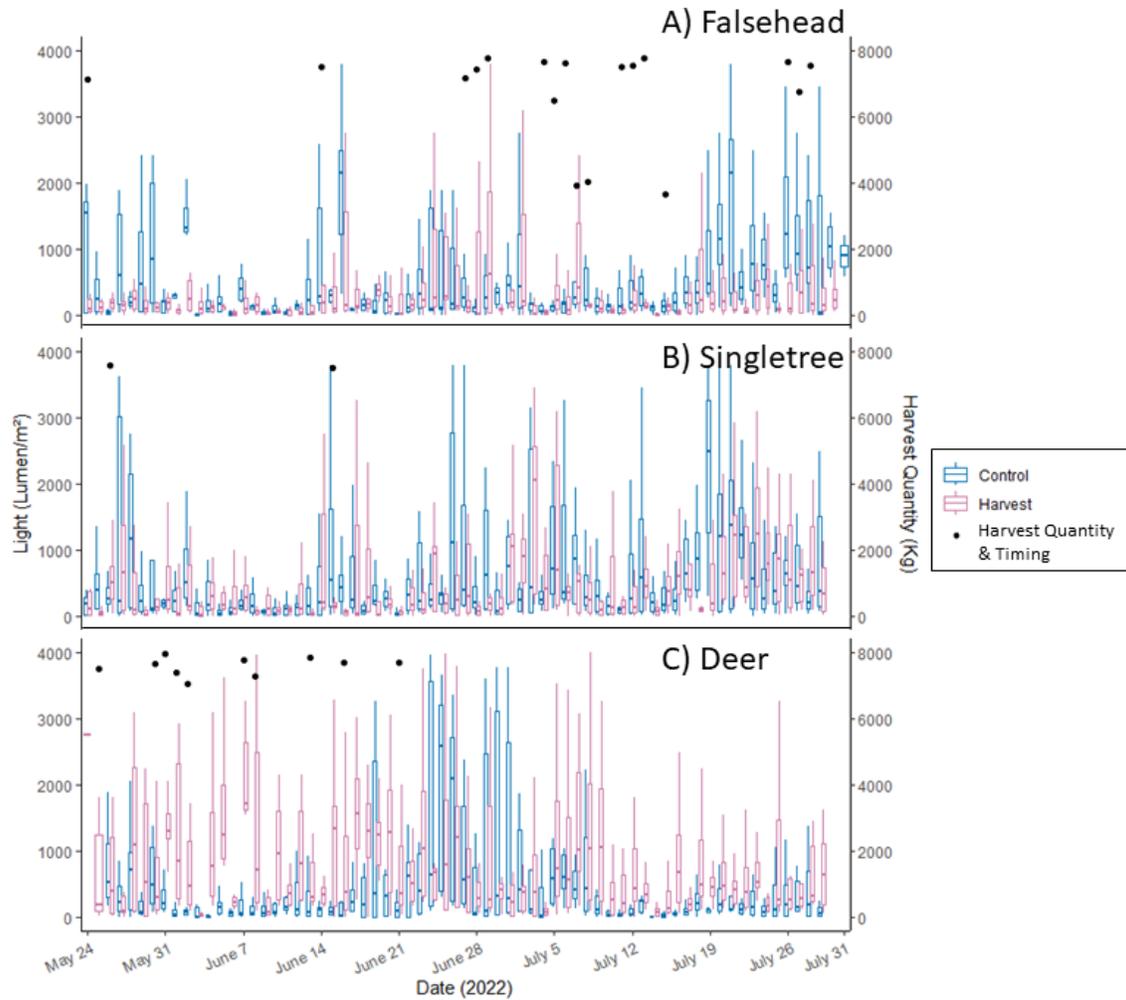


Figure 5: Daily light (Lumen/m^2) recorded by top and bottom loggers at 3 experimental kelp forests; A) Falsehead B) Singletree and C) Deer Island in control (blue) and harvested (pink) sections of the forest. Black dots denote when and how much harvest occurred (Kg).

Effect of Harvest on Kelp Forest Temperature, Light and Water Flow

Single Pulse Harvest

Light

We found no evidence for an effect of a one-day harvest event on benthic light intensity within two experimental kelp forests (Figure 6). Specifically, benthic light levels in the kelp forest at Singletree were variable both pre and post harvest, in control and

harvested sections of the forest (Figure 6 A). Consequently, no significant difference in light between control and harvested sections of the forest post harvest were detected by our linear model (p -value = 0.2). While a linear response in the difference in light between harvested and control sections of the kelp forest post harvest was best supported by the data relative to other models (Figure 6 C, Appendix B.1), only 2.6% of the variation in these differences was attributable to a linear response to harvest (Adj $R^2=0.0263$). Standard deviations between the pre-harvest and post harvest light quantities in the harvest and control sections were similar. (SD pre-harvest control section=59.2, SD pre-harvest harvest section=23.83, SD post-harvest control section=36.41, SD post-harvest harvest section=23.94).

Similarly, our winning model found no evidence for an effect of harvest on benthic light levels in the kelp forest at Falsehead (p -value = 0.25, Figure 6 E, Appendix B.1). Again here, a linear response to harvest was best supported by the data, but only 1.5% of the variation in the difference in light between control and harvested sections of the kelp forest post harvest was attributable to harvest (Adj $R^2=0.0151$). Over the time series, benthic light levels tended to be more variable in the control section of the forest pre harvest and became less variable in both sections after harvest, except for a one-time spike in light in the control section immediately post harvest (Figure 6 D, E, Appendix B.1). The control section post harvest experienced large spikes in average daily light quantities, with a larger standard deviation in the post harvest period than for the pre-harvest period (SD pre-harvest control section=56.16, SD post-harvest control section=137.08).

Temperature –

We found strong evidence for an effect of a single, pulse harvest event on benthic seawater temperatures at one experimental kelp forest but not the other (Figure 7). Following the harvest at the Singletree kelp forest, temperatures diverged significantly between control and harvested sections (p -value = $2.76e-11$). While benthic seawater rose in temperature in both sections, temperatures remained on average 1.41°C (+/- 0.59) degrees cooler in the harvested section post harvest. Here, 83% of the variation in the difference in benthic sea water temperature between control and harvested sections could be explained by a linear response to harvest. A linear model was best supported by the data (Figure 7 C) and estimated an increase in the magnitude

of difference between the harvest and control sections of 0.14°C per day (95% CI: -0.16 - -0.11 ; P-value = $2.76\text{e-}11$) after a single harvest event. The standard deviation of the post harvest control section was half a degree higher than the pre-harvest control section, showcasing the high variability of the data (SD pre-harvest control section= 0.46 , SD post harvest control section= 0.91).

In contrast, following the single harvest at the Falsehead kelp forest, the step model found no significant divergence in benthic seawater temperatures between control and harvested sections (p-value = 0.49 , Figure 7 D). Instead, temperatures rose consistently at control and harvested sections of the forest. While a step function response in benthic temperature post harvest was best supported by the data (Figure 7 F, Appendix B.2), the model explained only 2.1% of the variation in the difference in temperature between control and harvested sections of the kelp forest.

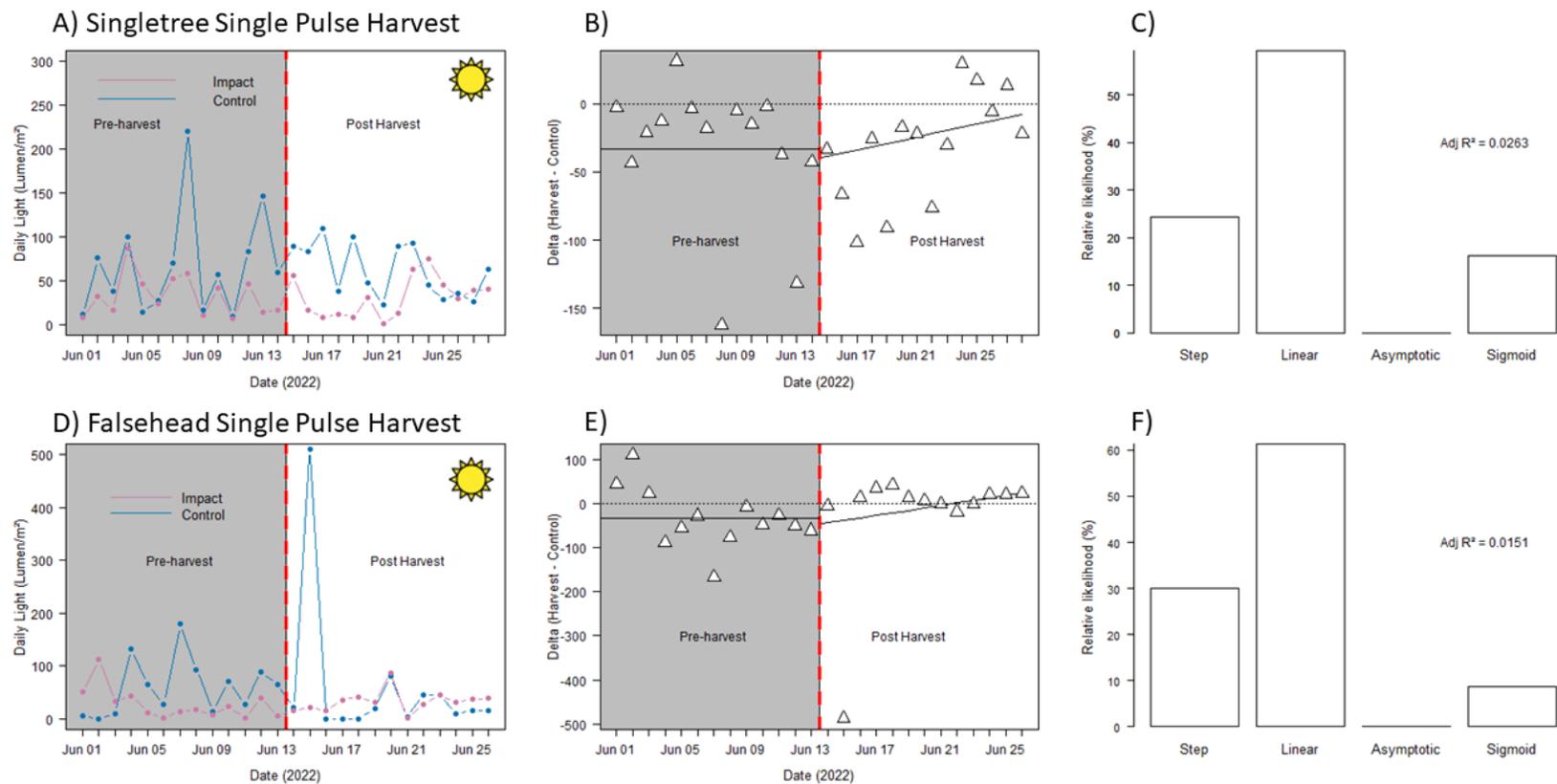


Figure 6: Effects of a single pulse harvest event on benthic kelp forest light intensity (Lumen/m²) at A,B,C Singletree and D,E,F) Falsehead in control (blue) and harvested (pink) sections of the forest, pre and post harvest.

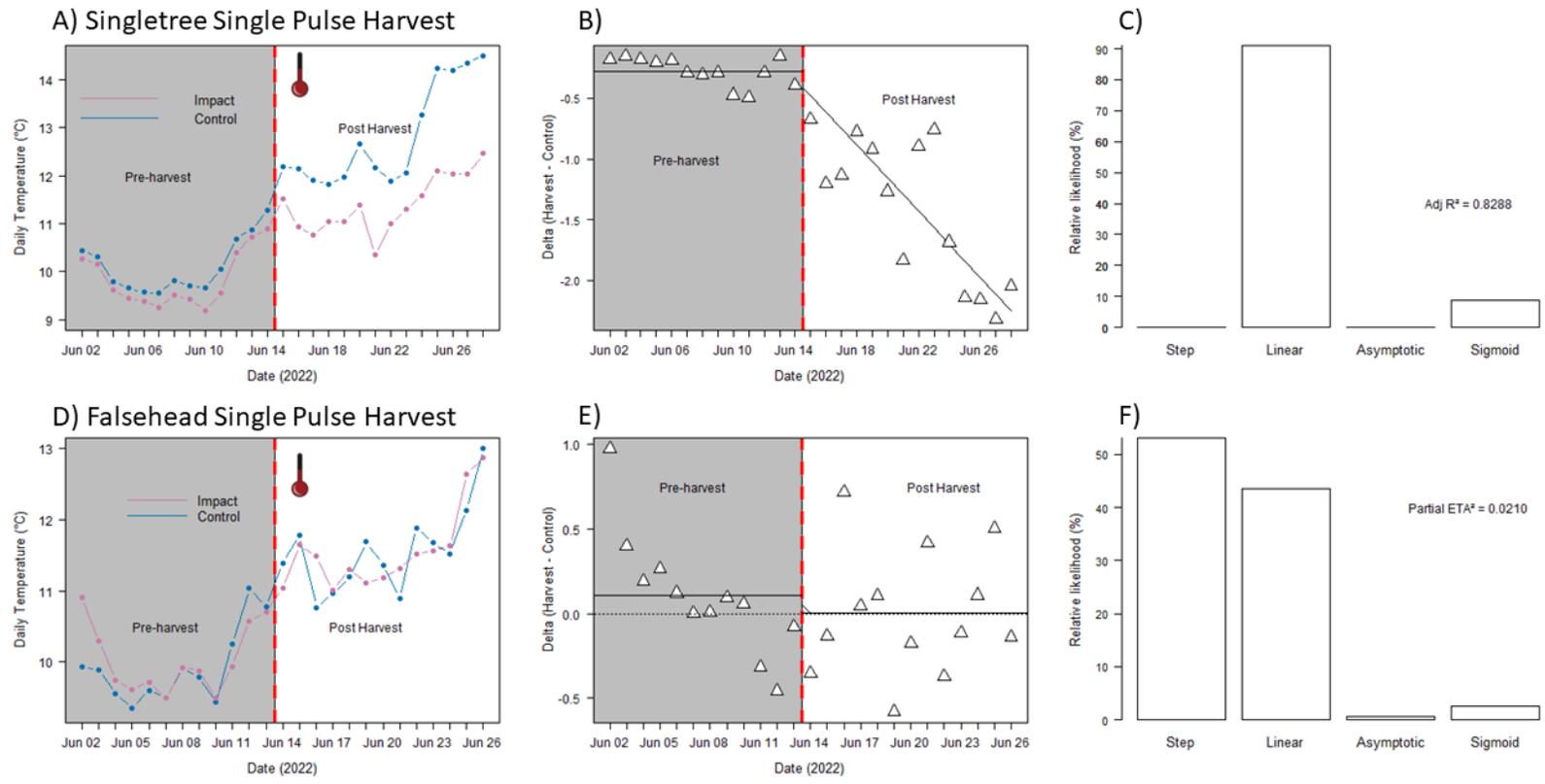


Figure 7: Effects of a single pulse harvest event on benthic kelp forest sea water temperature (°C) at A,B,C) Singletree and D,E,F) Falsehead in control (blue) and harvested (pink) sections of the forest, pre and post harvest.

