Received Date : 12-May-2016

Revised Date : 20-Sep-2016

Accepted Date : 25-Oct-2016

Article type : Articles

Running Head: Ecosystem consequences of kelp harvest

Assessing the ecosystem-level consequences of a small-scale artisanal kelp fishery within the context of climate-change

Krumhansl K. A.[1, 2*], Bergman J. N.[3], Salomon A. K.[1, 2]

[1.] School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC Canada V5A 1S6; [2.] Hakai Institute, PO Box 309, Heriot Bay, BC Canada V0P 1H0; [3.] Florida Fish and Wildlife Research Institute, 100 8th Ave ST, St. Petersburg Florida USA 33701

Abstract

Coastal communities worldwide rely on small-scale artisanal fisheries as a means of increasing food security and alleviating poverty. Even small-scale fishing activities, however, are prone to resource depletion and environmental degradation, which can erode livelihoods in the long run. Thus, there is a

---

[*] kkrumhan@sfu.ca

pressing need to identify viable and resilient artisanal fisheries, and generate knowledge to support management within the context of a rapidly changing climate. We examined the ecosystem-level consequences of an artisanal kelp fishery (*Macrocystis pyrifera*), finding minimal impacts of small-scale harvest on kelp recovery rates, survival, and biomass dynamics, and abundances of associated commercial and culturally important fish species. These results suggest that small-scale harvest poses minimal trade-offs for the other economic benefits provided by these ecosystems, and their inherent, spiritual, and cultural value to humans. However, we detected a negative impact of warmer seawater temperatures on kelp recovery rates following harvest, indicating that the viability of harvest, even at small scales, may be threatened by future increases in global ocean temperature. This suggests that negative impacts of artisanal fisheries may be more likely to arise in the context of a warming climate, further highlighting the widespread effects of global climate change on coastal fisheries and livelihoods.

Key Words: kelp, harvest, artisanal fishery, small-scale fishery, climate change, seaweed, *Macrocystis pyrifera*

Introduction

Informing the trade-offs between ecosystem conservation, food security & poverty alleviation presents one of the greatest challenges of our time (Foley et al. 2005, Karieva and Marvier 2012, Batista et al. 2015). Moreover, conservation and management decisions must be navigated within the contemporary context of climate change (Cloern et al. 2016). Along coastlines of the world's temperate oceans, where communities are faced with depleted fisheries (Costello et al. 2016), increasing temperature anomalies (Hansen et al. 2010), and new and sometimes conflicting market opportunities (Foley et al. 2005), informing these decisions with empirical evidence has become even more pressing. The need for balancing these trade-offs is heightened in coastal indigenous communities where food insecurity is growing (Turner and Turner 2008) and economic opportunities are constrained (Mackey and Strathdee 2015).

Small-scale subsistence and artisanal fisheries (i.e. traditional fisheries involving a small amount of capital and energy) (FAO 2014) have been shown to increase food security, provide economic benefits, and support social welfare in coastal communities worldwide (Allison and Ellis 2001, Berkes et al. 2001, Salas et al. 2007, Poe et al. 2015). Unfortunately, many areas where artisanal fisheries are most common also lack sufficient resources for monitoring and management, leading to ecosystem degradation and further marginalization of impoverished communities (Allison and Ellis 2001, Salas et al. 2007). In most cases, the scientific research needed to support the development of sound management practices is lacking in part because of a spatial mismatch between where artisanal fisheries operate and where the majority of scientific research is conducted (Oliviera Junior et al. 2016). As a result, research supporting the development of sustainable and resilient artisanal fisheries is desperately needed.

For some coastal communities, commercial seaweed harvest may represent an important new economic opportunity given that seaweed species are generally easy to access and harvest, and many have a high natural capacity to recover from disturbances (Dayton et al. 1992). While harvest of seaweed has been practiced among indigenous communities for millennia (Turner 2001, Erlandson 2007), new and diverse markets for seaweed products have recently increased the demand for commercial harvest (McHugh 2003, Buschmann et al. 2014, Correa et al. 2016). Seaweeds are now used in the production of agriculture and aquaculture products (fertilizers, feed) (Chopin et al. 2001, Correa et al. 2016), food and pharmaceuticals (Vea and Ask 2011), and biofuels (Adams et al. 2011, Hafting et al. 2012). Seaweeds have, in fact, been named a new “super food”.

Kelps, seaweeds in the order Laminariales, have been targeted for harvest because they have some of the fastest growth rates of any primary producer on the planet (Mann 1973), and they generally occur at very high levels of biomass throughout coastal zones of temperate and arctic areas worldwide. Early research identified rapid recovery rates of some species of kelp following harvest (i.e. giant kelp; *Macrocystis pyrifera*) and minimal resulting impacts to long-term yield (Kimura and Foster 1984, Barilotti and Zertuche-González 1990, Vásquez 1995). This led to wide-scale harvests throughout North America starting in the 1970s. In some areas of the world, however, increases in kelp harvest rates have triggered concerns about the ability of wild stocks to sustain harvest (Vásquez 2008, Buschmann et al. 2014). Slow recovery rates and depleted kelp stocks would have broad implications for coastal ecosystems because of the role that kelp forests play as foundation species (Dayton 1972). By providing structural habitat and food resources, kelps can enhance species diversity and productivity locally and over broad spatial scales (Dayton 1985, Duggins et al. 1989, Krumhansl and Scheibling 2012).

Consequently, kelp harvest may impose trade-offs among the ecosystem services provided by kelp forests, which have been valued in the range of billions of dollars annually (Smale et al. 2013, Vásquez et al. 2014, Bennett et al. 2016). These services include the provisioning of lucrative commercial fin and shellfish fisheries, the cycling of nutrients and energy, the storage of atmospheric carbon, and the protection of shorelines from incoming swells (Reed and Brzezinski 2009, Smale et al. 2013, Vásquez et al. 2014). Much of the value of kelp forests to faunal communities is attributed to their physical structure, which provides habitat and protection from predators (Carr 1989), enhances larval retention by slowing currents (Gaylord et al. 2007, Almanez et al. 2012), and increases trophic complexity (Graham 2004). Thus, removing the physical structure of kelps during harvest may negatively impact associated commercial fin and shellfish fisheries. Moreover, kelp forests have intrinsic, social, and cultural value for coastal peoples, featuring prominently in the oral histories and traditions of indigenous communities (Turner 2001). Whether kelp harvest may trigger trade-offs among these other important ecosystem services and values remains unclear.

Giant kelp (*Macrocystis pyrifera*) is targeted for harvest throughout western coastlines of North and South America, with the most intensive harvests occurring in Northern and Central Chile (Vásquez 2008). Previous studies have determined that this species, particularly the rhizomatous form, has a unique capacity for re-growth relative to other kelps following removal of floating canopies only (Figure S1) (Borras-Chavez et al. 2012, Westermeyer et al. 2014), with minimal resulting impacts on kelp growth, survivorship, and canopy area (Barilotti et al. 1985, Barilotti and Zertuche-González 1990, Geange 2014). Some studies, however, have identified potential implications for the long-term persistence of populations through changes in reproductive dynamics (Reed 1987, Geange 2014). Previous studies of kelp harvest have mainly been designed to demonstrate the potential impacts of harvest on the kelp itself, but little attention has been directed towards generating knowledge to inform best harvest practices and assess trade-offs with other ecosystem services and values. Moreover, kelp harvest management has not largely considered the modern context of climate change, despite the fact that kelp biomass and population dynamics are tightly regulated by environmental conditions such as temperature and nutrients, which are tightly correlated (Parnell et al. 2010), and storm frequency and intensity (Reed et al. 2011, Bell et al. 2015). Warming seawater temperatures have previously been linked to declines in kelp resilience (Wernberg et al. 2010).

In this study, we asked: 1) what factors drive spatial variability in the recovery of *M. pyrifera* following small-scale harvest, and 2) what is the response of fish and understory kelp communities to varying harvest intensities (% canopy removal)? This research addresses key gaps in our understanding of how kelp forest ecosystems respond to small-scale artisanal harvest, and generates valuable information relevant to the conservation and ecosystem-based management of this important foundation species in the face of increasing global harvest pressure and changing ocean climate. Such information can directly inform management and conservation practices, and provide better projections for how climate change may impact recovery rates, harvest yields and thus kelp population dynamics.

Methods

We conducted two small-scale experimental harvests of *M. pyrifera*: 1) an individual *M. pyrifera* harvest, where five plants were harvested at each of five sites to examine the relative influences of individual (kelp size), bed (kelp density and biomass), and site-level factors (temperature and wave exposure) in driving spatial variation in recovery, and 2) a small-scale artisanal harvest experiment, where separate plots (30m x 30m) at a single site were harvested at varying intensities (0-100% canopy removal) to determine how communities associated with *M. pyrifera* would respond to different levels of harvest. The plot size used in this study mimics the size of most *M. pyrifera* beds along the Central Coast of British Columbia (Figure 1a), which occur patchily on semi-protected to protected reefs. Moreover, the spatial scale used in the study reflects the scale at which harvest is feasible locally (4000 lbs. of kelp per bed per day) given the constraints of the fishing fleet (e.g. boats < 6 m in length with 3-4 harvesters harvesting by hand).

Study sites

Individual *M. pyrifera* harvests were conducted at five sites spanning a 50 km stretch of coastline (Figure 1b, Table S1). Sites were selected where beds dominated by *M. pyrifera* occurred between 0-5m depth (mean low water, MLW). The small-scale artisanal harvest intensity experiment was conducted in a continuous bed of *M. pyrifera* spanning 600m of the eastern side of a small group of islands in the same region, ranging in depth from the intertidal to ~6m MLW (Figure 1c).