Sequential Press Harvest

Light -

We found evidence for an effect of sequential press harvest on benthic light intensity in the kelp forests at Deer Island and Falsehead (Figure 8). In both kelp forests, light intensity declined on the seafloor following harvest, but the response trajectory differed among kelp forests. Specifically, after ten days of harvesting the kelp forest off Deer Island in late May to late June, removing 75,897 kg total of kelp, we detected a significant linear decline in light level differences between harvested and control sections post harvest (P-value=4.45e-4). Initially following harvest light quantity within the harvested section was greater, however the differences decline for ~3 weeks until hitting zero, then gradually increasing at a rate of 15.45 Lumens/m². Only 16% of the variation in these differences however is described by a linear response model to harvest (Figure 8 A, B, C, Appendix B.3, adj R²= 0.16). The variability of the light data was high in the harvest section, with a greater standard deviation in the harvest section post press harvest (SD during sequential harvest harvest section=242.83, SD post harvest harvest section=500.03).

After twelve days of harvest at Falsehead that removed 74,655 kg total of kelp, later in the growing season (from late June to mid July) we found that benthic light levels in the harvested section of the forest dropped significantly below those of the control section four days after harvest (p-value = 1.9e-06). In this case, a sigmoidal response in the difference in light levels between control and harvested sections of the kelp forest was best supported by the data (Figure 10 F, Adj R² =0.554) revealing an eventual average difference of 157.94 Lumen/m² between control and harvested sections (95% CI: -208.68 - -107.19) seven days post harvest. The control section experienced high variability of the data, with a standard deviation 8 times greater post sequential harvest (SD during sequential harvest control section=16.97, SD post harvest control section=132.62).

Temperature –

We detected significant yet variable effects of sequential harvest on benthic seawater temperatures across two kelp forests (Figure 9). Specifically, we found evidence for an effect of sequential kelp harvest on benthic seawater temperatures at

the kelp forest off Deer Island, which was harvested early in the growing season (Figure 9 A, B, C). There, the sigmoidal model detected a significant yet ephemeral increase in temperatures in the harvest section compared to the control (p -value= $3.09e-4$), however only 14% of the variation in the difference in temperature between control and harvested sections of this kelp forest is described by a sigmoidal response to harvest (adj $R^2=0.14$).

We also detected strong evidence of an effect of press harvest on benthic seawater temperature at Falsehead (p -value = $8.52e-16$), which was harvested later in the growing season (Figure 9 D, E, F). At Falsehead, kelp forest temperatures in the control and harvested sections of the forest rose and diverged, with the harvested section experiencing a steadily increasing, linear cooling response (Figure 9 D, E, F Table B.4). The strongly supported linear response in temperature differences between control and harvested sections of the Falsehead kelp forest suggest an increase in temperature differences of 0.15°C per day post sequential press harvest (95% CI: $-0.17 - -0.13$) (Figure 9 E, F, Table B.4). Variability in temperature in the control section of the forest was higher than the harvest section post sequential harvest (SD during press harvest control section= 0.53 , SD post harvest control section= 0.81 , SD during press harvest harvest section= 0.53 , SD post harvest harvest section= 0.69).

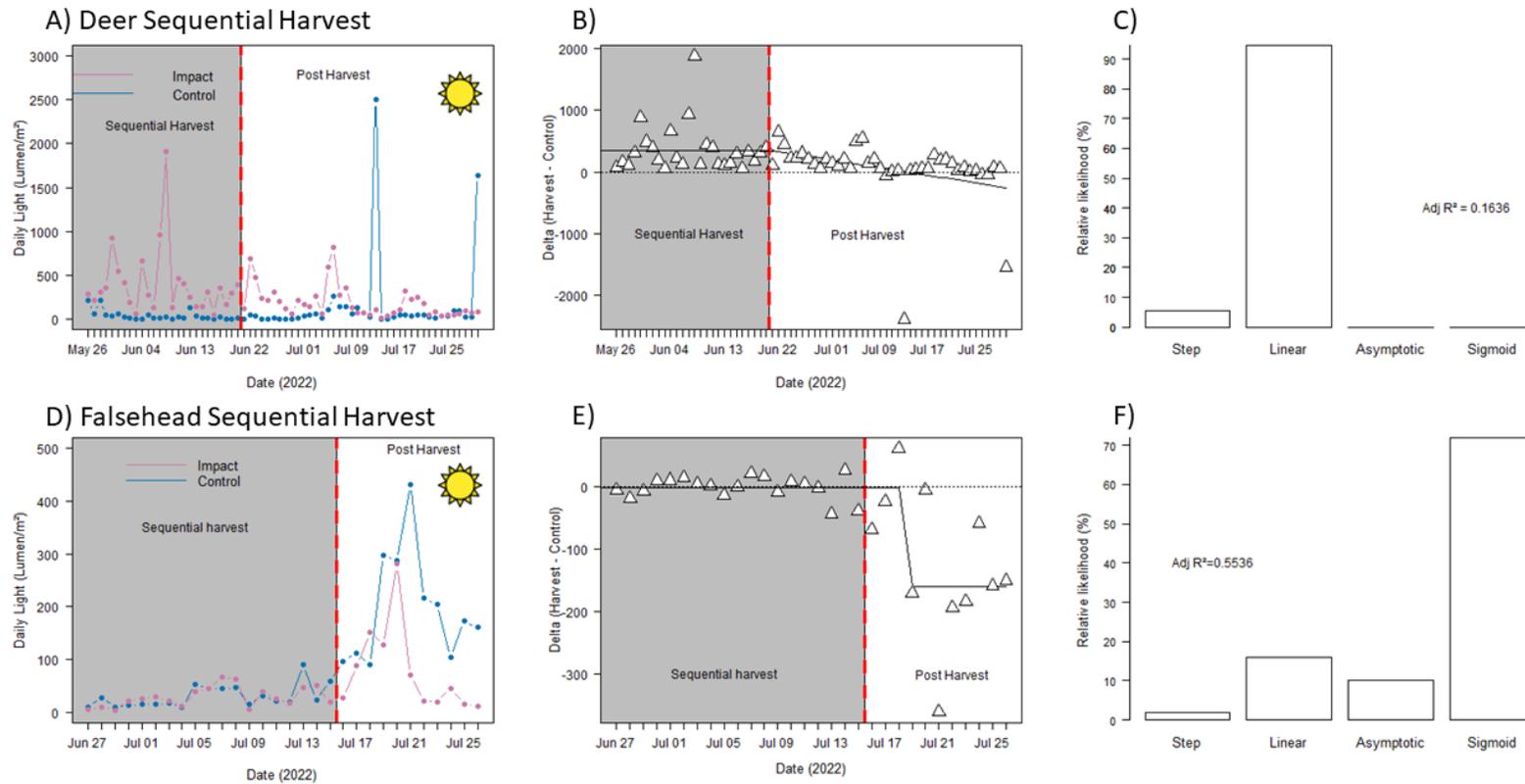


Figure 8: Effects of sequential press harvest on benthic kelp forest light intensity (Lumen/m²) at A,B,C) Deer Island and D,E,F) Falsehead in control (blue) and harvested (pink) sections of the forest, during and post harvest.

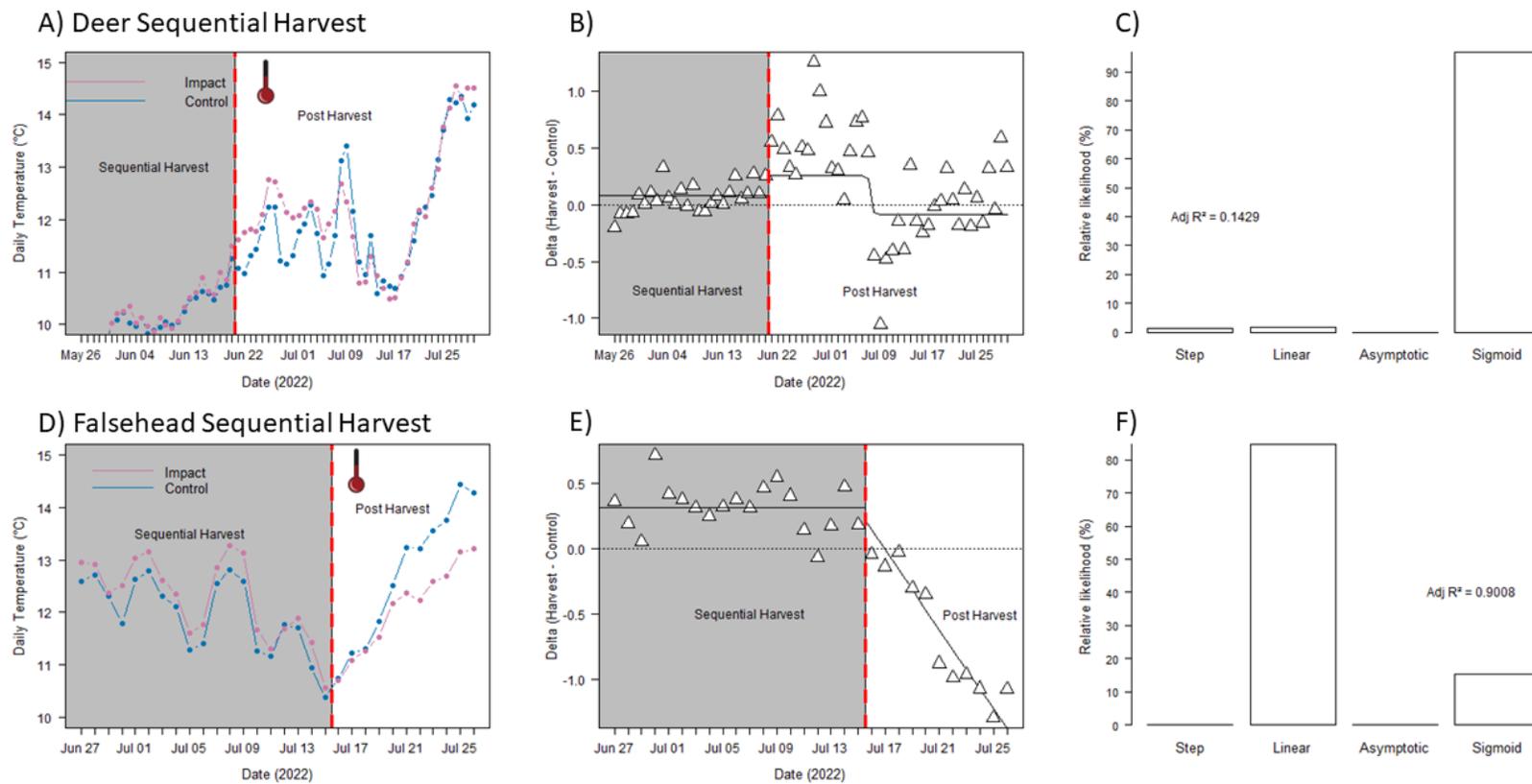


Figure 9: Effects of sequential press harvest on benthic kelp forest seawater temperature (°C) at A,B,C) Deer Island and D,E,F) Falsehead in control (blue) and harvested (pink) sections of the forest, during and post harvest.

Effect of Pulse and Press Harvest Disturbances on Water Flow

We did not detect an effect of a single, early season pulse harvest event on seawater flow at the kelp forests off Falsehead and Singletree (Figure 10 A, B, Appendix D.1, D.2). Immediately after harvest, both sections of the kelp forests experienced on average higher flow rates, but these differences were not significant.