Individual M. pyrifera harvest experiment

In each location, canopies were harvested from five individual plants at low tide (0.8-1.6m) from June 2-6, 2014. Plants in 2.5-6.5m of water along the edge of *M. pyrifera* beds were selected for harvest to avoid entanglement with other plants and to aid in relocation. To harvest, a surface swimmer pulled all the fronds from a plant until they could feel that the fronds were tight to the bottom, and then used a knife to cut all fronds at the surface of the water. These fronds were retained for later measurements. Following the harvest of a frond, that frond was tagged with a colored cable tie just below the point of harvest. At the time of harvest, the number of fronds at the surface and the total surface length (length of the longest frond) of the harvested plant were measured. Within three hours of harvest, the length of each harvested frond was measured (10cm accuracy) and the frond was weighed (0.1 kg accuracy). From this, we calculated the total canopy biomass removed from each plant.

Plants were revisited at each site four weeks later. At this time point, the maximum surface length of fronds was assessed, and the number of new fronds and remaining fronds tagged during the previous interval were counted. Any new fronds at the surface were tagged with cable ties. Divers also descended on each individual to count the number of sporophylls that had reproductive sori relative to the total number of sporophylls. Plants were revisited a final time 14 weeks following harvest, at which point divers repeated the measurements described above, and collected harvested individuals. Each frond was then weighed on the surface and cut at the location on the plant where the initial harvest occurred. The re-harvested material was then weighed to calculate canopy biomass recovered.

Canopy growth (m frond^{-1} d^{-1}) was assessed after each interval using the net change in maximum surface length (0m at harvest) divided by the initial (pre-harvest) number of fronds at the surface, and the elapsed time (# of days). Surface frond production and loss were calculated by enumerating the number of new and lost fronds (assessed using fronds tagged at harvest), and dividing these quantities by the elapsed time. Canopy recovery was related to measures of ambient frond and plant density at each site, which were measured along three, 2m x 20m transects placed within the kelp bed adjacent to the harvested plants. Reproduction of non-harvested plants was assessed by counting the number of reproductive sporophylls on five plants randomly selected along the three transect lines.

Small-scale artisanal harvest intensity experiment

In the McMullins Islands, a series of eight, 30 x 30m plots were demarcated using surface floats at a minimum distance of 30m apart. In the center of each plot, one 20m belt transect made of lead line was laid perpendicular to the shore and secured using underwater epoxy and metal clips to ensure that transects remained in the same location for the duration of the study. Each plot was randomly assigned a harvest intensity of 0, 15, 30, 45, 60, 70, 90, or 100% canopy removal, and harvested at this rate throughout the 30m x 30m area once in early June 2015. Harvesting was done by hand at low tide (0.5-1.5m) from a small boat, as above. Material was retained from the 100% harvest plot and measured as the number of full ~3.5m^3 containers (10 containers total, with 300-400lbs of kelp each). This quantity was then used to determine how much canopy material was to be taken from the other experimental plots (e.g. 30% = 3 full containers). This assumes relatively constant surface biomass across plots, so harvest intensities were also visually verified from the surface, and confirmed 24 hours post-harvest by divers who counted the number of cut fronds relative to total fronds reaching the surface along the central transect line. The proportion of fronds cut along each transect line was a good approximation of harvest intensity in each plot ($p<0.01$, $R^2=0.76$), so the assigned harvest treatment value (0-100% canopy removal) was used for later analysis.

Fish surveys

Underwater visual transects (4m x 20m) were completed along the central transect line in each harvest plot prior, 24 hours, three weeks, and 10 weeks post-harvest. In each plot, fish size (total length, TL) and density were estimated in one benthic transect (4m x 20m, 0-2m above bottom), and one canopy transect (4m x 20m, 0-2m below surface). PVC measuring sticks were used to estimate fish size, and disturb the understory and surface kelp canopies to ensure that all fish within the transect zone were counted. The canopy diver remained at least three meters from the benthos, and the benthic diver remained at least five meters behind the canopy diver to reduce the possibility of disturbing fish in each zone prior to census. Fish surveys were completed prior to any other measurements in each plot.

M. pyrifera surveys

To capture short-term recovery dynamics of *M. pyrifera* following harvest, measurements of *M. pyrifera* were taken immediately prior, 24 hours, and three weeks post-harvest along the central 20m transect in each plot. The total length and number of fronds ≥1m were recorded for each individual within 1m of either side of the transect line. Five plants within each plot were tagged with numbered tags, and used for measurements of plant loss, frond production, frond loss, and reproductive potential. To measure frond production and loss, all fronds were tagged at the holdfast with a cable tie prior to harvest and enumerated. The number of tagged fronds remaining after three weeks was then subtracted from the initial number of tagged fronds and divided by the elapsed time (# of days) to generate a measure of frond loss (fronds d^{-1}). The number of new, untagged fronds present after three weeks was used to calculate frond production (fronds d^{-1}). The persistence of tagged kelps throughout the duration of the study was also used to assess survivorship in harvest plots. Reproductive potential in each harvest plot was measured by counting the percentage of sporophylls with reproductive sori.

M. pyrifera biomass was calculated at each interval following methods described in detail in Rassweiler et al. 2008. Briefly, standing biomass (kelp biomass minus the holdfast) was calculated from an estimate of the total length of each plant. This length estimate was generated by summing length estimates across the subsurface section of the plant (consisting of the portion of the plant that does not reach the surface), the water column section of the plant (consisting of the sub-surface portion of the surface-reaching fronds), and the canopy section of the plant (consisting of the portion of the fronds at the sea surface). Total length estimates for these three portions of each plant were calculated using measures of the number of fronds ≥ 1m, the number of fronds that reach the surface of the water, the surface length of the canopy, and the depth of the water using equations in Rassweiler et al. (2008). The summed length measure was converted to biomass using a length to weight relationship ($R^2>0.80$), established by measuring the length and weight of fronds from plants harvested from all sites in June, August, and September 2014 (n=75 total). Growth was calculated using the linear rate of change in biomass between the pre-harvest and three week post-harvest intervals, accounting for biomass due to frond loss.

Understory kelp surveys

Understory kelp density, biomass, and size distribution were measured in each plot prior, three weeks, and 10 weeks post-harvest. Divers enumerated and measured the total length of each understory kelp (*Pterygophora californica, Saccharina groenlandica, Saccharina latissima, Laminaria setchelii, Agarum fimbratum, Costaria costata,* and *Cymathere triplicata*) in eight, $1m^2$ quadrats randomly placed within ~5m of either side of the central transect line. At the conclusion of the experiment, divers harvested 15-30 individuals of each understory species, and brought them to the surface to measure their total length and weight. These measurements were used to generate an estimate of the length to weight relationships for each kelp species (linear regressions, $R^2 > 0.85$) and estimate biomass from underwater length data.

Abiotic conditions

For both experiments, temperature and light level data were collected using one HOBO Pendant temperature logger mounted to the bottom within the harvested area in each plot at each site. Temperature conditions were summarized as the mean, maximum, and standard deviation. Wave exposure at each site was assessed using a relative wave exposure index (details in Krumhansl and Scheibling 2011), which calculates exposure in each compass direction in increments of 22.5°, by multiplying fetch, average wind speed (km hr^{-1}), and wind frequency from that direction. Values are then summed across compass directions to generate a single estimate of wave exposure at each site. Wind data are from Environment Canada’s National Climate Data and Information Archive (http://climate.weather.gc.ca). Light data were averaged across each plot in the harvest intensity experiment. All temperature measures and the index of wave exposure were used for analyses in the individual harvest experiment, while average temperature and light levels were related to observed patterns in the harvest intensity experiment.

Statistical Analysis

We used a model selection approach to assess the strength of evidence for the effect of each predictor variable on metrics of *M. pyrifera* recovery and community response following harvest in both experiments (Burnham and Anderson 2002). For the individual harvest experiment, mixed effects models with site as a random factor were used to assess the relative influence of individual (initial size), bed (population characteristics), and site level variables (temperature, wave exposure) on individual kelp recovery rates (canopy growth, frond production, frond loss, and total biomass recovered). For the small-scale artisanal harvest experiment, generalized linear models with specified likelihoods or linear models with Gaussian likelihoods were used to test the effects of harvest intensity (treatment; % canopy removed) and initial conditions (plant or frond density, biomass) on the density of *M. pyrifera* fronds and plants, biomass, growth, reproduction, and the density of juveniles (< 2m) at three weeks post-harvest. The effects of harvest intensity (treatment; % canopy removed) and time interval post-harvest (24 hours, three and 10 weeks post-harvest) on total abundance, and the abundances of canopy, benthic, and rockfish species was assessed using generalized linear models, while linear models were used to assess the effects of the same predictor variables on the total abundance (density and biomass) of understory kelp species, and the abundances of *Saccharina sp.* and *P. californica* separately. Linear models were also used to assess the effects of harvest treatment and initial density of *M. pyrifera* (plants and fronds) on light levels in harvest plots during the first three weeks post-harvest.

For all response variables, we chose models a priori containing 2 or fewer predictor variables based on prior knowledge from the literature and our understanding of the natural history of each species (Burnham and Anderson 2002). Models were limited to ≤2 parameters because AICc performs poorly as a model selection tool if the number of parameters is high relative to the sample size (Burnhan and Anderson 2002). Models were compared using delAICc values and cumulative model weights (Burnham and Anderson 2002). Summing Akaike weights across all models containing each parameter generated Relative Variable Importance (RVI) estimates. Prior to analysis, residuals were inspected to confirm that data meet the assumption of homogeneity of variances, and data were transformed where necessary to meet this assumption. Collinearity between predictor variables was assessed using Variance Inflation Factors (VIF<10), but was not found to be an issue in any of the models considered. Where generalized linear models were used, chi-squared tests were used to determine the appropriate likelihood. Mixed effects models were fit with the nlme package in R. Generalized linear models with a negative binomial error distribution were modeled using the MASS package in R, and models with a Poisson distribution were run using the stats package in R. Model selection and model averaging were done using the AICcmodavg (linear models, and GLMs with poisson distribution) and MuMin (GLMs with negative binomial error distribution) packages in R.