We detected variable effects of sequential press harvest on seawater flow at the kelp forests off Deer Island and Falsehead (Figure 11 A, B, Appendix D.3, D.4, D.5). Specifically, immediately after eight days of harvest at Deer Island from late May to mid June, we detected a significant 7-fold increase in waterflow in the harvested section of the kelp forest (p -value = $9.24e-5$). Moreover, repeated measures of waterflow at the Deer Island kelp forest through the harvest season indicate significant increases in water flow in the harvested sections of the forest (p -value = $4.37e-06$) (Figure 12). In contrast, at Falsehead, after six days of sequential press harvest from late June to early July, we found no difference in waterflow between control and harvested sections of the kelp forest (Appendix D.3)

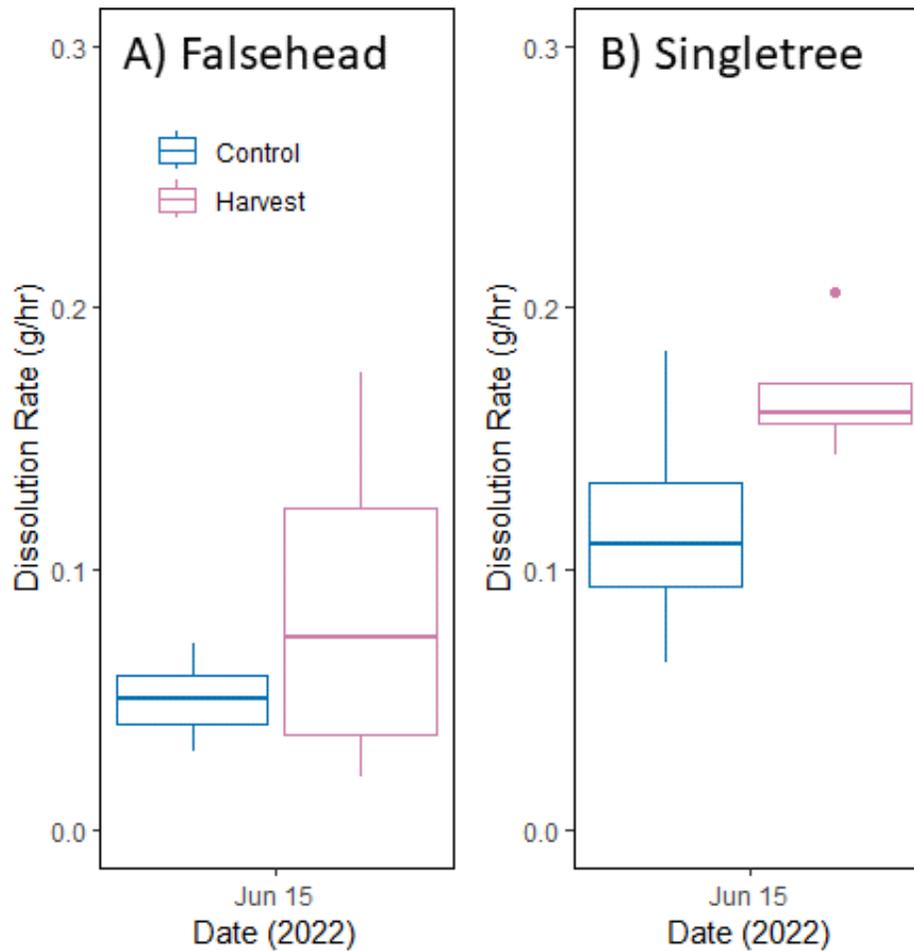


Figure 10: Dissolution rate (g/hr), a metric of water flow, in the harvested (pink) and control (blue) sections of the experimental kelp forest at A) Falsehead and B) Singletree after a single pulse harvest event in June.

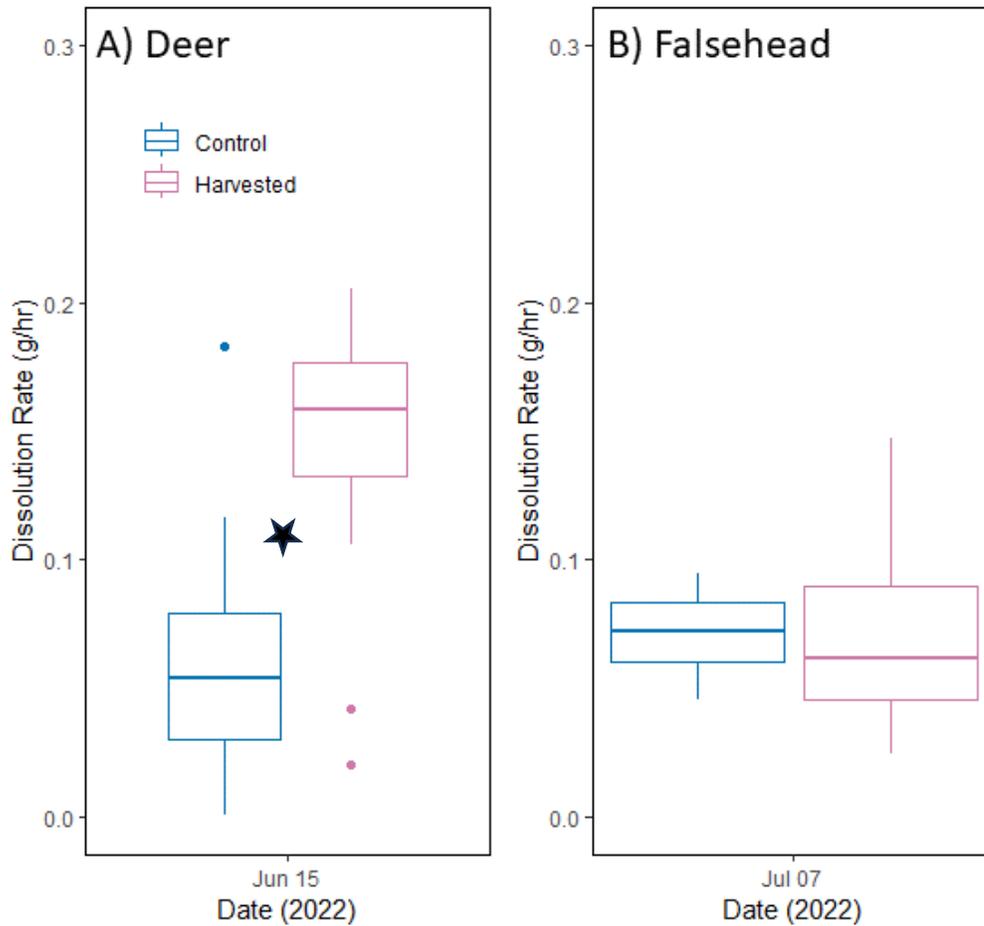


Figure 11: Dissolution rate (g/hr), a metric of water flow, in the harvested (pink) and control (blue) sections of the experimental kelp forests after 6 to 8 days of repeated press harvest at A) Deer Island early in the growing season and B) Falsehead later in the growing season. * indicates significant differences.

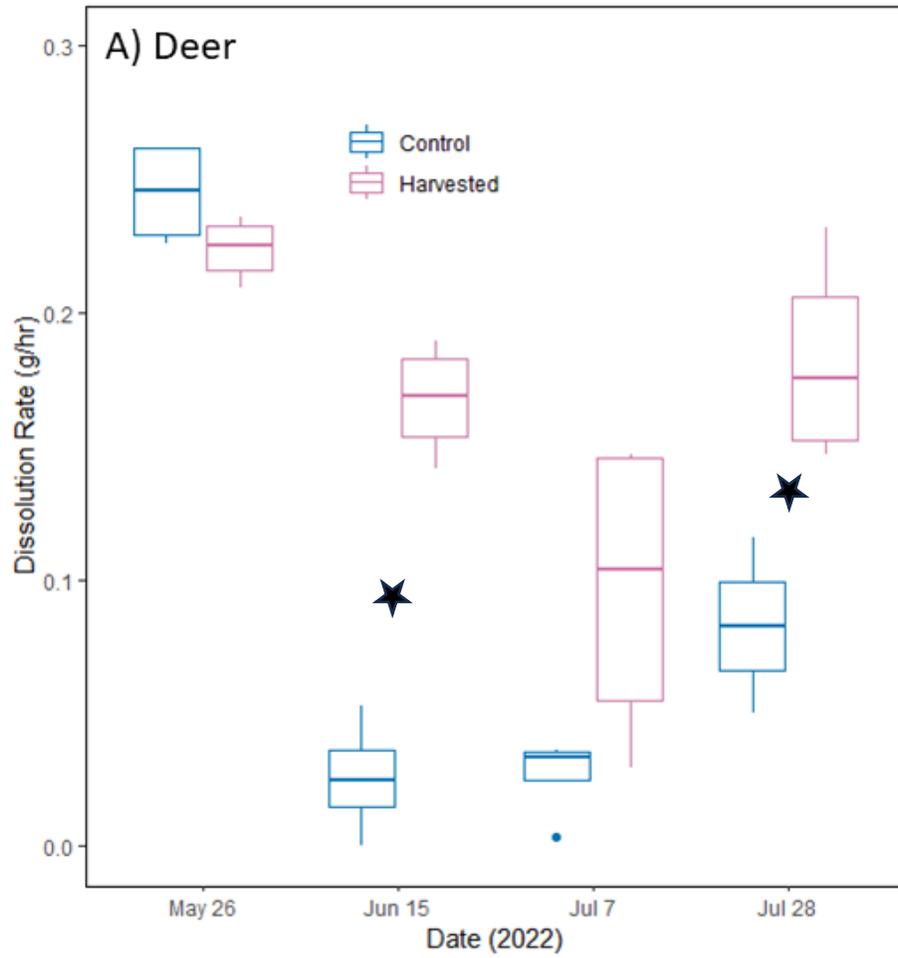


Figure 12: Dissolution rate (g/hr), a metric of water flow, in the harvested (pink) and control (blue) sections of Deer Island throughout the entire harvest season. * indicates significant differences.

Effect of Harvest on Surface Frond Densities and Bryozoan Cover

We found that harvest influenced the density of surface fronds at only one of our three experimental kelp forests (Figure 13, Appendix E.1). Specifically, at Deer Island, where a sequential press kelp harvest was imposed for 10 days at the beginning of the growing season, surface frond density was on average 2 times lower in the harvested section of the forest (11 ± 1.07 fronds/m²) relative to the unharvested control where average frond densities were 20 ± 1.24 fronds/m². This impact was seasonally influenced, with July 10 surface frond density at Deer Island not differing between the harvest and control sections but early season and late season frond densities being impacted by harvest.

While we detected a significant effect of harvest on bryozoan cover, the effect varied across kelp forest and season (Figure 14 Appendix E.2). All sites had significant impact of harvest on bryozoan coverage in July, however Falsehead was the only site to have significant differences in late July and there was no impact of harvest on bryozoan coverage across all sites in June (Appendix E.2). A significant 3-fold increase in bryozoan coverage was found in the control section compared to the harvested area at Singletree on July 7, with the control section having on average $8.58\% \pm 1.22$ compared to the $2.96\% \pm 0.43$ for the harvest section. In contrast, Falsehead and Deer had higher bryozoan coverage in the harvest section compared to the control section in early July. Falsehead had on average $0.87\% \pm 0.13$ bryozoan coverage in the harvest and $0.18\% \pm 0.11$ in the control section on July 11. Deer had an average bryozoan coverage of $1.95\% \pm 0.27$ in the control and $3.24\% \pm 0.46$ in the harvest on July 10 (Figure 14). Bryozoan coverage was lowest at the beginning of June and peaked at the beginning of July, with twice as much bryozoan in July as other times in the season. Overall, Singletree had 1.7 times more coverage of bryozoan compared to Deer, and 4 times more bryozoan than Falsehead (Figure 14).

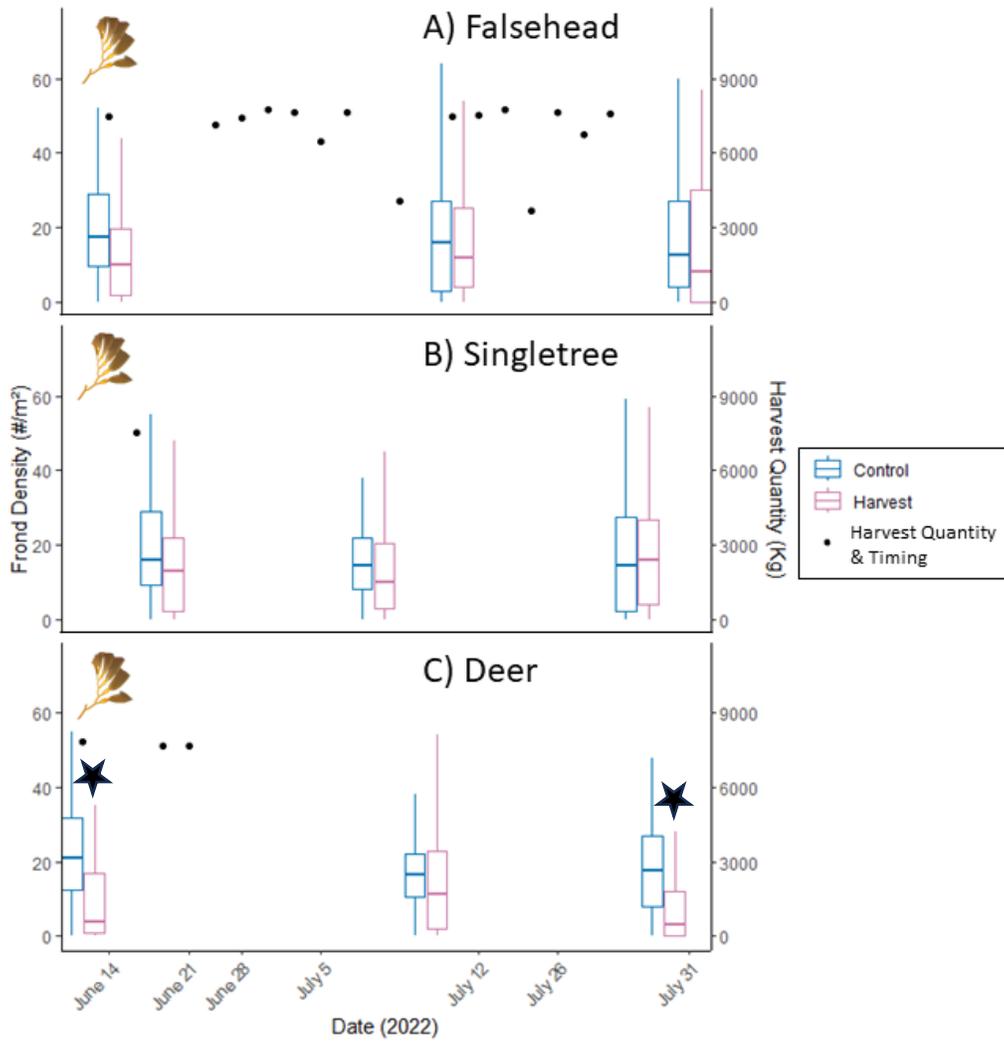


Figure 13: Surface frond density (#/m²) at A) Falsehead, B) Singletree, and C) Deer Island in control (blue) and harvested (pink) sections of the kelp forests measured after harvest. Black dots denote when and how much harvest occurred (Kg). * indicates significant differences.

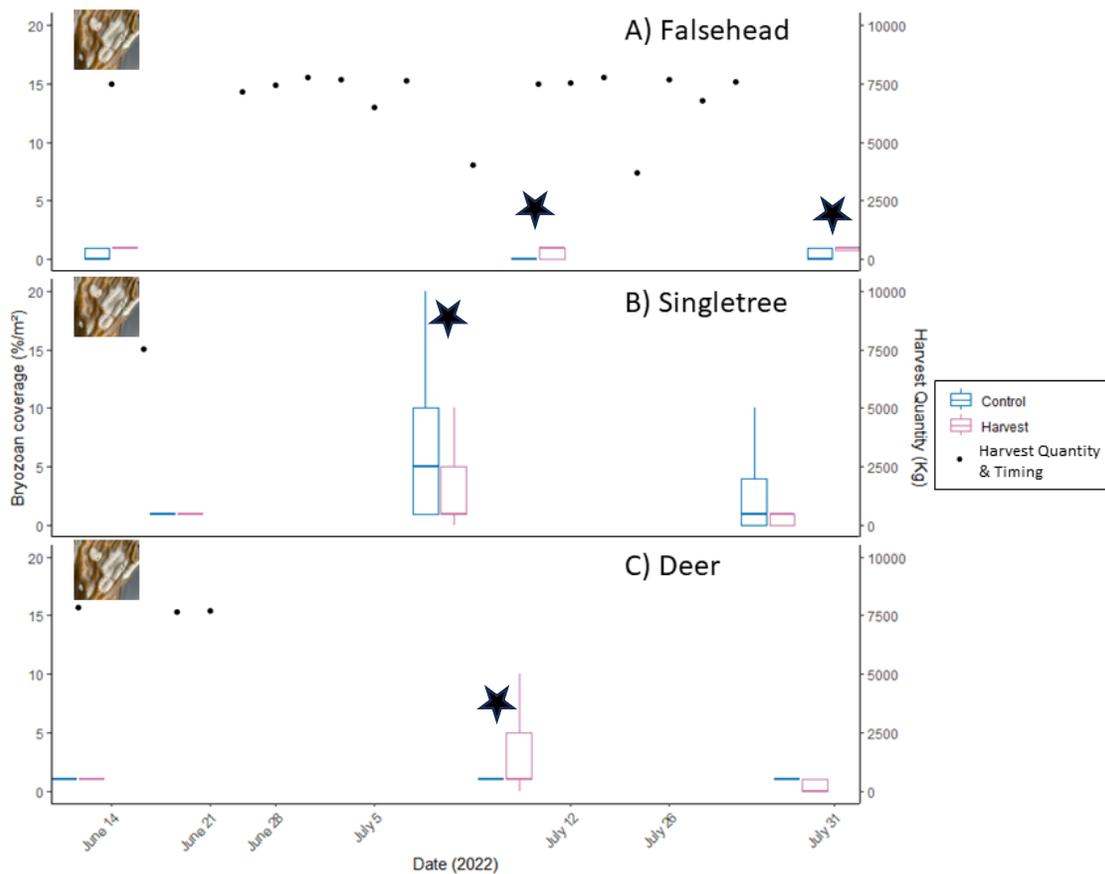


Figure 14: Bryozoan coverage (%/m²) at A) Falsehead, B) Singletree, and C) Deer Island in control (blue) and harvested (pink) sections of the kelp forests measured after harvest. Black dots denote when and how much harvest occurred (Kg). * indicates significant differences.

Effect of Harvest on Subsurface Fronds and Reproduction

We did not detect an effect of harvest on the number of subsurface kelp fronds at the kelp forests off Falsehead, Singletree and Deer Island (Figure 15, Appendix F). The number of new or alive fronds did not differ significantly between harvested and control sections. The dead fronds did not differ between section at Singletree or Deer Island, however at Falsehead the number of dead fronds in the harvested section compared to the control section was significant later in the season (average 9 dead fronds/kelp +/- 2.28 in the harvest section, 1.62 +/- 0.73 dead fronds/kelp in the control section) (Figure 15, Appendix F.4).

We detected no effect of harvest on the potential reproductive output of kelp plants at Falsehead, Singletree and Deer Island across the entire season looking at number of reproductive sporophylls (Figure 16, Appendix G.1, G.2). The number of sori patches on individual kelp plants were not significantly different between the harvest section or the control section at any of the kelp forests. There was also no significant effect of harvest on the number of sporophylls between the three kelp forests (Appendix G). Singletree had the highest number of sori patches, 3 times higher than Falsehead (Figure 16). The peak of reproduction was observed at the beginning of July, with the control section having 1.5 times more sporophylls than the harvest section during that period. The average percentage of reproductive sporophylls for the control and harvest sections was 6% and 5% respectively.

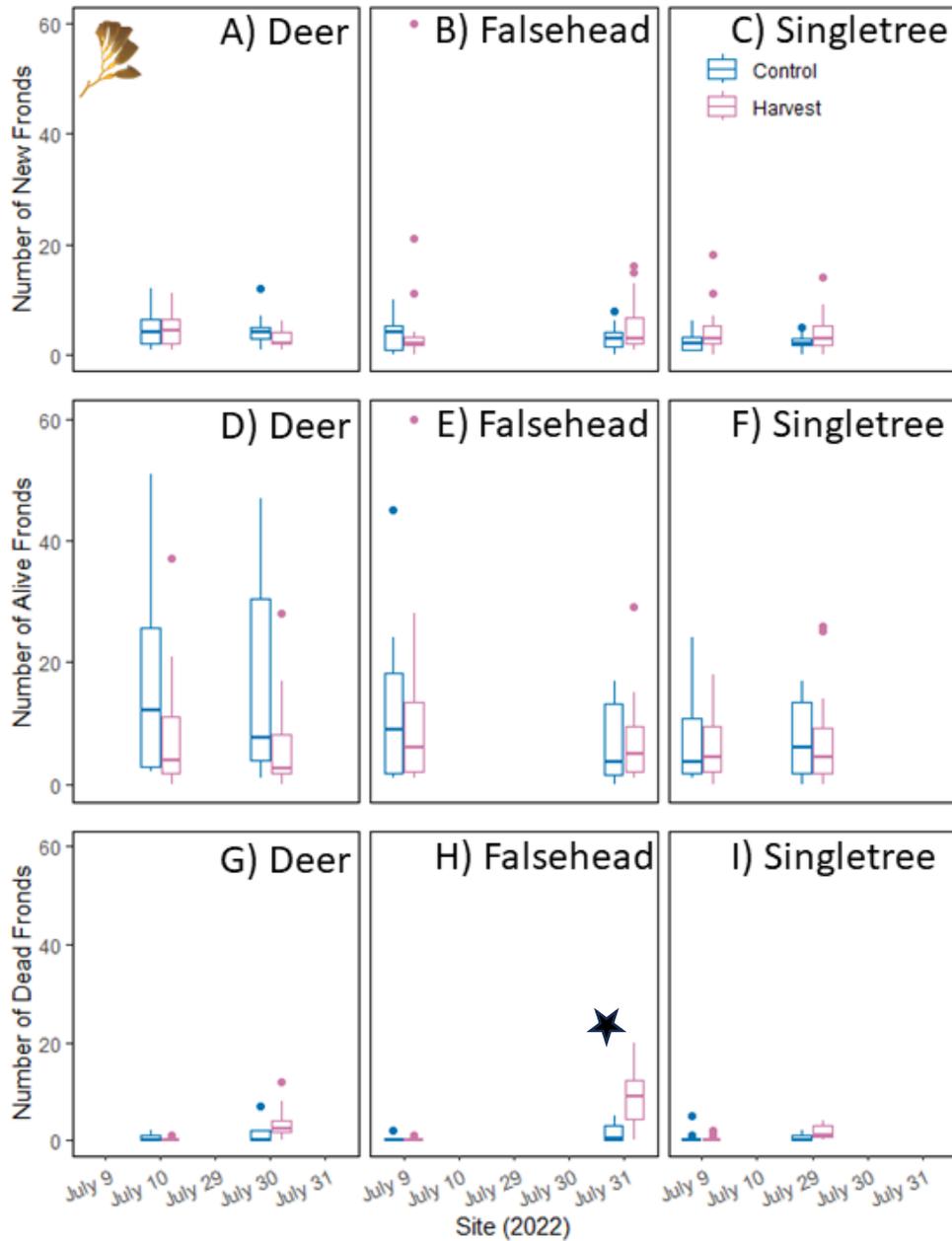


Figure 15: Number of new fronds, alive fronds and dead fronds at Deer Island, Falshead, and Singletree in control (blue) and harvested (pink) sections of the kelp forests measured after harvest. * indicates significant differences.

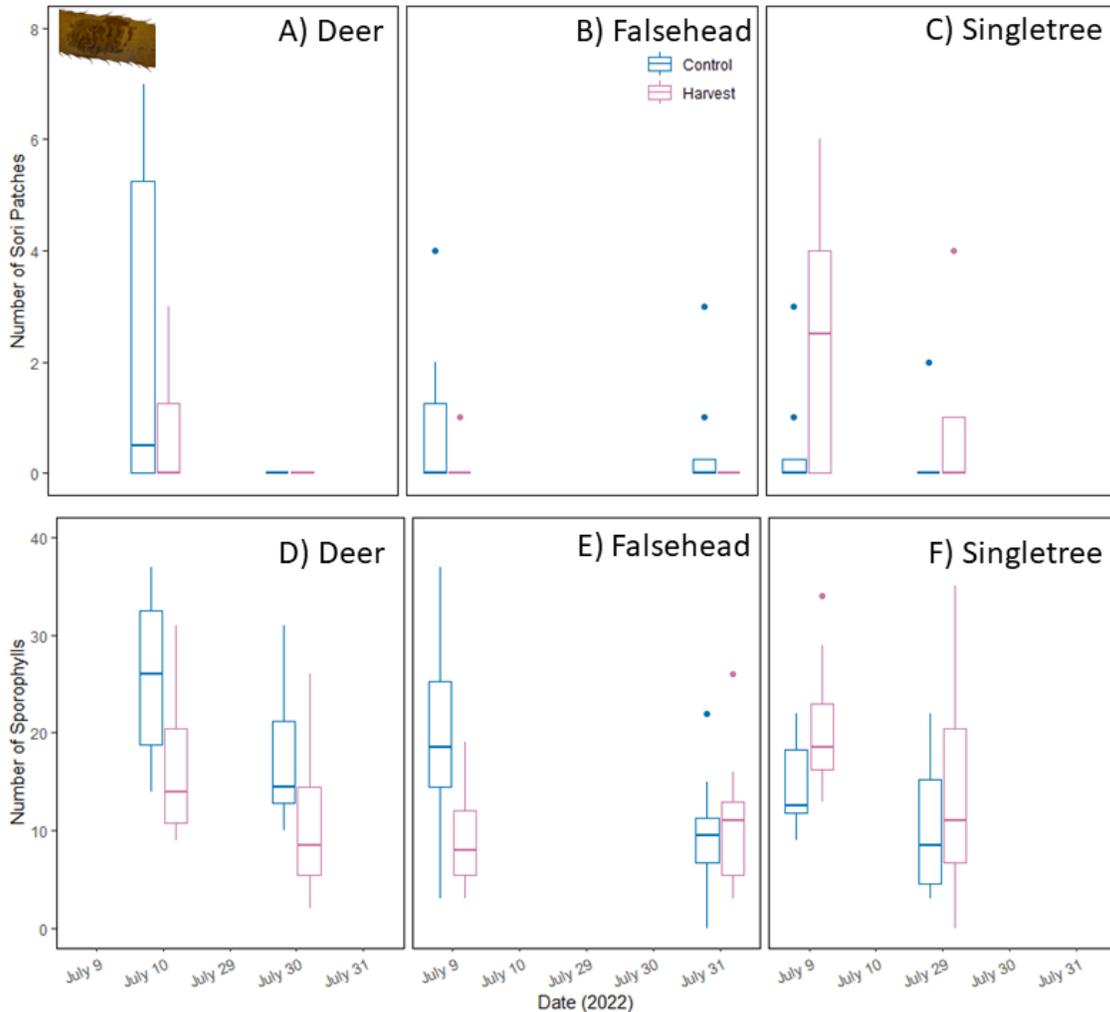


Figure 16: Number of sori patches at A) Deer Island, B) Falsehead, C) Singletree and number of sporophylls at D) Deer Island, E) Falsehead, F) Singletree from tagged kelps in control (blue) and harvested (pink) sections of the kelp forests measured after harvest.