Results

Temperature and light conditions

During the 2014 individual *M. pyrifera* harvest experiment, average daily temperatures ranged from 8.3-16.6°C across sites, with site level averages ranging from 11.9-12.7°C (Figure S2a, b). In 2015, average temperatures during the first three weeks of the small-scale artisanal harvest intensity experiment at the one experimental site (11.5-11.9°C) were warmer than those observed during the same period across the 5 experimental sites in 2014 (10.4-11.2 °C) (Figure S2c). Light conditions varied widely across harvest intensity plots (Figure S2d), with initial frond and plant density explaining the most variation (Table S2, Figure S2e, f). Light levels did not appear to vary with harvest treatment (Table S2, Figure S2g).

Individual kelp harvest experiment

In 2014, the recovery of individually harvested *M. pyrifera* canopies occurred at a rate of 4-30 cm d^{-1} across sites, resulting in the recovery of 35-150% of the initial, pre-harvest canopy biomass at four weeks post-harvest. When calculated for the entire 14-week experimental period, canopy growth rates were somewhat lower (7-10 cm d^{-1}), suggesting a reduction in canopy growth rate as the season progressed. This resulted in an overall recovery of canopy biomass that ranged from 6-139% of initial spring biomass across harvest sites after 14 weeks. Canopy growth rate was most strongly influenced by a negative relationship with average seawater temperature (RVI=0.9, Table S3, Figures 2a, 3a). The total amount of canopy biomass recovered (kg) and the production of fronds also declined with increasing average seawater temperature, but temperature was relatively less important than metrics of initial plant size (initial surface length: RVI=0.84, initial surface fronds: RVI=0.97, respectively) (Table S3, Figures 2b,c, 3b, c). Frond loss increased somewhat with average seawater temperature, but this response variable was also most strongly influenced by the initial size of the harvested plant (initial surface fronds: RVI=1) (Table S3, Figures 2d, 3d). Reproduction (% reproductive sporophylls) was not significantly different between harvested and unharvested plants at all sites (Table S4, Figure S3a).

Small-scale artisanal harvest intensity experiment

M. pyrifera

At three weeks following harvest, *M. pyrifera* canopy biomass had recovered to within 87-137% of the pre-harvest biomass in all plots. The highest levels of recovery were at intermediate harvest intensities, where biomass exceeded or equaled initial biomass (100-137% recovery at 30-70% canopy removal). Recovered biomass at the highest harvest intensities (90-100% canopy removal) was lower than the initial, pre-harvest biomass (87-89% recovery), while recovered biomass at the lowest harvest intensities (0-15%) was roughly equal to initial biomass (96-103% recovery).

Variation in growth over the three-week period was mainly determined by initial biomass in the plots pre-harvest (Figure 4a), although the intercept model performed best out of those considered, indicating only a weak effect of initial biomass, and no effect of harvest treatment (Table 1, Figure 4e). The density (fronds and individuals) and total standing biomass of *M. pyrifera* at three weeks post-harvest were also most strongly related to characteristics of the *M. pyrifera* population prior to harvest (initial biomass, initial frond density, and initial plant density) (Table 1, Figure 4b, c, d). Changes in biomass and frond density (from pre-harvest to three weeks post-harvest) were not strongly influenced by harvest treatment (Figure 4f, g), but treatment had a negative effect on individual plant density (Table 1, Figure 4h). In particular, juvenile densities (<2m TL) decreased with harvest intensity, with net losses of juveniles at some higher levels of harvest (60, 100%), and increases at lower harvest rates (0-30%) (Table 1, Figure S4). Survivorship (0% plant loss across plots) and reproduction (Table S4, Figure S3b) were also not impacted by harvest intensity.

Understory Kelp Species

The main understory species observed in plots included *Agarum fimbratum*, *Costaria costata*, *Cymathere triplicata*, *Laminaria setchellii*, *P. californica*, *Saccharina groenlandica*, and *Saccharina latissima*, with the latter three species being the most abundant (Figure S5). There was moderately strong evidence that the model containing harvest treatment and time interval post-harvest was the best model out of those considered for predicting biomass of *Saccharina* spp. (*S. latissima*, *S. groenlandica*), with slight declines in biomass at higher harvest intensities three and 10 weeks post-harvest (Figure 5, Table 2). There was also some weak evidence that density of *Saccharina* spp. decreased somewhat with harvest intensity (Table 2). Treatment had a slight positive effect on the density of *P. californica*, particularly at 10 weeks post-harvest, but was less important in driving variation in the biomass of *P. californica* (Figure 6, Table 2). Total understory kelp density and biomass declined somewhat throughout the experimental period, with the model containing time interval post-harvest being the most parsimonious out of those considered for both measures (Figure S5, Table 2). Harvest treatment had little overall effect on total understory density and biomass (Figure S5, Table 2).

Fish Species

The fish species observed in kelp canopies included: *Sebastes melanops*, *Clupea pallasii*, *Rimicola muscarum*, *Brachyistius frenatus*, *Embiotoca lateralis*, *Aulorhynchus flavidus*, and juvenile rockfish (likely *Sebastes melanops*, *Sebastes caurinus*, and *Sebastes maliger*) (Figure S6). In the benthos, species included *Sebastes melanops*, *Scorpaenichthys marmoratus*, *Sebastes caurinus*, *Hexagrammos decagrammus*, *Brachyistius frenatus*, *Ocylebius pictus*, *Rhacochilus vacca*, *Sebastes emphaeus*, *Embiotoca lateralis*, and juvenile rockfish (Figure S6). There was strong evidence that time interval post-harvest was the most important variable influencing fish abundance, with increases in all groups of fish species over the experimental period (Table 3). There was some weak evidence for increases in fish abundance with harvest intensity at 10 weeks post-harvest, particularly for benthic associated species (Figure 6), but this effect was small relative to the effect of time since harvest (Table 3).

Discussion

Overall, our results indicate that small-scale harvest of the world's fastest growing kelp, *M. pyrifera*, had minimal effects on the plant itself and associated fish assemblages, suggesting that *M. pyrifera* harvest at this spatial scale has the potential to support economic growth and local livelihoods without negatively impacting biodiversity or the other benefits that humans derive from these ecosystems. However, the strong relationship we detected between *M. pyrifera* recovery and temperature (Figures 2,3) indicates that the impacts of harvest may be largely context-dependent, varying according to local temperature regimes. Other studies have identified that kelp ecosystems respond to synergies between local stressors (e.g. fishing and pollution) and climate change differently than they respond to single stressors alone (Connell et al. 2008, Ling et al. 2009, Connell and Russell 2010, Filbee-Dexter et al. 2016), highlighting the important role that effective management of local stressors can play in reducing the negative impacts of climate change on kelp forest ecosystems. In the context of kelp harvest, our results suggest that harvest management plans should consider the potential for harvest to interact with regional changes in ocean temperature, which can negatively impact harvest yields, kelp recovery rates, and in turn, the benefits humans derive from kelp forest ecosystems.

Importantly, the effect of temperature on *M. pyrifera* growth rates in our study occurred over a relatively narrow range (0.8°C). Previous experimental and observational studies have identified that rising temperatures can decrease kelp survival, growth, photosynthesis, spore production, spore germination, recruitment, and harvest yield (Valdez et al. 2003, Davoult et al. 2011, Harley et al. 2012, Wernberg et al. 2013, Brown et al. 2014). However, these effects were generally observed over temperature ranges that span 2-20°C over ambient (Fain and Murray 1982, Deysher and Dean 1986, Wernberg et al. 2010, Wernberg et al. 2013, Brown et al. 2014). Response to such a small increase in temperature as that which was observed in this study may be expected where a species is near its physiological temperature tolerance limit. However, the mean temperatures observed in this study (11.9-12.7°C) are well within the thermal range known for *M. pyrifera* (8-23°C) (Schiel and Foster 2015). Kelp populations are known to be locally adapted to the conditions they typically experience, with populations displaying different responses to changes in temperature throughout a latitudinal range (Buschmann et al. 2004, Mohring et al. 2014). Our results may indicate that *M. pyrifera* in this region of British Columbia are adapted to relatively small fluctuations in temperature such that even slight shifts in mean conditions may reduce the resilience *of M. pyrifera* populations to disturbance events such as storm surge, intense grazing pulses, and harvest. It is also possible that the effect we observed is driven in part by other factors that co-vary with temperature, such as nutrient concentrations or salinity (Zimmerman and Kremer 1984, Bell et al. 2015). More broadly, our results highlight the importance of considering the potential for temperature to impact kelp growth and recovery over relative small gradients.

Interestingly, characteristics of the *M. pyrifera* population at the time of harvest (density and biomass) were more important in driving variation in *M. pyrifera* biomass, density, and growth across plots than the magnitude of harvest (Figure 4, Table 1). There were some indications that higher growth rates at intermediate harvest intensities led to greater increases in *M. pyrifera* biomass and frond density in these plots, but evidence for this was weak (Figure 4, Table 1). We did observe a decline in juvenile *M. pyrifera* (<2m TL) densities at higher harvest rates (Figure 5), however, which contrasts previous studies showing increases in *M. pyrifera* recruits following canopy removal (Kimura and Foster 1984). The declines we observed may have been caused by competitive interactions with other understory kelp species, as we saw slight increases in the biomass and density of *P. californica* at higher harvest intensities relative to other kelp species in the understory (Figure 6) (Druehl and Breen 1986, Arkema et al. 2009, Miller et al. 2011). The decline in recruitment we observed suggests harvest regimes involving the removal of entire *M. pyrifera* canopies in this region, even at the small spatial scale at which our harvest experiment was conducted, may have long-term implications for *M. pyrifera* population dynamics and harvest viability, but this warrants further study.

In contrast to findings by Reed (1987) and Geange (2014), we did not detect a negative effect of canopy harvest on the reproductive output of *M. pyrifera*. Canopies of *M. pyrifera* are responsible for 95% of organic production (Towle and Pearse 1973), and with a limited capacity to store nitrogen and photosynthates, canopy removal can cause significant declines in the overall energy available for growth and reproduction (Geange 2014). In previous studies that have demonstrated negative effects of harvest on reproductive output, floating canopies have been removed down to 1.2 m below the surface (Geange 2014), or entire fronds have been cut from the holdfast (Reed 1987, Bourraz-Chavez et al 2012). In our study, fronds were cut at the surface of the water, leaving the blade biomass that is in the top one meter of the water column. Our findings may indicate that this remaining biomass is capable of mitigating the negative effects of canopy removal on reproductive output, which is an important consideration for future population persistence and thus management. Different results in our study may also be due to the timing of harvest, which in our case occurred during the season with maximal growth and biomass (Druehl and Wheeler 1986), and thus recovery potential (Gao et al. 2014). In general, the response of *M. pyrifera* to harvest is likely to vary widely across geographic locations according to local population dynamics, individual adaptation, environmental regimes, and specific morphologies of their holdfasts (Figure S1) (Graham et al. 2007).

Seasonality in fish community composition, abundance, and species behavior has been linked to changes in the biomass of *M. pyrifera* (Bodkin 1986, Angel and Ojeda 2001, Hamilton and Konar 2007), with *M. pyrifera* removals causing detectable changes in fish communities (Bodkin 1988, Carr 1989). In our study, higher intensity harvests were associated with slight increases in fish abundance at 10 weeks post-harvest (Figure 6). Given that adult rockfish have relatively small home range sizes ($30m^2$), and have been known to actively move between areas to select suitable habitat (Matthews 1990), we expected to see short (24 hours to three weeks) and potentially longer-term (10 weeks) declines in abundance of canopy fish in areas where canopies were removed. Contrary to these expectations, we did not detect any negative impacts to canopy-dwelling species immediately or three weeks post-harvest. Juvenile rockfish appeared in kelp canopies in nearly all plots in late June (three weeks post-harvest) and then moved to benthic habitats by August (10 weeks post-harvest), as has been observed elsewhere (Carr 1991). These results suggest minimal direct effects of canopy harvest on fish communities. However, the timing of harvest may again play an important role in driving these effects, as very few fish were observed in kelp canopies prior to or immediately following harvest. Different effects may be observed had harvest occurred later in the season when more juvenile fish are occupying kelp canopies.

The increases in fish abundance we detected at 10 weeks post-harvest mainly reflect increases in benthic reef-associated species. These species occupy benthic zones because of the high structural complexity of benthic algal species and rocky substrates (Trebilco et al. 2015), which afford protection from predators and refugia for fish prey (Eibling et al. 1980, Efird and Konar 2014). Removals of *M. pyrifera* have been shown to alter understory algal community dynamics, which in turn influence the abundances of benthic invertebrate species (Arkema et al. 2009, Miller et al. 2015). Shifts in the abundance and biomass of understory kelps in our study (Figure 5) may thus have altered shelter and prey dynamics for associated fish, leading to increases in benthic fish abundances at higher harvest intensities (Figure 6). Thus, our results indicate that the indirect effects of harvest on fish communities may be stronger than the direct effects of removing canopy habitat. However, these indirect effects most likely represent a relatively small-scale shift in behavior rather than a regional population increase, especially at the small spatial scale at which these experiments were carried out.

Our findings have broad implications for coastal communities navigating the trade-offs between economic opportunities, poverty alleviation, food security and biodiversity conservation. Small-scale artisanal fisheries can bring many benefits to coastal communities, but scientific knowledge to inform management of these fisheries is often lacking, which can lead to ecosystem degradation (Olivier Junior et al. 2016). Our research supports the viability of a small-scale artisanal fishery for *M. pyrifera* by indicating that harvest may not represent a trade-off with other important ecosystem services and values provided by these kelp forests. Specifically, harvest at the scale studied did not have strong negative impacts on the plant itself or associated fish species. A broader examination of the literature highlights that the response of kelp ecosystems to harvest is largely scale and species-dependent, with larger-scale harvests being associated with regional kelp decline (Buschmann et al. 2014), and harvests of kelp species with single stipes having more dramatic ecological effects (e.g. Lorentsen et al. 2010). This suggests that high-value markets that maintain small-scale harvests may have the greatest chances of success. In particular, a small-scale seasonal kelp harvest timed for the period of maximum growth (early summer in this case) would not only result in minimal ecological impacts, but also leave opportunities for local people to diversify their livelihoods and engage in other economic activities (Salas et al. 2007).

Although we detected minimal impacts of small-scale harvest on *M. pyrifera* population dynamics and associated species, our results provide indications that warming regional climates have the potential to threaten the ability of kelp forests to sustain harvest yields, even over small spatial scales. Identifying negative impacts over such a narrow range of temperatures highlights just how extensively climate change threatens coastal fisheries (Weatherdone et al. 2016). Artisanal fisheries have the greatest potential for success in the face of rising global temperatures if they are designed to enable participants to respond dynamically to resource fluctuations related to variable regional temperatures (Allison and Ellis 2001). More broadly, our results highlight the need to consider the ways in which artisanal fisheries may interact with climate change and other human stressors to threaten the ability of coastal systems to provide ecosystem benefits vital to the health and livelihoods of coastal communities.

Acknowledgements

This research was conducted in collaboration with the Heiltsuk Integrated Management Department and the Hakai Institute. Funding was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Postdoctoral Fellowship to K. Krumhansl, an NSERC Undergraduate Student Research Award to J. Bergman and an NSERC Discovery grant and Canadian Foundation for Innovation Grant to A. K. Salomon. We thank Mike Reid, Gary Wilson, and Kelly Brown for valuable guidance on the project, and Richard Reid, Jordan Wilson, Victoria Burdett-Coutts, and Jonah Bernstein for field support. We also thank two anonymous reviewers for their thorough feedback on our manuscript.

Literature Cited

Adams, J.M.M., T.A. Troop, I.S. Donnison, and J.A. Gallagher. 2011. Seasonal variation in *Laminaria digitata* and its impact on biochemical conversion routes to biofuels. Bioresource Technology 102:9976-9984.

Allison, E. H., and F. Ellis. 2001. The livelihoods approach and management of small-scale fisheries. Marine Policy 25:377-388.

Almanza, V., A. H. Buschmann, M. C. Hernández-González, M. A. Henriquez. 2012. Can giant kelp (*Macrocystis pyrifera*) enhance invertebrate recruitment in southern Chile? Mar Biol Res 8:855-864.

Angel, A., and F. P. Ojeda. 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. Marine Ecology Progress Series 217:81-91.

Arkema, K. K., D. C. Reed, and S. C. Schroeter. 2009. Direct and indirect effects of giant kelp determine benthic community structure and dynamics. Ecology 90:3126-3137.

Barilotti, D. C., and J. A. Zertuche-González. 1990. Ecological effects of seaweed harvesting in the Gulf of California and Pacific Ocean off Baja California and California. Thirteenth International Seaweed Symposium. Springer Netherlands 204/205:35-40.

Barilotti, C. D., R. H. McPeak, and P. K. Dayton. 1985. Experimental studies on the effects of commercial kelp harvesting in central and southern California *Macrocystis pyrifera* kelp beds. California Fish and Game 71:4-20.

Batista, V. S., N. N. Fabre, A. C. C. Malhado, R. J. Ladle. 2015. Trophic artisanal coastal fisheries: challenges and future directions. Reviews in Fisheries Sciences & Aquaculture 22:1-15.

Bell, T.W., K.C. Cavanaugh, D.C. Reed, and D.A. Siegel. 2015. Geographical variability in the controls of giant kelp biomass dynamics. Journal of Biogeography 42:2010-2021.

Bennett S., T. Wernberg, S.D. Connell, A.J. Hobday, C.R. Johnson, and E.S. Poloczanska. 2016. The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. Marine and Freshwater Research 67:47-56

Berkes F., R. Mahon, P. McConnet, R. Pollnac, R. Pomeroy. 2001. Managing Small-scale Fisheries: Alternative Directions and Methods. International Development Research Centre, Ottawa, Ontario, Canada.

Bodkin, J. L. 1986. Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California. Fishery Bulletin 84:799-808.

Bodkin, J. L.1988. Effects of kelp forest removal on associated fish assemblages in central California. Journal of Experimental Marine Biology and Ecology 117:227-238.

Borraz-Chavez, R., M. Edwards, J.A. Vásquez. 2012. Testing sustainable management in Northern Chile: harvesting *Macrocystis pyrifera* (Phaeophyceae, Laminariales). A case study. Journal of Phycology 24:1655-1665.

Brown, M. B., M. S. Edwards, and K .Y. Kim. 2014. Effects of climate change on the physiology of giant kelp, *Macrocystis pyrifera*, and grazing by purple urchin, *Strongylocentrotus purpuratus*. Algae 29:203-215.

Burnham, K. L., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second Edition. Springer, New York, USA.

Buschmann, A. H., J. A. Vásquez, P. Osorio, E. Reyes, L. Filún, M. C. Hernández-González, and A. Vega. 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis spp*. (Phaeophyta) at different latitudes in Chile. Marine Biology 145:849-862.

Buschmann, A. H., S. Prescott, P. Potin, S. Faugeron, J. A. Vásquez, C. Camus, J. Infante, M. C. Hernández-González, A. Gutíerrez, and D. A. Varela. 2014. The status of kelp exploitation and marine agronomy, with emphasis on *Macrocystis pyrifera* in Chile. Advances Botanical Research 71:161-188.

Carr, M. H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 126:59-76.

Carr, M. H. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 146:113-137.

Chopin, T., A.H. Buschmann, C. Halling, M. Troell, N. Kautsky, A. Neori, G.P. Kraemer, J.A. Zertuche-Gonzalez, C. Yarish, and C. Neefus. 2001. Integrating seaweeds into aquaculture systems. Journal of Phycology 37:975–986.