Effect of Harvest on Aerial Surface Coverage of Kelp

Patterns of kelp canopy coverage were inconsistent between the harvest and control sections of Falsehead, Singletree and Deer Island (Figure 17). Kelp coverage in the harvested sections tended to increase over the harvest season. Surface kelp coverage was 3.4x higher at Falsehead compared to Singletree and Deer Island across sections through time due to the larger size of the forest (Figure 17). Seasonal timing of

peak kelp coverage was not the same between kelp forests, with Falsehead having the highest canopy coverage in August, Singletree in June, and Deer in May (Figure 17).

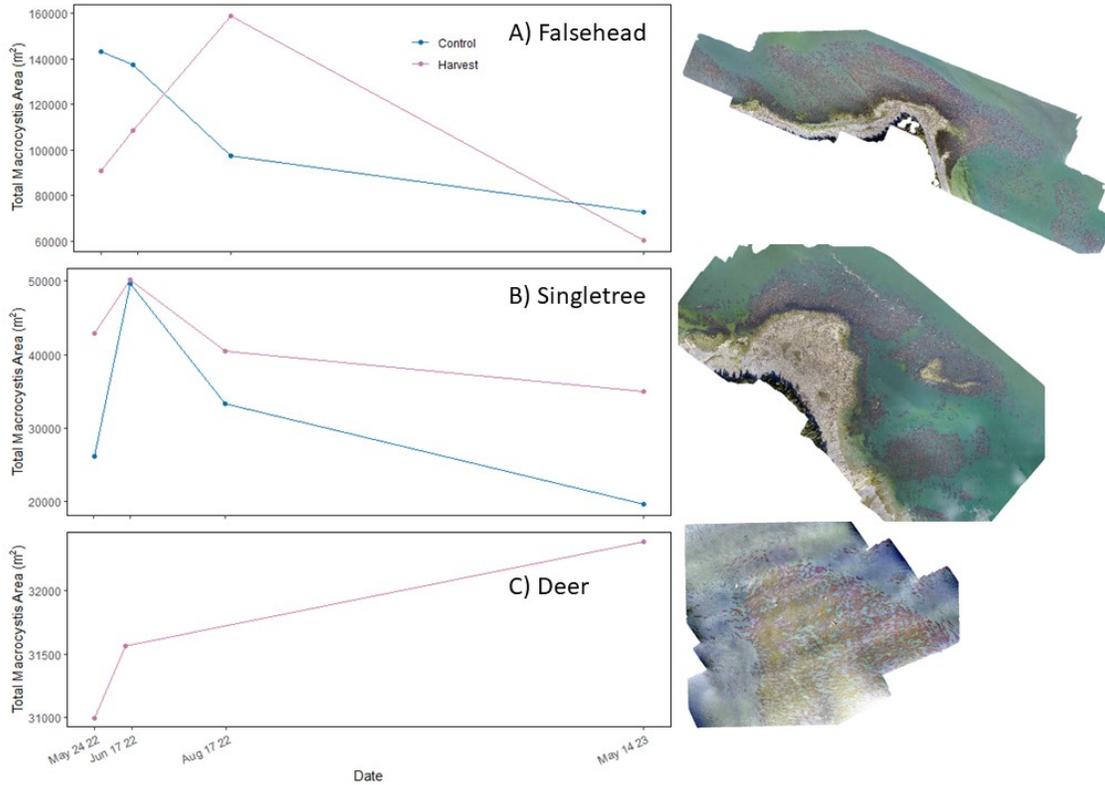


Figure 17: Total Macrocyctis area at A) Falsehead, B) Singletree, C) Deer Island in control (blue) and harvested (pink) sections of the kelp forests.

Discussion

The expansion of kelp harvest has been identified as a pathway to support emerging blue economies among temperate coastlines worldwide. Here, we found that kelp forests in Kwakiutl territory of the Pacific Northwest coast of North America appear to be resilient to current kelp harvest levels and practices. Specifically, the hand harvest of surface canopy fronds removing <10% of available canopy biomass had surprisingly small effects on kelp forest surface density, subsurface frond recovery, canopy kelp area, and potential reproductive output of kelp plants. Sequential kelp harvest reduced benthic light levels at one site, possibly due to accumulation of cut fronds on the benthos, and marginally increased light at another site. Press harvest also altered sea water temperatures in kelp forests, ephemerally warming benthic sea water in one case and cooling it in another case.

Specifically, there were relatively small changes in kelp forest density detected post-harvest. Surface kelp frond density was empirically reduced by harvest at one site, but harvest was not found to influence changes in kelp density at the other two sites, frond recovery below the surface or trends in overall surface kelp coverage. The contextual nature of kelp harvest effects was highlighted by the surprising reduction in light levels at one site and variable impacts on temperature and water flow following repeat and single harvests. Overall, our results underscore the reciprocal and dynamic nature of ecological interactions within harvested kelp forests and the importance of empirical assessments when determining kelp forest changes after disturbances. This includes the relationships between kelp harvesters, kelp forests and a diversity of social-ecological conditions and constraints. Our findings suggest that kelp management will need to be assessed at the forest scale and that harvest effort may need to be fine tuned to local kelp forest conditions.

Kelp Forest Characteristics are Variably Affected by Harvest

One of the many challenges for marine managers is to determine if current harvest quantities and techniques support the recovery and sustained use of a kelp forest (Krumhansl et al., 2016; Kobluk et al., 2021). In our study, we found that kelp harvest reduced the number of surface fronds at Deer Island but not at Falsehead or

Singletree. Press harvests at Deer occurred in early June, whereas press harvests at Falsehead were later in the season and Singletree only had pulse harvests. Our results suggest that seasonal timing of press harvests may influence frond density both immediately after harvest and later in the season. The lack of frond reductions across sites and season post-harvest may also be influenced by the overall density. The average density across all kelp forests was 15 fronds/m² in the harvest section, with Deer Island having the lowest harvest sections density on June 15 at 11 fronds/m². The lowest density section of the lowest density kelp forest during the time of year with the lowest densities we assessed still had very dense kelp forests. 11 fronds/m² is higher than densities of unharvested giant kelp forests from different temperate regions globally, which range from 6 fronds/m² in southern California (Reed et al., 2009), 15 fronds/m² in the Falkland Islands (Tussenbroek, 1993), 2.45 fronds/m² in Alaska (van Tamelen & Woodby, 2001) and 4.45 fronds/m² in British Columbia (Sutherland et al., 2008). This result suggests that kelp forests in Kwakiutl territory are significantly denser than in other parts of the province and the world, even after repetitive commercial harvests. In addition, there were not consistent trends from aerial imagery of kelp canopy area reductions after harvest, suggesting that harvest does not always reduce overall canopy size or coverage. Aerial imagery of kelp forests in California, where harvest yields are 300 to 550 metric tons wet weight per harvest and forests are harvested twice a year have also been found to show minimal effects on canopy area (Kimura & Foster, 1984; Barilotti & Zertuche-Gonzalez, 1990). Ultimately these results suggest that harvest at the intensity and temporal rate we studied maintains high density of kelp fronds.

Following the removal of kelp fronds, compensatory growth allows kelp to recover and tolerate moderate levels of loss (Cerda et al., 2009). Harvest methodologies which focus on selective frond removal instead of whole plant harvest have been suggested by managers to maintain sustainability of harvest, due to increased replacement of fronds (Levitt et al., 2002; Krumhansl et al., 2017). Our study did not find that harvesting of giant kelp increased the number of new or alive fronds. These results are echoed by other work which also did not find harvest to increase the production or growth of new fronds (Geange et al., 2014). However, our results also did not find a significant decrease in the number of alive fronds following harvest compared to our control section. This result suggests that either the removal of harvestable sized canopy

fronds is mimicking natural loss and frond replacement of non-harvested plants or that compensatory growth is replacing harvested fronds. Previous research has shown that small scale kelp harvest mimics natural frond loss, has minimal impacts on kelp biomass and in some cases can stimulate increased biomass production (Krumhansl et al., 2017; Kobluk et al., 2021). Based on these results, the harvest effort, and practices we studied had relatively small impacts on kelp density and through hand harvests of upper portions of fronds kelp forests can be maintained through time.

Warmer and denser kelp forests are more susceptible to bryozoan settlement and growth (Saunders & Metaxas, 2008), leading to the hypothesis that intentional kelp thinning could be used as a proactive tool to reduce the amount of bryozoan cover in kelp forests (Denley et al., 2022). We did detect an effect of kelp harvest on bryozoan coverage at all three kelp forests, however bryozoan cover varied inconsistently between harvest and control sections among kelp forests throughout the harvest season. Warmer periods of the harvest season had higher impacts of harvest on bryozoan, although the directionality of these impacts varied. Falsehead and Deer Island had higher bryozoan coverage in harvested sections during the warmer period while Singletree had lower coverage in the harvested section during this same period. Additionally, part of this variability may be due to selective harvest of kelp by harvesters, who target healthy fronds due to the lower market value of heavily colonized fronds (Walls et al., 2017). Calcification of bryozoan on kelp changes pH dynamics of harvested fronds, reducing the ability for resale of kelp as fertilizer, the main economic use for Kwakiutl commercially harvested kelp. These social-ecological influences may contribute to observations of higher bryozoan cover in selectively harvested kelp forests, where harvesters will leave heavily fouled kelp fronds.

While our study found differences in trends of bryozoan cover following harvest, the overall cover of bryozoan we found were relatively small. Previous research on the Central Coast in British Columbia found peak seasonal bryozoan coverage averaged 25%-50%, with maximum coverage of 75%, however methodology of quantification varied from ours slightly (Denley et al., 2022). The statistically significant differences between the harvest and control sections we found were differences of less than 2%, which we predict would not be ecologically relevant differences. The only site that had higher coverage of bryozoans, Singletree, followed hypothesized trends of lower bryozoan coverage in the harvested section. Future analyses on the impacts of

commercial kelp harvest on bryozoan cover should focus on regions with higher quantities of bryozoan coverage to further illuminate the role harvest has on bryozoan populations and coverage.

Reproductive strategies of giant kelp in the northern hemisphere consist of year-round production of a high number of sporophylls, with the majority of those sporophylls producing sporogenous sori (Buschmann et al., 2006). The removal of kelp biomass has been found to have negative consequences on the production of reproductive blades, with certain cases leading to complete sterility (Graham, 2022). In California one study of *Macrocystis pyrifera* found a removal of 75% of kelp fronds led to a ~75% decrease in reproductive blades (Reed, 1987), and in New Zealand, harvest was found to cause an 86% reduction in reproduction (Geange et al., 2014). In contrast, our study did not find an effect of harvest on the number of reproductive blades or the number of sori patches. These results may be due to the small density changes caused by harvest, which removed <10% of the total surface canopy over the season and was found to minimally affect frond density across kelp forests through the harvest season. Additionally, our study assessed reproduction over a relatively short period of time, 3 months. Research on harvest impacts over a longer time frame and through multiple seasons is needed to truly assess the long-term impacts of harvest on the reproductive output of perennial giant kelp plants.

Changes in Biophysical Properties of Kelp Forests Not Consistently Correlated with Kelp Forest Density Changes

While we detected changes in the biophysical properties of light quantity, seawater temperature and water flow between harvested and control sections at our three experimental kelp forest, these properties were not consistently linked to changes in kelp forest densities following harvest. At Deer Island, water flow was greater in the harvested compared to control sections in early June and late July, corresponding to significant reductions in frond density at harvested sections during those times (Figure 12, 13). Water flow at Deer Island did not differ between sections in mid June, consistent with a lack of difference in frond density during that same time period (Figure 12, 13). However, at Deer Island benthic sea water temperatures did ephemerally increase in the harvest section following harvest compared to the control section, despite increased flow rates. Additionally, temperature and light differences following harvest were observed at

Falsehead and Singletree following pulse and press harvests, despite no detectable difference in kelp density between experimental sections during this time. This suggests that the changes in biophysical characteristics of the kelp forests at the spatial and temporal rate we studied were not closely related to significant reductions in frond density due to harvest. Instead, biophysical characteristics appear to be highly site specific, possibly reflecting the magnitude and seasonal timing of the harvest disturbance experienced at each kelp forest.