Cloern, J. E., P. C. Abreu, J. Cartensen, L. Chauvaud, R. Elmgren, J. Grall, J. Greening, J. O. R. Johansson, M. Kahru, E. T. Sherwood, J. Xu, and K. Yin. 2016. Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. Global Change Biology 22:513-529.

Connell, S.D., B.D. Russell, D.J. Turner, S.A. Shepherd, T. Kildea, D. Miller, L. Airoldi, and C. Cheshire. 2008. Recovering a lost baseline: missing kelp forests from a metropolitan coast. Marine Ecology Progress Series 360:63-72.

Connell, S.D., and B.D. Russell. 2009. The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. Proceedings of the Royal Society B 277:1409-1415.

Correa, T., A. Guitierrez, R. Flores, A.H. Buschmann, P. Cornejo, C. Bucarey. 2016. Production and economic assessment of giant kelp *Macrocystis pyrifera* cultivation for abalone feed in the south of Chile. Aquaculture Research 47:698-707.

Costello, C., D. Ovando, T. Clavelle, C. K. Strauss, R. Hilborn, M. C. Melnychuk, T. A. Branch, S. D. Gaines, C. S. Szuwalski, R. B. Cabral, and D. N. Rader. 2016. Global fishery prospects under contrasting management regimes. Proceedings of the National Academy of Sciences 201520420.

Dayton PK. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. In: Proceedings of the Colloquium on Conservation Problems in Antarctica, edited by BC Parker. Lawrence, Kansas. Allen Press.

Dayton, P. K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16:215-245.

Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1991. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs 62:421-445.

Deysher, L. E., and T. A. Dean. 1986. In situ recruitment of sporophytes of the giant kelp, *Macrocystis pyrifera* (L.) CA Agardh: effects of physical factors. Journal of Experimental Marine Biology and Ecology 103:41-63.

Druehl, L. D., and P. A. Breen. 1986. Some ecological effects of harvesting *Macrocystis integrifolia*. Botanica Marina 29:97-104.

Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170-173.

Efird, T. P., and B. Konar. 2014. Habitat characteristics can influence fish assemblages in high latitude kelp forests. Environmental Biology of Fishes 97:1253-1263.

Eibling, A.W., R.J. Larson, W.S. Alevizon, and R.N. Bray. 1980. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. Fishery Bulletin 78:361-377.

Erlandson, J. M., M. H. Graham, B. H. Bourque, D. Corbett, J. A. Estes, and R. S. Steneck. 2007. The kelp highway hypothesis: Marine ecology, the coastal migration theory, and the peopling of the Americas. The Journal of Island and Coastal Archaeology 2:161-174

Fain, S. R., and S. N. Murray.1982. Effects of light and temperature on net photosynthesis and dark respiration of gametophytes and embryonic sporophytes of *Macrocystis pyrifera*. Journal of Phycology 18:92-98

Filbee-Dexter, K., C. J. Feehan, and R. E. Scheibling. 2016. Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. Marine Ecology Progress Series 543:141-152.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, and J. H. Helkowski. 2005. Global consequences of land use. Science 309:570-574.

Gao X., H. Endo, M. Yamana, K. Teniguchi, and Y. Agatsuma. 2014. Compensatory abilities depending on seasonal timing of thallus excision of the kelp *Undaria pinnatifida* cultivated in Matsushima Bay, northern Japan. Journal of Applied Phycology 25:1331-1340

Gaylord B., J. H. Rosman, D. C. Reed, J. R. Koseff, J. Fram, S. MacIntyre, K. Arkema, C. McDonald, Brzeinski M. A., J. L. Largier, S. G. Monismith, P. T. Ramondi, and B. Mardian. 2007. Spatial patterns of flow and their modification within and around a giant kelp forest. Limnology and Oceanography 52:1838-1852.

Geange, S. W. 2014. Growth and reproductive consequences of photosynthetic tissue loss in the surface canopies of *Macrocystis pyrifera* (L.) C. Agardh. Journal of Experimental Marine Biology and Ecology 453:70-75.

Hafting, J. T., A. T. Critchley, M. L. Cornish, S. A. Hubley, A.F. Archibald. 2012. On-land cultivation of functional seaweed products for human usage. Journal of Applied Phycology. 24:385-392.

Hamilton, J., and B. Konar. 2007. Implications of substrate complexity and kelp variability for south-central Alaskan nearshore fish communities. Fishery Bulletin 105:189-196.

Hansen, J., R. Ruedy, M. Sato, J. Lo. 2010. Global surface temperature change. Reviews of Geophysics 48:1-29.

Harley, C. D., K. M. Anderson, K. W. Demes, J. P. Jorve, R. L. Kordas, T. A. Coyle, and M. H. Graham. 2012. Effects of climate change on global seaweed communities. Journal of Phycology 48:1064-1078.

Kareiva, P., and M. Marvier. 2012. What is conservation science? Bioscience 62: 962-969.

Kimura, R. S., and M. S. Foster. 1984. The effects of harvesting *Macrocystis pyrifera* on the algal assemblage in a giant kelp forest. In Eleventh International Seaweed Symposium. Springer Netherlands 425-428.

Krumhansl, K. A., and R. E. Scheibling. 2012. Production and fate of kelp detritus. Marine Ecology Progress Series 467:281-302.

Krumhansl, K. A., and R. E. Scheibling. 2011. Detrital production in Nova Scotian kelp beds: patterns and processes. Marine Ecology Progress Series 421:67-82.

Ling, S. D., C. R. Johnson, S. D. Frusher, and K. R. Ridgway. 2009. Overfishing reduces the resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences of the USA 106:22341-22345

Lorentsen, S-H, K. Sjotun, D. Gremillet. 2010. Multi-trophic consequences of kelp harvest. Biological Conservation 143:2054-2062

Mackey, T. K., and S. A. Strathdee. 2015. Big events and risks to global substance using populations: unique threats and common challenges. Substance Use & Misuse 50:885-890.

Mann, K.H. 1973. Seaweeds: Their productivity and strategy for growth. Science 182:975-981.

Matthews, K. R. 1990. An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (Sebastes spp.). Environmental Biology of Fishes 29:161-178.

McHugh, D. J. 2003. A guide to the seaweed industry. Food and Agriculture Organization of the United Nations Technical Paper, Rome, Italy.

Miller, R. J., D. C. Reed, and M. A. Brzesinski. 2011. Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. Limnology and Oceanography 56:119-132.

Miller, R. J., H. M. Page, and aD. C. Reed. 2015. Trophic versus structural effects of a marine foundation species, giant kelp (*Macrocystis pyrifera*). Oecologia 179:1199-1209.

Mohring, M. B., T. Wernberg, J. T. Wright, S. D. Connell, B. D. Russell. 2014. Biogeographic variation in temperature drives performance of kelp gametophytes during warming. Marine Ecology Progress Series 513:85-96.

Olivera Junior, J. G. C., L. .P. S. Silva, A. C. M. Malhado, V. S. Batista, N. N. Fabre, R. J. Ladle. 2016. Artisanal fisheries research: a need for globalization? PLoS ONE 11:e0150689.

Parnell, P.E, E.F. Miller, C.D. Lennert-Cody, P.K. Dayton, M.L. Carter, T.D. Stebbins. 2010. The response of giant kelp (*Macrocystis pyrifera*) in southern California to low-frequency climate forcing. Limnology and Oceanography 55:2686-2702

Poe, M. R., P. S. Levin, N. Tolimieri, and K. Norman. 2015. Subsistence fishing in a 21st century capitalist society: From commodity to gift. Ecological Economics 116:241-250.

Rassweiler, A., K. K. Arkema, D. C. Reed, R. C. Zimmerman, and M. A. Brzesinski. 2008. Net primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern California. Ecology 89:2068-2081.

Reed, D. C. 1987. Factors affecting the production of sporophylls in the giant kelp *Macrocystis pyrifera* (L.) C. Ag. Journal of Experimental Marine Biology and Ecology 113:61-69.

Reed, D. C., and M. A. Brzezinski. 2009. Kelp Forests. In: Laffoley, D.d'A. and Grimsditch, G. (eds) The Management of Natural Coastal Carbon Sinks. IUCN, Gland, Switzerland:31-37.

Salas, S., R. Chuenpagdee, J. C. Seijo, and A. Charles. 2007. Challenges in the assessment and management of small-scale fisheries in Latin America and the Caribbean. Fisheries Research 87:5-16.

Shiel, D. R., and M. S. Foster. 2015. Giant Kelp Forests. University of California Press, Oakland, California, USA.

Smale, D. A., M. T. Burrows, P. Moore, N. O'Connor, and S. J. Hawkins. 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. Ecology and Evolution 3:4016-4038.

Towle, D. W., and J. S. Pearse. 1973. Production of giant kelp, *Macrocystis*, estimated by in situ incorporation of C-14 in polyethylene bags. Limnology and Oceanography 18:155-158.

Trebilco, R., N. K. Dulvey, H. Stewart, A. K. Salomon. 2015. The role of habitat complexity in shaping the size structure of a temperate reef fish community. Marine Ecology Progress Series 532:197-211.

Turner, N. J., and K. L. Turner. 2008. Where our women used to get the food: cumulative effects and loss of ethnobiotanical knowledge and practice; case study from coastal British Columbia. Botany 86:103-115.

Turner, N. J. 2001. Coastal peoples and marine plants on the northwest coast. International Association of Aquatic and Marine Science Libraries and Information Centers:69-76.

Valdez, M. C., E. S. Zaragoza, D. L. Belda, R. Marcos, and R. A. Ramírez. 2003. Effect of climatic change on the harvest of the kelp *Macrocystis pyrifera* on the Mexican Pacific coast. Bulletin of Marine Science 73:545-556.

Vásquez, J. A. 1995. Ecological effects of brown seaweed harvesting. Botanica Marina 38:251-258.

Vásquez, J. A. 2008. Production, use and fate of Chilean brown seaweeds: re-sources for a sustainable fishery. Journal of Applied Phycology 20:457-467.

Vásquez, J. A., S. Zuñiga, F. Tala, N. Piaget, D. C. Rodríguez, and J. A. Vega. 2014. Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. Journal of Applied Phycology 26:1081-1088.

Vea, J., E. Ask. 2011. Creating a sustainable commercial harvest of *Laminaria hyperborea*, in Norway. Journal of Applied Phycology 23:489-494.

Wernberg, T., D. A. Smale, F. Tuya, M. S. Thomsen, T. J. Langlois, T. de Bettignies, S. Bennett, and C. S. Rousseaux. 2013. An extreme climative event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change 3:78-82.

Wernberg, T., M. S. Thomsen, F. Tuya, G. A. Kendrick, P. A. Staehr, and B. D. Toohey. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecology Letters 13:685-694.

Weatherdon, L. V., Y. Ota, M. C. Jones, D. A. Close, W. and W. L. Cheung. 2016. Projected scenarios for coastal First Nations' fisheries catch potential under climate change: management challenges and opportunities. PLoS ONE 11:e0145285.

Zimmerman, R.C., J.N. Kremer, J.N. 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. Journal of Marine Research, 42, 591–604.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data associated with this paper have been deposited in a Dryad digital repository http://dx.doi.org/10.5061/dryad.9j346

Table 1. Model selection parameters (K, AICc, delAICc, LL, and AICc weights) for linear models predicting the effects of harvest treatment (% canopy removal) and initial conditions (frond density, plant density, biomass, and juvenile abundance [<2m TL]) on frond density, plant density, biomass, growth, and the number of juveniles in small-scale artisanal harvest plots (n=8) at three weeks post-harvest. Likelihoods are specified for each response variable.

Frond density (fronds 40 m^{-2}) *Negative binomial					
Model	K	AICc	delAICc	LL	AICc Wt
Initial frond density	3	78.0	0.00	-33.02	0.99
Initial frond density + Treatment	4	87.3	9.24	-32.97	0.01
Intercept	2	89.4	11.38	-41.51	0.00
Treatment	3	95.0	16.98	-41.51	0.00
Plant density (plants 40 m^{-2}) *Poisson					
Model	K	AICc	delAICc	LL	AICc Wt
Initial plant density	3	54.1	0.00	-23.85	0.73
Initial plant density + Treatment	4	56.2	2.07	-22.09	0.26
Intercept	2	63.4	9.34	-30.39	0.01
Treatment	3	64.3	10.16	-28.93	0.01
Biomass *Gaussian					
Model	K	AICc	delAICc	LL	AICc Wt
Initial Biomass	3	14.70	0.00	-1.35	0.98
Initial Biomass + Treatment	4	22.84	8.13	-0.75	0.02
Intercept	2	26.77	12.07	-10.18	0.00
Treatment	3	32.36	17.66	-10.18	0.00
Growth rate (kg d^{-1}) *Gaussian					

Model	K	AICc	delAICc	LL	AICc Wt
Intercept	2	22.57	0.00	-8.09	0.71
Initial Biomass	3	25.01	2.43	-6.50	0.21
Treatment	3	27.06	4.49	-7.53	0.08
Treatment + Initial Biomass	4	33.14	10.57	-5.91	0.00
Juvenile density (juveniles 40 m^{-2}) *Poisson					
Model	K	AICc	delAICc	LL	AICc Wt
Treatment	2	45.67	0.00	-19.63	0.70
Treatment + Initial no. Juveniles	3	48.54	2.88	-18.27	0.16
Treatment + Initial abundance	3	50.52	4.86	-19.26	0.06
Initial no. Juveniles	2	50.92	5.25	-22.26	0.05
Intercept	1	51.00	5.34	-24.17	0.05

Table 2. Model selection parameters (K, AICc, delAICc, LL, and AICc weights) for generalized linear models predicting the effects of harvest treatment (% canopy removal) and time interval (pre-harvest, three and 10 weeks post-harvest) on understory kelp abundance (density and biomass of all understory species, *Saccharina sp.*, and *P. californica*) in small-scale artisanal harvest plots (n=8).

Total Understory Kelp Density (plants m^{-2})					
Model	K	AICc	delAICc	LL	AICC wt
Interval	3	1088.0	0.00	-540.9	0.64
Intercept	2	1090.5	2.52	-543.2	0.18
Treatment*Interval	3	1091.5	3.57	-542.7	0.11
Treatment	3	1092.5	4.57	-543.2	0.07

Total Understory Kelp Biomass (kg m^{-2})					
Model		AICc	delAICc	LL	AICC wt
Interval	3	489.6	0.00	-241.7	0.49
Treatment	3	489.6	0.00	-241.7	0.48
Intercept	2	495.8	6.22	-245.9	0.02
Treatment*Interval	3	497.5	7.95	-245.7	0.01
Density of *Saccharina sp.* (plants m^{-2})					
Model		AICc	delAICc	LL	AICC wt
Treatment	3	677.9	0.00	-335.9	0.35
Intercept	2	678.2	0.25	-337.1	0.30
Interval	3	678.7	0.78	-336.3	0.23
Treatment*Interval	3	680.1	2.14	-334.8	0.12
Biomass of *Saccharina sp.* (kg m^{-2})					
Model		AICc	delAICc	LL	AICC wt
Treatment*Interval	3	368.4	0.00	-181.1	0.80
Treatment	3	371.5	3.08	-182.7	0.17
Intercept	2	376.3	7.91	-186.1	0.02
Interval	3	377.1	8.66	-185.4	0.01
Density of *P. californica* (plants m^{-2})					
Model		AICc	delAICc	LL	AICC wt
Treatment	3	425.4	0.00	-209.6	0.77
Interval	3	428.4	3.07	-211.1	017
Intercept	2	431.2	5.88	-213.6	0.04
Treatment*Interval	3	432.6	7.25	-213.2	0.02
Biomass of *P. californica* (kg m^{-2})					
Model		AICc	delAICc	LL	AICC wt
Interval		706.6	0.00	-350.2	0.40
Treatment		707.2	0.55	-350.5	0.30

Intercept	708.8	1.21	-351.9	0.22
Treatment*Interval	709.8	3.21	-351.8	0.08

Table 3. Model selection parameters (K, AICc, delAICc, LL, and AICc weights) for generalized linear models predicting the effects of harvest treatment (% canopy removal) and time interval (pre-harvest, three and 10 weeks post-harvest) on total, canopy, benthic, and rockfish abundance in small-scale artisanal harvest plots (n=8).

Total Fish Abundance (fish 320m^{-2})					
Model	K	AICc	delAICc	LL	AICC wt
Interval	5	242.6	0.00	-115.2	0.99
Treatment*Interval	6	251.6	8.9	-118.1	0.01
Intercept	2	257.8	15.1	-126.7	0.00
Treatment	3	260.0	17.4	-126.6	0.00
Canopy Fish Abundance (fish 320m^{-2})					
Model	K	AICc	delAICc	LL	AICC wt
Interval	5	182.7	0.0	-85.2	0.93
Treatment*Interval	6	188.8	6.1	-86.7	0.04
Intercept	2	190.3	7.7	-93.0	0.02
Treatment	3	192.7	10.1	-92.9	0.01
Benthic Fish Abundance (fish 320m^{-2})					
Model	K	AICc	delAICc	LL	AICC wt
Interval	5	193.0	0.00	-91.8	1
Treatment*Interval	6	223.0	29.97	-105.3	0
Treatment	3	410.0	216.9	-202.8	0
Interval	2	417.2	224.2	-207.5	0

Rockfish Abundance (fish 320m^{-2})

Model	K	AICc	delAICc	LL	AICC wt
Interval	5	163.9	0.00	-77.2	1
Treatment*Interval	6	193.1	29.26	-90.4	0
Intercept	2	427.2	263.3	-211.4	0
Treatment	3	435.8	271.9	-216.8	0

Figure 1. a) Overview of the British Columbia, Canada coastline with the study region highlighted. b) Frond harvest experiments were conducted at Stryker, Simmonds, Golden, Triquet, and Meay, while the harvest intensity experiment was conducted at the McMullins, c.) where the magnitude of harvest was randomly assigned among eight, 30m x 30m plots. Plots were placed in a continuous kelp bed running alongshore, the offshore extent of which is shown by a black line.

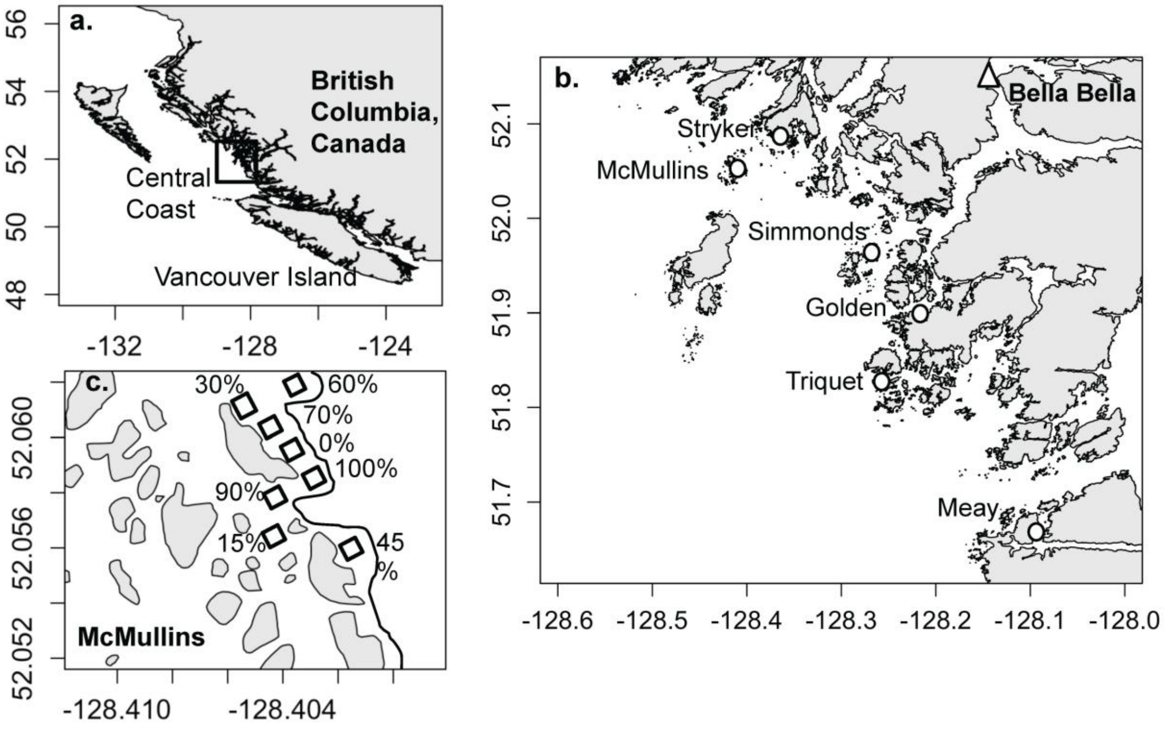
Figure 2. Parameter estimates and relative variable importance (RVI) calculated from AICc weights of linear mixed effects models of a) growth (m frond^{-1} d^{-1}), b) the amount of biomass recovered (kg), c) frond production (fronds frond^{-1} d^{-1}), and d) frond loss (fronds frond^{-1} d^{-1}) from individual *M. pyrifera* harvested at five different sites (n=23). Predictor variables considered include metrics of temperature (°C; average, maximum, standard deviation), wave exposure, initial kelp size (initial canopy length [m], initial number of surface fronds), and plant and frond density (plants m^{-2}, fronds m^{-2}).