While temporal and spatial context is important, our findings suggest that commercial hand harvest of <10% of total giant kelp surface canopy has no impact on light after a single pulse harvest event but reduced light after repeated harvest pressure at one site and marginally increased it at another (Figure 6, 8, Appendix B & C). Contrary to our predictions, benthic light levels at Falsehead were reduced at harvested sections relative to the control sections following harvests, likely due to shading from deteriorating cut fronds. Specifically, at Falsehead following press harvest in mid July light levels in the harvest section decreased, this correlated with significantly higher quantities of dead fronds in the harvested section of Falsehead in late July (Figure 8, 15). The harvest methodologies used in this study did not remove the entire kelp, instead, the top ~5 m of canopy fronds was hand cut, leaving large proportions of subtidal fronds intact after harvest. These fronds, now lacking a scimitar and thus the ability to grow, gathered below the canopy to decay, creating large masses that reduced light levels. This short-term increase in detrital production following pulse harvests may have implications for ecological communities present in the kelp understory, including populations of detritivores. Further work is needed to understand the impacts kelp harvest is having on secondary production and on associated abiotic and biotic changes.

The inconsistent changes in light levels following harvest demonstrates that implications of harvests are context-dependent, based on site specific reactions to harvest and harvest frequency, which may influence ecological dynamics within harvested forests. Light is closely related to canopy density and in high density kelp forests irradiance at 1m depth is often low enough to limit photosynthesis even during sunny conditions (Gerald, 1984). Previous work has found that kelp surface canopies can reduce bottom light by 30%, which has the potential to decrease kelp gametophyte reproduction and vegetative growth through changes to light intensity and quality (Bularz et al., 2022; Ebbing et al., 2020). The arrival and survival of kelp predators, such as sea

urchins, and the presence of competitive understory algae is also influenced by light changes (Reed & Foster, 1984). Studies of 50% kelp canopy removal found major changes in light attenuation, which in turn reduced shade adapted understory algae and fauna who rely on the canopy for shelter (Wernberg et al., 2020; Norderhaug et al., 2020). In contrast, our work suggests that kelp harvest at our documented intensity and extent does not increase light, potentially maintaining these benthic communities due to stability of benthic light availability. However, our work did not normalize benthic light quantity to the incoming photosynthetically usable radiation, limiting our ability to compare impacts of harvest on light quantity or quality between sites. Overall, the impact of harvest on light is dynamic, variable, and further research is needed to understand harvest impacts on benthic communities.

Our work highlights that kelp harvest can alter sea water temperatures, particularly in forests experiencing instances of warmer seasonal water temperatures (Figure 7, 9, Appendix B & C). While our results were not consistent across all kelp forests, we found temperatures diverged between control and harvested sections of Singletree after a single pulse harvest with the harvested section having consistently lower temperatures. Similarly, the harvested sections of the Deer and Falsehead kelp forests were relatively cooler after a period of sequential harvest. Singletree was the shallowest of our experimental kelp forests, with the forest residing on a shallow bench with an average depth of ~3m below chart datum. The control section of Singletree experienced significantly higher temperatures earlier in the season than any other forest and any other section, likely due to the shallow nature of the kelp forest (Figure 4, 7, 9). In contrast, the temperatures of the harvested side of Singletree during the same period were significantly lower. Additionally, during the hottest period of our experiment Falsehead exhibited lower temperatures in the harvest section compared to the control section. Deer Island after sequential harvest, initially experienced warmer temperatures in the harvested section, however once ambient air temperatures rose at the beginning of July in the harvest section, sea water temperatures dropped. These results suggest that harvest has a possible buffering effect on temperatures during times of high heat. While these reductions in temperatures were not correlated with subsurface water flow except at Deer Island, greater analyses of water flow across seasons and depths are needed. Ultimately, if kelp harvest can reduce sea water temperatures during periods of

high ambient temperature, then small-scale harvest could positively alter the persistence and integrity of cold-water kelp forest ecosystems.

Through this study we have shown that kelp forests in Kwakiutl territory are resilient to current kelp harvest levels and practices, conclusions that can only be drawn from working directly with harvesters following established harvest methodologies. We acknowledge that many challenges arise when implementing sea-scape level experiments with harvesters that are constrained by weather conditions, sea state, kelp forest conditions, travel time, time of year, and approved provincial harvest quotas. This work focused on drawing inferences from typical Kwakiutl kelp harvest practices without altering when or which kelp forest to harvest, maintaining harvester decision making processes. While we established harvested and control sections of three experimental kelp forests, we did not control the timing or magnitude of the harvest itself. Our analysis focused on differing spatial temporal pulse and press instances of harvest, limiting the inferences we can make on the effects of harvest on light, temperature, and water flow changes. Overall, more work across a wide range of kelp forest distributions and ecological environments will illuminate these uncertainties. However, we strove to include communities and practitioners in this research thereby increasing the legitimacy and relevance of this research to collaborating communities and practitioners. Overall, we found that harvest impacts are minimal, variable over time and context dependent.

The Future of Kelp Harvest in Canada

Worldwide, seaweed cultivation generated USD \$14.7 billion in 2019, with Canada accounting for only 0.04% of world production (Cai et al., 2021). To meet climate and economic goals, Canada plans to grow their blue economy through the commercial development and support of emerging kelp fisheries (Fisheries and Oceans Canada, 2022). Management policies for kelp harvest that can provide sustainable yields, minimize bryozoan fouling, maintain ecological integrity and complexity, and promote kelp forest growth are required to maintain the sustainability of harvest practices. With increasing threats to kelp forests caused by climate change and land use changes it is important to understand the consequences of kelp harvest and minimize them whenever possible.

In British Columbia, current provincial kelp harvest regulations dictate that kelp must be hand harvested and that stipes must be cut above the holdfast (BC Fish and seafood licensing regulation, 2016). Further provincial regulations dictate a maximum of 20% of any one kelp forest can be harvested and a maximum of 20% of the total kelp biomass can be harvested within a given harvest area. This quota was chosen conservatively based on data available to resource managers at the time which suggested that kelp could recover from harvest levels of 30 – 70% (Krumhansl et al., 2017). Our research confirms the potential of these policies to support kelp recovery post harvest, however our results were highly variable between kelp forests. Trends across kelp forests following singular or repetitive harvests varied, with individual kelp forest characteristics altering the magnitude of harvest impacts. Additionally, influences of harvest on abiotic conditions known to influence kelp growth and persistence were inconsistent and seasonal. Ultimately, kelp forest management must be on the forest-scale, with managers who are aware of local abiotic and biotic conditions within kelp forests making decisions on when, where, and how much to harvest.

The Kwakiutl Nation has expressed interest in furthering the development of kelp operations within their territory. While the financial gain of increased kelp harvest and aquaculture could have positive community-level effects, the primary focus of expanding kelp mariculture within the community is to increase connection with and access to kelp for all people of the Nation (Gutzmann, 2023). Kwakiutl governance principles for kelp which include responsibility, *namwayut* (we are all one), reciprocity, and *maya'xala* (respect) will maintain the sustainability of kelp practices, while providing the Nation with reconnection to their lands and waters, asserting land sovereignty, and facilitating Kwakiutl knowledge exchange (Gutzmann, 2023). While in this research we measured ecological outcomes of kelp harvest, our results cannot be isolated from the broader cultural context of Kwakiutl values and principles, which have sustained harvest practices through time (Artelle et al., 2018).

Overall, our results underscore the reciprocal and dynamic nature of ecological interactions within kelp forests and the importance of empirical assessments when determining kelp forest changes after disturbances. This collaborative kelp harvest experiment has implications for future kelp management within Kwakiutl territory and more widely for within the province of British Columbia. Firstly, future kelp harvest rates should be adapted to local conditions. Our work shows that each kelp forest reacts and

recovers slightly differently after harvest and these differences need to be considered when setting harvest rates. Second, future harvest rates should reflect kelp forest productivity and ecosystem change amid a warming ocean. Kelps are incredibly unique due to their thermal tolerance across their range; however, previous work highlights that kelp recovery rates post harvest are extremely temperature sensitive, with as little as 0.7 degrees of warming reducing recovery rates (Krumhansl et al., 2017). Future research should focus on modelling kelp forest productivity, amid a warming ocean, to be able to better predict harvest impacts. Finally, future harvest rates should be cautious of ecological thresholds. Kelp harvesters, regulators, and decision makers should be cognizant of tipping points, especially as market demands continue to grow and harvests become more efficient.

In Canada, we are situated to enhance the resilience of kelp forests and coastal communities to the impacts of harvest through kelp management practices that utilize diverse knowledges and democratizing conservation practices (Salomon et al., 2018). We have shown that harvested kelp forests are social-ecological systems where interconnected relationships between harvesters and kelp forests dictate the outcomes of harvests. The transition from colonial and centralized management to place-based governance systems with local culture, knowledge and management at the core would focus kelp harvest policy to the forest-scale, facilitating more equitable and resilient kelp forest-human relationships into the future.

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Appendix A.

Magnitude of the Harvest

Table A.1: Mean length and weight of harvested kelp fronds for each site (Falsehead, Singletree & Deer) at each measurement period.

Site	Measurement Date (2022)	Mean Length (m)	Length Standard Error	Mean Weight (kg)	Weight Standard Error	Number of harvested fronds
Falsehead	May 26	-	-	2.58	0.89	10
	June 17	5.90	0.81	3.27	1.35	18
	July 8	4.08	1.81	-	-	151
	July 9	6.97	1.87	1.59	0.55	20
	July 28	3.75	1.89	-	-	169
	July 31	8.04	2.54	1.40	0.51	20
Singletree	May 26	-	-	1.99	0.53	15
	June 17	6.25	1.62	1.80	0.91	8
	July 7	4.04	0.71	1.98	0.54	21
	July 29	7.82	1.89	2.1	0.65	21
Deer	May 26	-	-	2.66	1.02	9
	June 13	3.59	1.51	1.86	0.74	26
	July 10	5.51	1.67	2.16	0.97	20
	July 30	1.91	1.68	1.37	0.60	20

Table A.2: Mean harvest quantity across time (May 24- August 12) at each site (Falsehead, Singletree and Deer).

Site	Mean Harvest Quantity (kg)	Mean Harvest Standard Error	Number of Harvest Days
Falsehead	7048.97	88.92	20
Singletree	6859.64	198.11	13
Deer	7394.25	91.32	11

Appendix B.

Benthic BACIPS Analysis

Benthic Pulse BACIPS Analysis

Table B.1: BACIPS outputs for benthic light levels (Lumen/m²) at Singletree and Falsehead after a single pulse harvest event. Significant p-values (>0.05) are highlighted in yellow.

	Singletree	Falsehead
Winning Model AICc Weight	59.23 (Linear)	61.3 (Linear)
Next Best Model AICc Weight	24.26 (Step)	29.98 (Step)
Best Model Estimated Effect Size	2.38 Lumens/m ²	5.62 Lumens/m ²
95% Confidence Interval	-1.37 – 6.11	-4.25 – 15.5
P-value	0.2	0.25
Standard Deviation Pre-Harvest Control Section	59.2	56.16
Standard Deviation Post Harvest Control Section	36.41	137.08
Standard Deviation Pre-Harvest Harvest Section	23.83	30.74
Standard Deviation Post Harvest Harvest Section	23.94	21.69

Table B.2: BACIPS outputs for benthic temperatures (°C) at Singletree and Falsehead after a single pulse harvest event. Significant p-values (>0.05) are highlighted in yellow.

	Singletree	Falsehead
Winning Model AICc Weight	91.1 (Linear)	53.16 (Step)
Next Best Model AICc Weight	8.9 (Sigmoid)	43.65 (Linear)
Best Model Estimated Effect Size	0.14 °C	0.1 °C
95% Confidence Interval	-0.16 - -0.11	-0.13 – 0.37
P-value	2.76e-11	0.49
Standard Deviation Pre-Harvest Control Section	0.46	0.53
Standard Deviation Post Harvest Control Section	0.91	0.59
Standard Deviation Pre-Harvest Harvest Section	0.5	0.48
Standard Deviation Post Harvest Harvest Section	0.5	0.57

Benthic Press BACIPS Analysis

Table B.3: BACIPS outputs for benthic light levels (Lumen/m²) at Deer and Falsehead after sequential press harvest events. Significant p-values (>0.05) are highlighted in yellow.