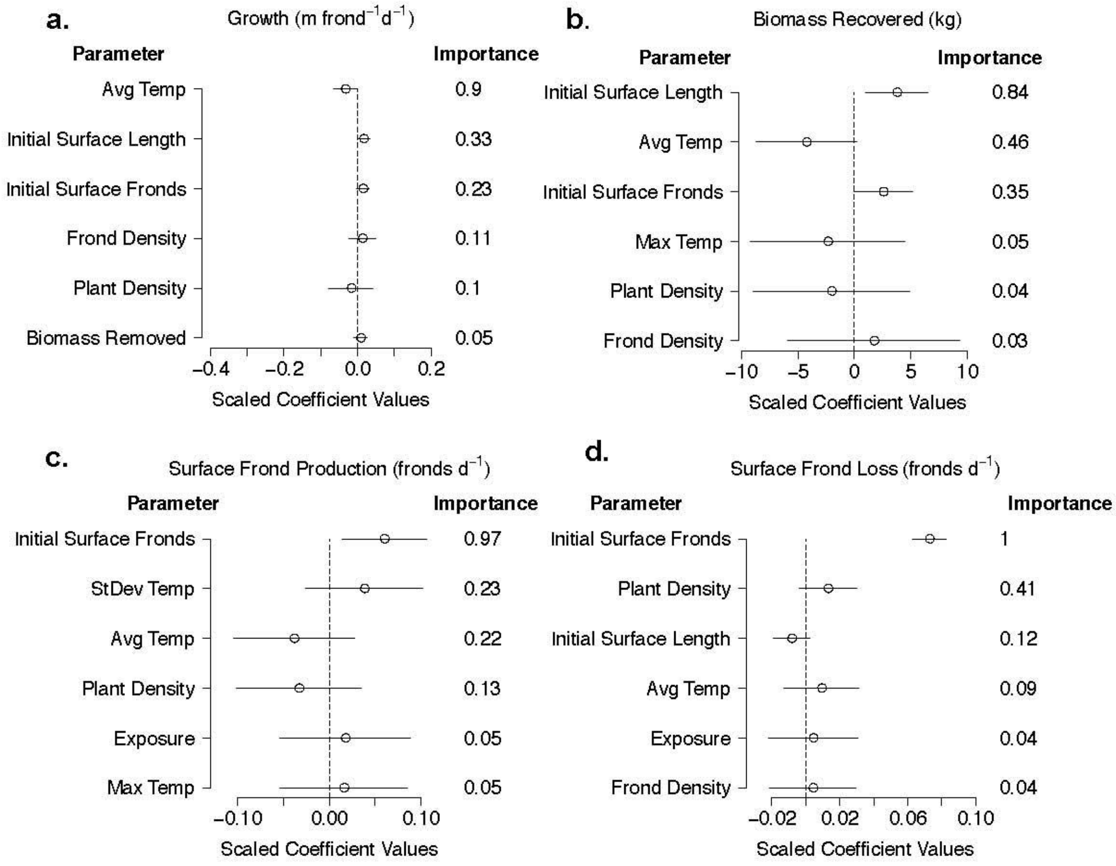
Figure 3. The relationship between average seawater temperature and a) growth, b) the amount of biomass recovered, c) frond production, and d) frond loss from individual *M. pyrifera* harvested at five different sites (n=23). Darker hues indicate overlapping data points.

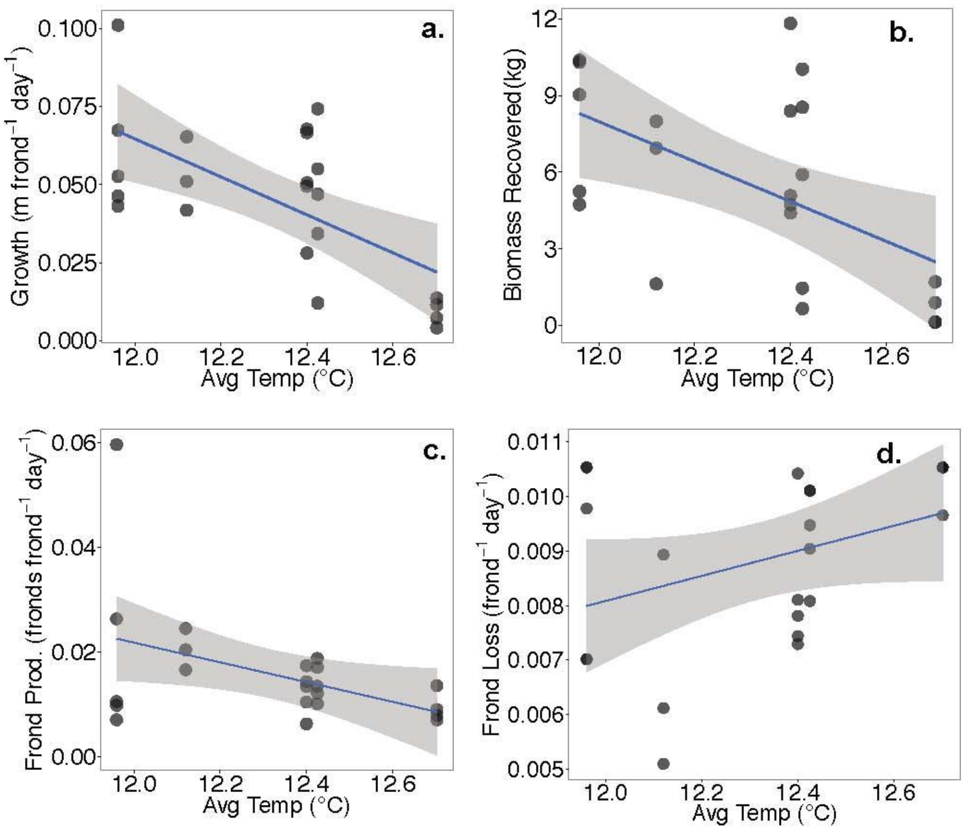
Figure 4. Plots (a-d) showing kelp parameters as a function of their most important predictor variables selected using delAICc and model weight: a) growth and b) biomass as a function of initial biomass; c) frond density as a function of initial frond density; d) plant density as a function of initial plant density. Also shown are e) growth, f) change in biomass, g) change in frond density and h) change in plant density as a function of % canopy harvest (n=8 plots, 1 transect per plot).

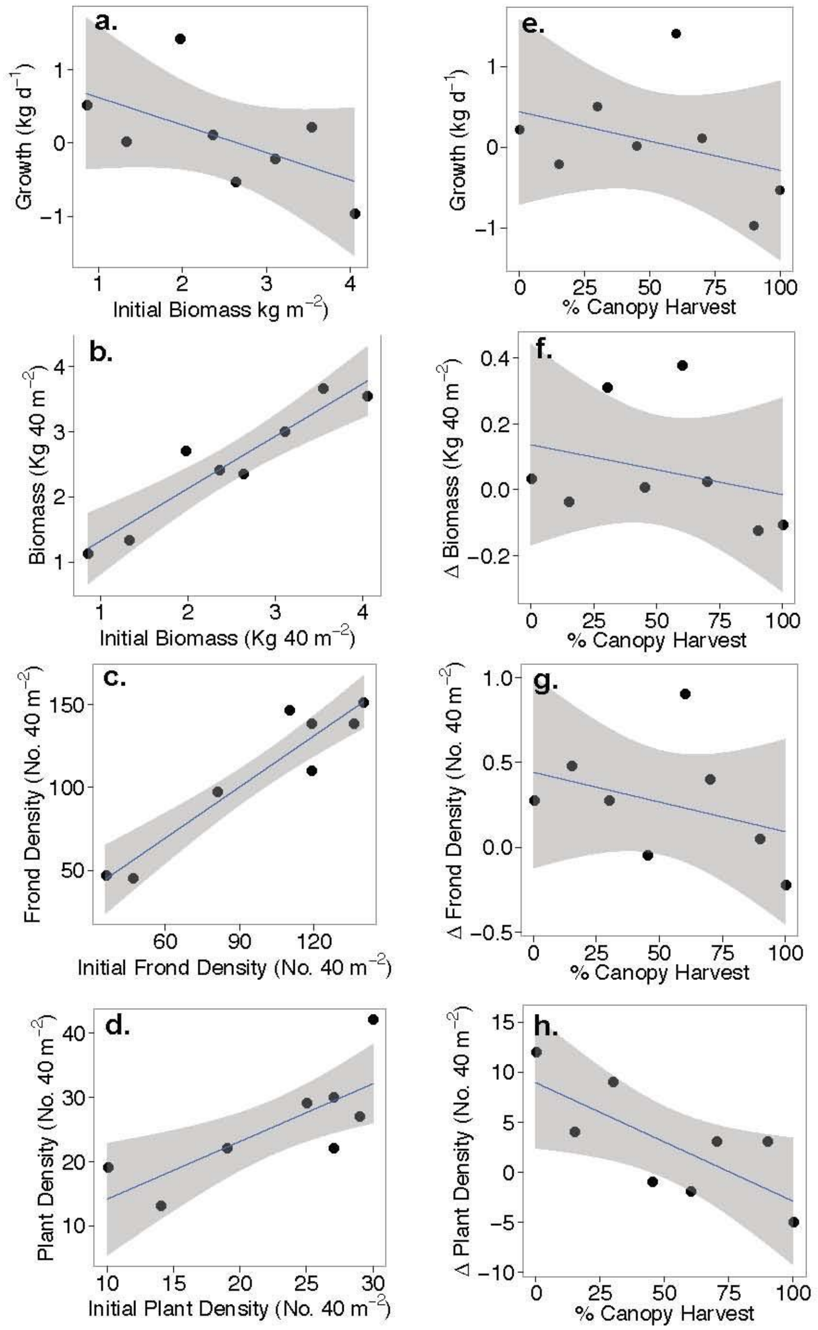
Figure 5. The biomass of *Saccharina sp.* and *P. californica* across harvest treatments (% canopy removal) in small-scale artisanal harvest plots at three time intervals. Plots are fitted with a linear model (n=8 per plot).

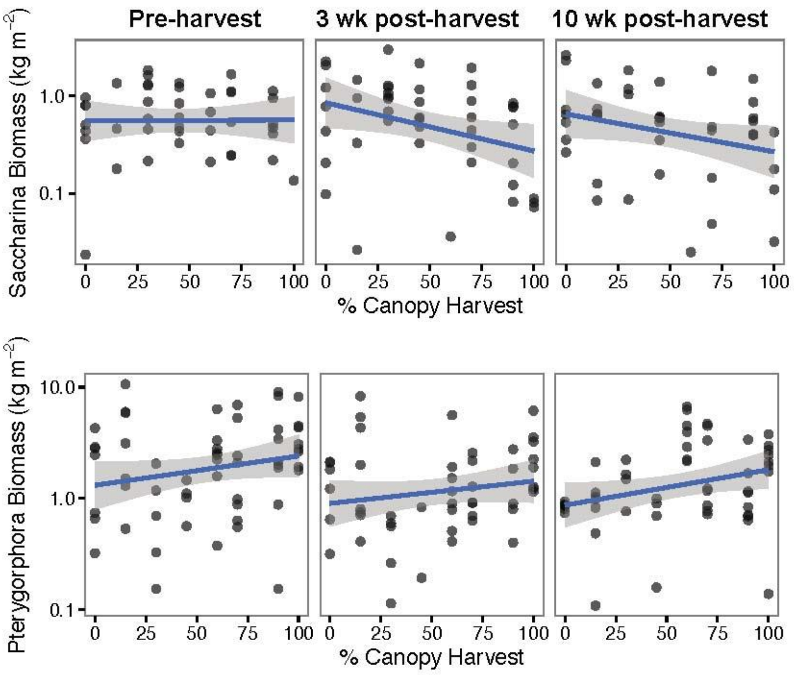
Figure 6. The relationship between % canopy harvest and the abundances of canopy and benthic reef-associated fish in harvest plots at each time interval (n=8 plots, 1 transect per plot).

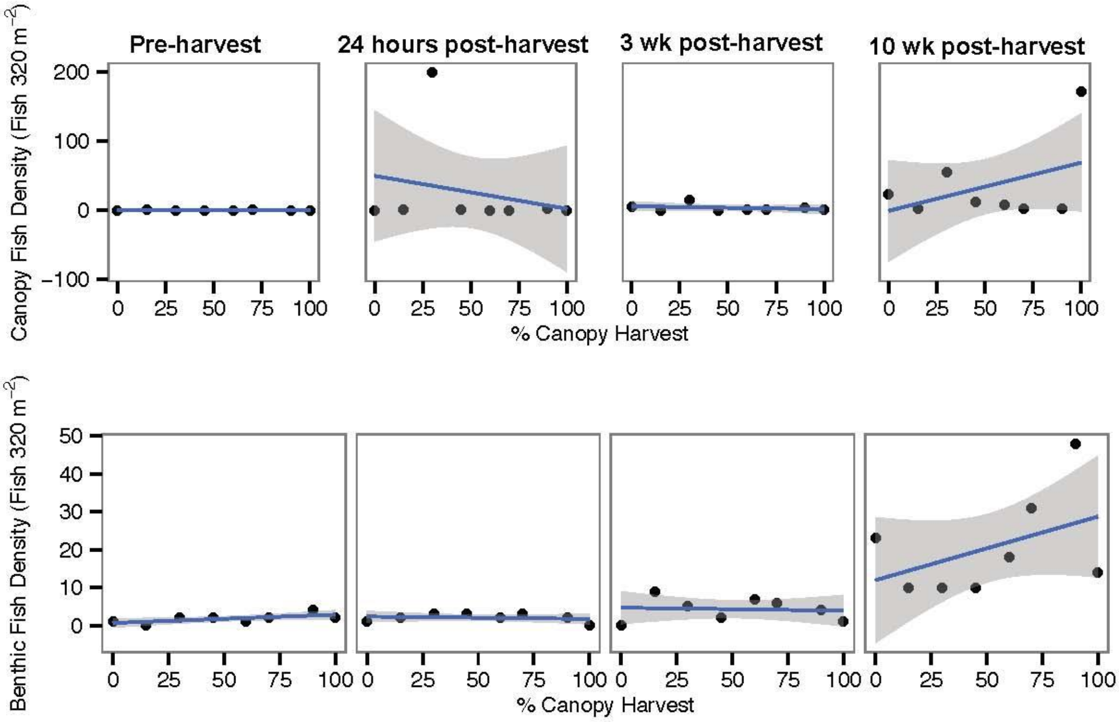



a.
Growth (m frond^{-1}d^{-1})
Parameter
Importance
Avg Temp
0.9
Initial Surface Length
0.33
Initial Surface Fronds
0.23
Frond Density
0.11
Plant Density
0.1
Biomass Removed
0.05
–0.4
–0.2
0.0
0.2
Scaled Coefficient Values
b.
Biomass Recovered (kg)
Parameter
Importance
Initial Surface Length
0.84
Avg Temp
0.46
Initial Surface Fronds
0.35
Max Temp
0.05
Plant Density
0.04
Frond Density
0.03
–10
–5
0
5
10
Scaled Coefficient Values
c.
Surface Frond Production (fronds d^{-1})
Parameter
Importance
Initial Surface Fronds
0.97
StDev Temp
0.23
Avg Temp
0.22
Plant Density
0.13
Exposure
0.05
Max Temp
0.05
–0.10
0.00
0.10
Scaled Coefficient Values
d.
Surface Frond Loss (fronds d^{-1})
Parameter
Importance
Initial Surface Fronds
1
Plant Density
0.41
Initial Surface Length
0.12
Avg Temp
0.09
Exposure
0.04
Frond Density
0.04
–0.02
0.02
0.06
0.10
Scaled Coefficient Values


a.
Growth (m frond^{-1} day^{-1})
0.100
0.075
0.050
0.025
0.000
12.0
12.2
12.4
12.6
Avg Temp (°C)
b.
Biomass Recovered (kg)
12
9
6
3
0
12.0
12.2
12.4
12.6
Avg Temp (°C)
c.
Frond Prod. (fronds frond^{-1} day^{-1})
0.06
0.04
0.02
0.00
12.0
12.2
12.4
12.6
Avg Temp (°C)
d.
Frond Loss (frond^{-1} day^{-1})
0.011
0.010
0.009
0.008
0.007
0.006
0.005
12.0
12.2
12.4
12.6
Avg Temp (°C)


a.
Growth (kg d^{-1})
1
0
−1
1
2
3
4
Initial Biomass kg m^{-2})
b.
Biomass (Kg 40 m^{-2})
4
3
2
1
1
2
3
4
Initial Biomass (Kg 40 m^{-2})
c.
Frond Density (No. 40 m^{-2})
150
100
50
60
90
120
Initial Frond Density (No. 40 m^{-2})
d.
Plant Density (No. 40 m^{-2})
40
30
20
10
10
15
20
25
30
Initial Plant Density (No. 40 m^{-2})
e.
Growth (kg d^{-1})
1
0
−1
0
25
50
75
100
% Canopy Harvest
f.
Δ Biomass (Kg 40 m^{-2})
0.4
0.2
0.0
−0.2
0
25
50
75
100
% Canopy Harvest
g.
Δ Frond Density (No. 40 m^{-2})
1.0
0.5
0.0
−0.5
0
25
50
75
100
% Canopy Harvest
h.
Δ Plant Density (No. 40 m^{-2})
15
10
5
0
−5
−10
0
25
50
75
100
% Canopy Harvest


Pre-harvest
3 wk post-harvest
10 wk post-harvest
Saccharina Biomass (kg m^{-2})
1.0
0.1
0
25
50
75
100
% Canopy Harvest
Pterygorphora Biomass (kg m^{-2})
10.0
1.0
0.1
0
25
50
75
100
% Canopy Harvest


Pre-harvest
24 hours post-harvest
3 wk post-harvest
10 wk post-harvest
Canopy Fish Density (Fish 320 m^{-2})
200
100
0
−100
0
25
50
75
100
% Canopy Harvest
Benthic Fish Density (Fish 320 m^{-2})
50
40
30
20
10
0
0
25
50
75
100
% Canopy Harvest