	Deer	Falsehead
Winning Model AICc Weight	94.66 (Linear)	71.85 (Sigmoid)
Next Best Model AICc Weight	5.32 (Step)	15.95 (Linear)
Best Model Estimated Effect Size	15.45 Lumens/m ²	157.94 Lumens/m ²
95% Confidence Interval	-23.18 - -7.72	-208.68 - -107.19
P-value	4.45e-4	1.9e-06
Standard Deviation Pre-Harvest Control Section	73.85	16.97
Standard Deviation Post Harvest Control Section	33.06	132.62
Standard Deviation Pre-Harvest Harvest Section	242.83	21.2
Standard Deviation Post Harvest Harvest Section	500.03	76.21

Table B.4: BACIPS outputs for benthic temperatures (°C) at Deer and Falsehead after sequential press harvest events. Significant p-values (>0.05) are highlighted in yellow.

	Deer	Falsehead
Winning Model AICc Weight	96.93 (Sigmoid)	84.61 (Linear)
Next Best Model AICc Weight	1.72 (Step)	15.39 (Sigmoid)
Best Model Estimated Effect Size	0.34°C	0.15°C
95% Confidence Interval	-0.51 - -0.17	-0.17 - -0.13
P-value	3.09e-4	8.52e-16
Standard Deviation Pre-Harvest Control Section	0.33	0.53
Standard Deviation Post Harvest Control Section	0.31	0.81
Standard Deviation Pre-Harvest Harvest Section	0.43	0.53
Standard Deviation Post Harvest Harvest Section	0.39	0.69

Appendix C.

Subsurface BACIPS Analysis

Subsurface Pulse BACIPS Analysis

Table C.1: BACIPS outputs for subsurface light levels (Lumen/m²) at Singletree and Falsehead after a single pulse harvest event. Significant p-values (>0.05) are highlighted in yellow.

	Singletree	Falsehead
Winning Model AICc Weight	71.05 (Linear)	56.14 (Asymptotic)
Next Best Model AICc Weight	23.35 (Step)	23.12 (Step)
Best Model Estimated Effect Size	-47.83 Lumens/m ²	-22.34 Lumens/m ²
95% Confidence Interval	-84.56 - -11.09	-188.83 – 144.14
P-value	0.0127	0.80
Standard Deviation Pre-Harvest Control Section	129.87	92.03
Standard Deviation Post Harvest Control Section	238.77	798.05
Standard Deviation Pre-Harvest Harvest Section	245.42	262.09
Standard Deviation Post Harvest Harvest Section	469.39	158.30

Table C.2: BACIPS outputs for subsurface temperatures (°C) at Singletree and Falsehead after a single pulse harvest event. Significant p-values (>0.05) are highlighted in yellow.

	Singletree	Falsehead
Winning Model AICc Weight	80.74 (Sigmoid)	49.33 (Step)
Next Best Model AICc Weight	18.56 (Linear)	48.10 (Linear)
Best Model Estimated Effect Size	-0.56 °C	-0.43 °C
95% Confidence Interval	-0.76 - -0.35	-0.65 - -0.21
P-value	1.84e-05	0.80
Standard Deviation Pre-Harvest Control Section	0.53	0.45
Standard Deviation Post Harvest Control Section	0.94	0.94
Standard Deviation Pre-Harvest Harvest Section	0.63	0.56
Standard Deviation Post Harvest Harvest Section	0.70	0.79

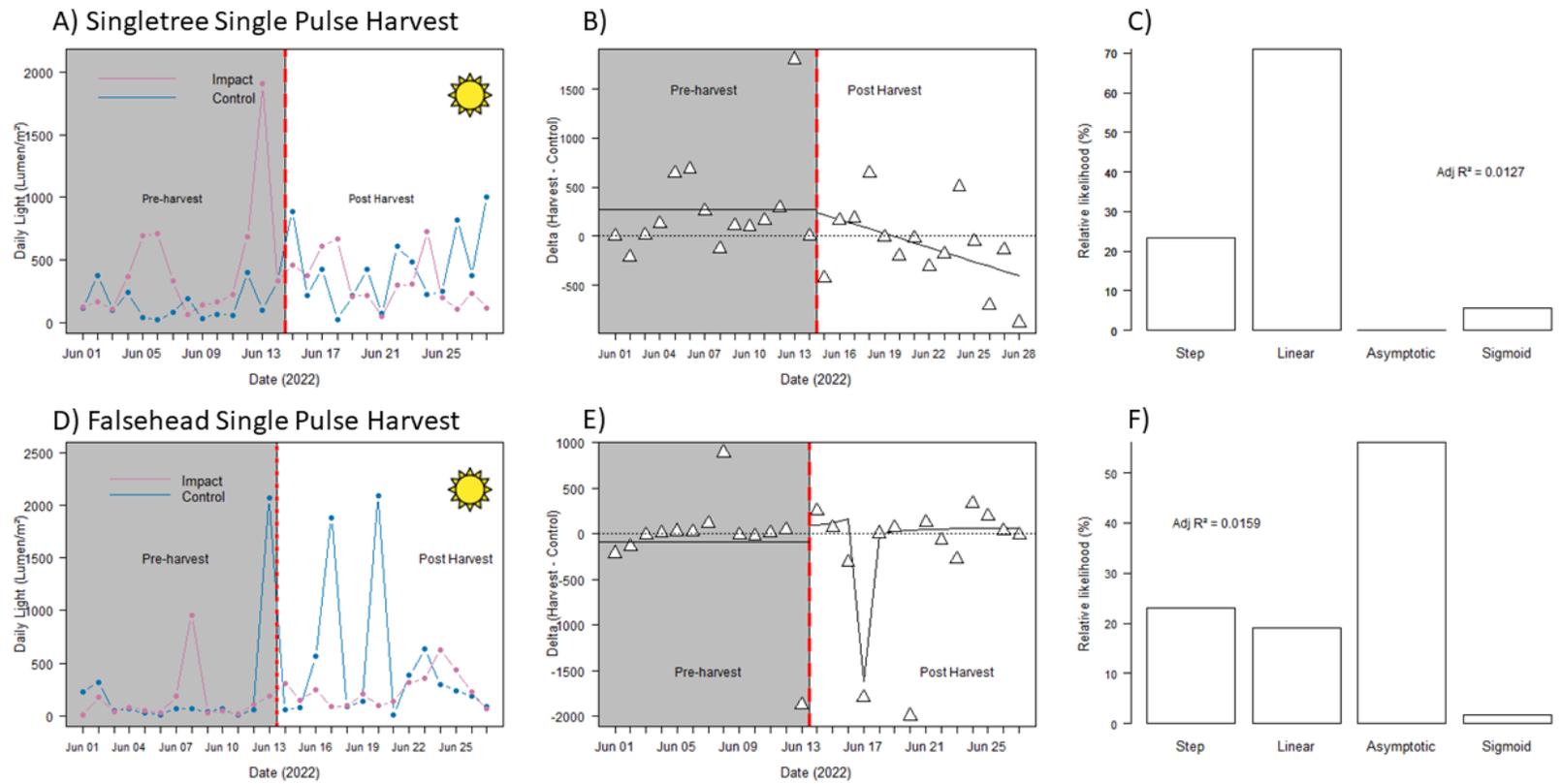


Figure C.1: Effects of a single pulse harvest event on subsurface kelp forest light intensity (Lumen/m²) at A,B,C) Singletree and D,E,F) Falsehead in control (blue) and impacted (pink) sections of the forest, pre and post harvest.

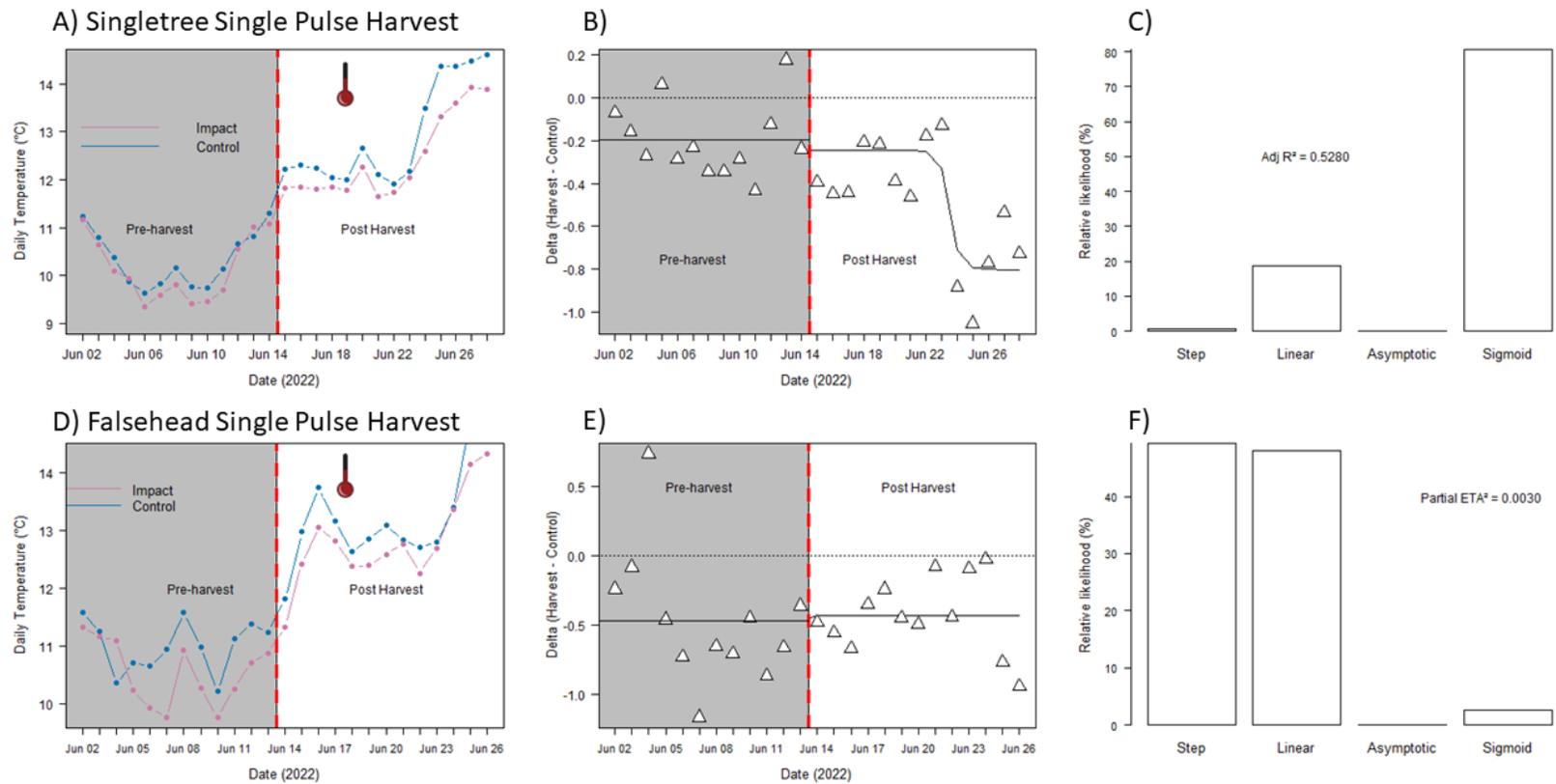


Figure C.2: Effects of a single pulse harvest event on subsurface kelp forest sea water temperature (°C) at A,B,C) Singletree and D,E,F) Falsehead in control (blue) and impacted (pink) sections of the forest, pre and post harvest.

Subsurface Press BACIPS Analysis

Table C.3: BACIPS outputs for subsurface light levels (Lumen/m²) at Deer and Falsehead after sequential press harvest events. Significant p-values (>0.05) are highlighted in yellow.

	Deer	Falsehead
Winning Model AICc Weight	88.71 (Linear)	82.02 (Linear)
Next Best Model AICc Weight	7.96 (Step)	15.77 (Step)
Best Model Estimated Effect Size	-39.01 Lumen/m ²	-59.97 Lumen/m ²
95% Confidence Interval	-74.18 - -3.85	-90.4 - -29.81
P-value	0.030	0.0004
Standard Deviation Pre-Harvest Control Section	157.47	154.83
Standard Deviation Post Harvest Control Section	1053.67	249.74
Standard Deviation Pre-Harvest Harvest Section	284.60	201.35
Standard Deviation Post Harvest Harvest Section	1064.13	137.19

Table C.4: BACIPS outputs for subsurface temperatures (°C) at Deer and Falsehead after sequential press harvest events. Significant p-values (>0.05) are highlighted in yellow.

	Deer	Falsehead
Winning Model AICc Weight	85.04 (Step)	59.77 (Linear)
Next Best Model AICc Weight	8.51 (Sigmoid)	30.38 (Step)
Best Model Estimated Effect Size	0.64 °C	0.024 °C
95% Confidence Interval	-0.093 – 2.21	-0.065 – 0.016
P-value	0.0067	0.24
Standard Deviation Pre-Harvest Control Section	0.58	0.83
Standard Deviation Post Harvest Control Section	0.60	0.88
Standard Deviation Pre-Harvest Harvest Section	0.70	0.78
Standard Deviation Post Harvest Harvest Section	0.47	0.96

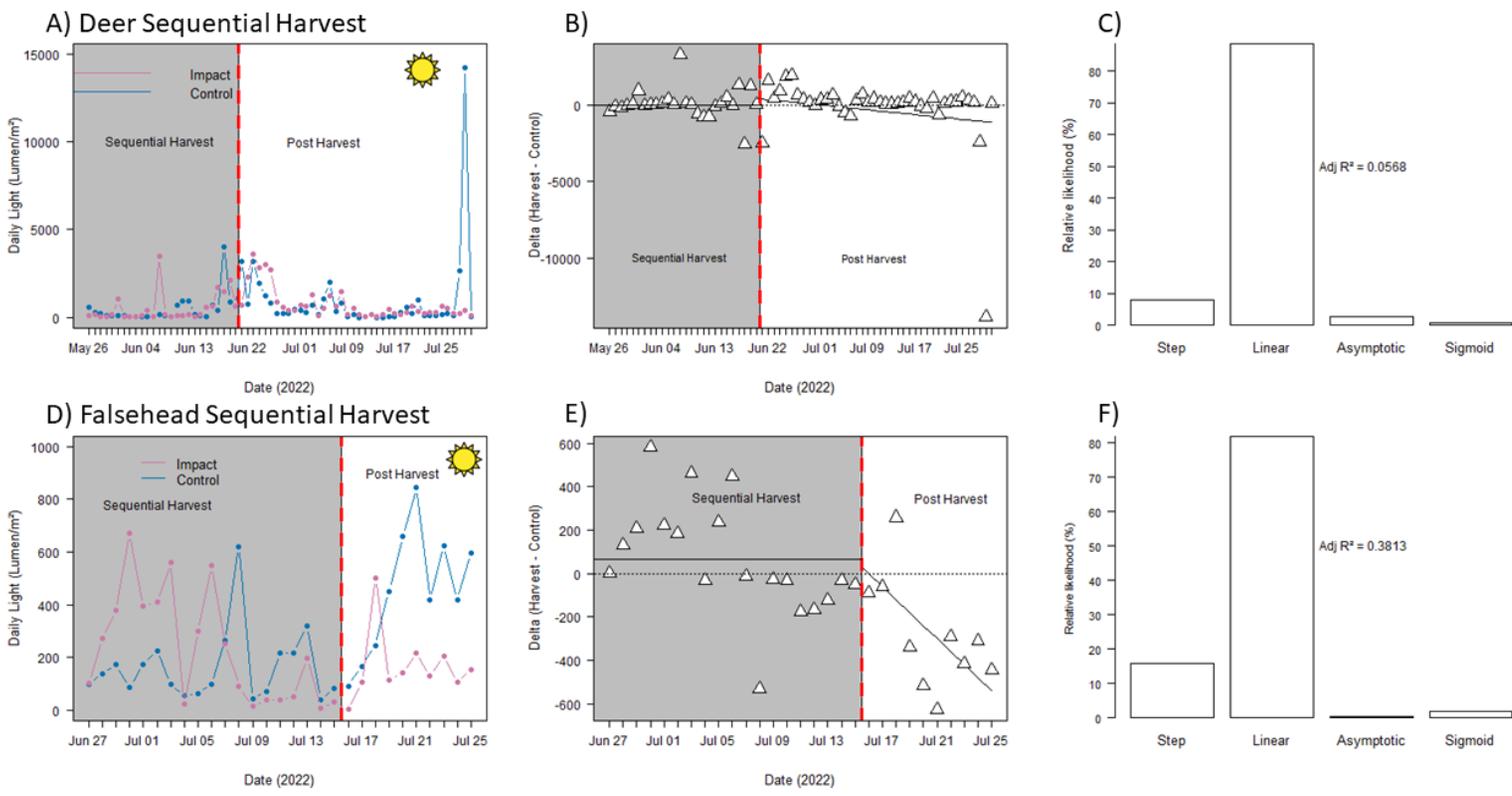


Figure C.3: Effects of sequential press harvest on subsurface kelp forest light intensity (Lumen/m²) at A,B,C) Deer Island and D,E,F) Falsehead in control (blue) and harvested (pink) sections of the forest, during and post harvest.

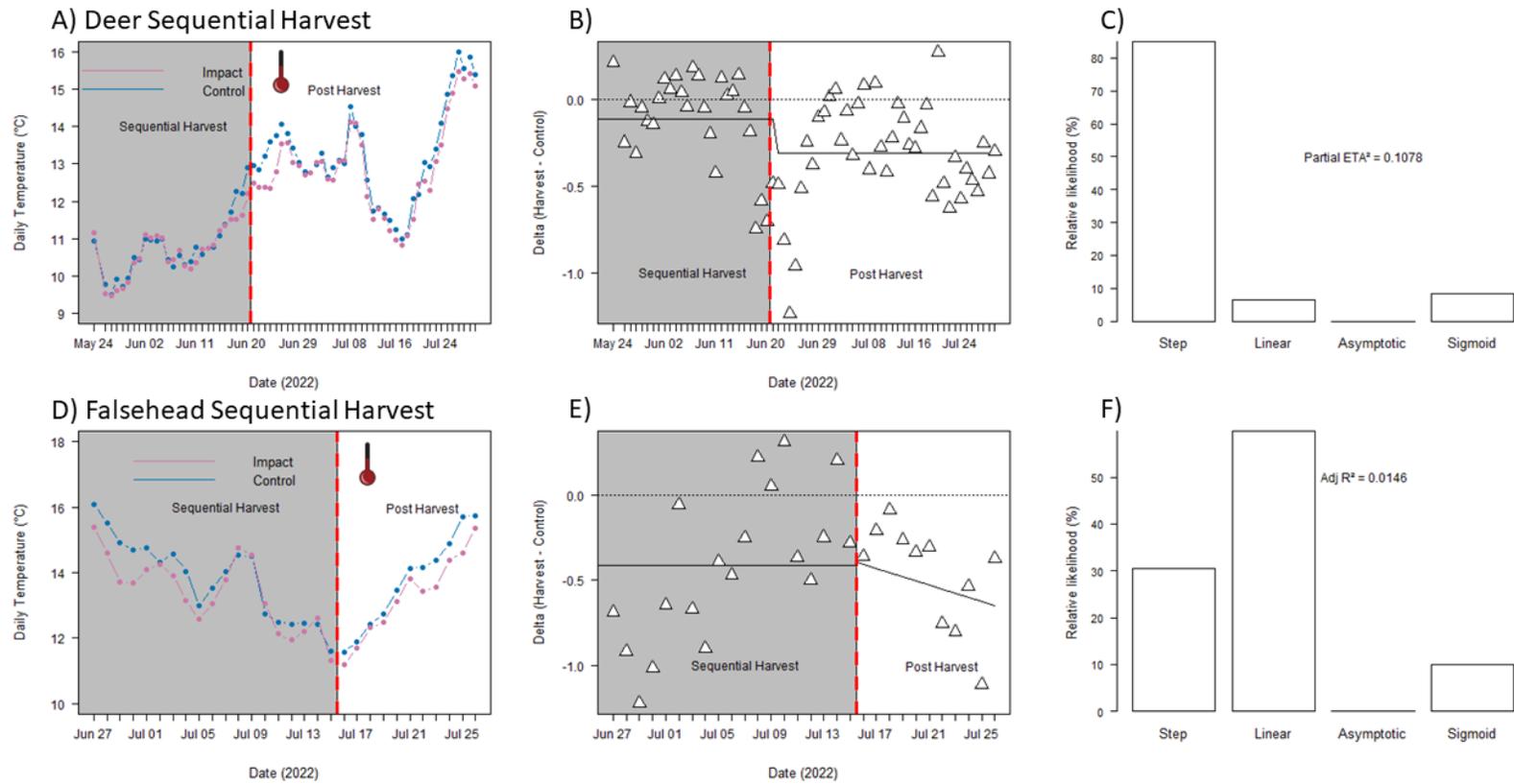


Figure C.4: Effects of sequential press harvest on subsurface kelp forest sea water temperature (°C) at A,B,C) Deer Island and D,E,F) Falsehead in control (blue) and harvested (pink) sections of the forest, during and post harvest.

Appendix D.

Water Flow

Pulse Harvest Water Flow

Table D.1: T-test for dissolution rate (g/hr) at Falsehead after a single pulse harvest in June. Significant p-values (>0.05) are highlighted in yellow which were then investigated using a Tukey HSD, significant (>0.05) Tukey HSD adjusted p-values were reported.

	Df	SS	MS	F	P-value	Tukey HSD adjusted p-value
Treatment	1	0.0025	0.0025	0.977	0.388	

Table D.2: T-test for dissolution rate (g/hr) at Singletree after a single pulse harvest in June. Significant p-values (>0.05) are highlighted in yellow which were then investigated using a Tukey HSD, significant (>0.05) Tukey HSD adjusted p-values were reported.

	Df	SS	MS	F	P-value	Tukey HSD adjusted p-value
Treatment	1	0.0051	0.0051	3.23	0.137	

Press Harvest Water Flow

Table D.3: T-test for dissolution rate (g/hr) at Falsehead in July after 6 days of sequential press harvests. Significant p-values (>0.05) are highlighted in yellow which were then investigated using a Tukey HSD, significant (>0.05) Tukey HSD adjusted p-values were reported.

	Df	SS	MS	F	P-value	Tukey HSD adjusted p-value
Treatment	1	0.00001	0.00001	0.007	0.936	

Table D.4: T-test for dissolution rate (g/hr) at Deer after 8 days of sequential press harvest in June. Significant p-values (>0.05) are highlighted in yellow which were then investigated using a Tukey HSD, significant (>0.05) Tukey HSD adjusted p-values were reported.

	Df	SS	MS	F	P-value	Tukey HSD adjusted p-value	Direction of Difference
Treatment	1	0.0399	0.0399	84.84	9.24e-05	9.23e-05	Harvest > Control

Table D.5: Repeat measures ANOVA for dissolution rate (g/hr) at Deer through the harvest season. Significant p-values (>0.05) are highlighted in yellow which were then investigated using a Tukey HSD, significant (>0.05) Tukey HSD adjusted p-values were reported. Significant Tukey results for Treatment:Date at the same sample period were reported.

	Df	SS	MS	F	P-value	Tukey HSD adjusted p-value	Direction of Difference
Treatment	1	0.0373	0.0373	36.56	4.37e-06	4.4e-06	Harvest > Control
Date	3	0.1343	0.0448	43.83	1.89e-09	June 15- May 26 1.0e-08 July 7- May 26 0.00 July 28- May 26 6.74e-07 July 28- July 7 0.0011	June 15 < May 26 July 7 < May 26 July 28 < May 26 July 28 > July 7
Treatment:Date	3	0.028	0.0093	9.14	0.0004	Harvest June 15- Control 6.35e-6 Harvest July 28- Control 0.028	Harvest > Control Harvest > Control

Appendix E.

Surface Surveys

Density of Surface Fronds

Table E1: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for surface frond density (#/m²) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	June 14	0.9977	
	July 11	0.9356	
	July 31	0.9999	
Singletree	June 16	0.7315	
	July 7	0.9997	
	July 29	0.9973	
Deer	June 13	7.35e-5	Control > Harvest
	July 10	0.8336	
	July 30	9.1e-5	Control > Harvest

Bryozoan Coverage

Table E2: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for surface bryozoan coverage (%/m²) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	June 14	0.2236	
	July 11	0.0059	Harvest > Control
	July 31	2.0e-5	Harvest > Control
Singletree	June 16	0.9238	
	July 7	0.00	Harvest < Control
	July 29	0.9966	
Deer	June 13	0.9999	
	July 10	0.0198	Harvest > Control
	July 30	0.4056	

Appendix F.

Scuba Surveys

All Fronds from Tagged Kelps

Table F.1: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for all underwater frond counts (#) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	July 9	0.9999	
	July 31	0.9397	
Singletree	July 9	0.9924	
	July 29	0.9917	
Deer	July 10	0.6383	
	July 30	0.6262	

Alive Fronds from Tagged Kelps

Table F.2: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for all alive underwater frond counts (#) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	July 9	0.9703	
	July 31	0.9786	
Singletree	July 9	0.9999	
	July 29	0.9999	
Deer	July 10	0.4822	
	July 30	0.1844	

New Fronds from Tagged Kelps

Table F.3: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for all new underwater frond counts (#) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	July 9	0.7882	
	July 31	0.9264	
Singletree	July 9	0.2225	
	July 29	0.4269	
Deer	July 10	0.9999	
	July 30	0.6905	

Dead Fronds from Tagged Kelps

Table F.4: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for all dead underwater frond counts (#) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	July 9	0.9998	
	July 31	0.0002	Harvest > Control
Singletree	July 9	0.9796	
	July 29	0.2909	
Deer	July 10	0.9989	
	July 30	0.1465	

Appendix G.

Reproductive Assessments

Sori from Tagged Kelps

Table G.1: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for all sori counts (#) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	July 9	0.3795	
	July 31	0.7008	
Singletree	July 9	0.0747	
	July 29	0.9045	
Deer	July 10	0.2192	
	July 30	1.00	

Sporophylls from Tagged Kelps

Table G.2: Harvest impacts from repeat measures ANOVA were investigated using a Tukey HSD for all sori counts (#) after harvest. Significant p-values (>0.05) are highlighted in yellow.

Site	Date	Tukey HSD adjusted p-value	Direction of Difference
Falsehead	July 9	0.6828	
	July 31	0.9945	
Singletree	July 9	0.4565	
	July 29	0.7485	
Deer	July 10	0.1243	
	July 30	0.3613	