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Bed-scale impact and recovery of a commercially important intertidal seaweed

Elliot M. Johnston [a,*], Hannah N. Mittelstaedt [a], Laura A. Braun [a], Jessica F. Muhlin [b], Brian J. Olsen [a], Hannah M. Webber [a,c], Amanda J. Klemmer [a]

[a] School of Biology & Ecology, University of Maine, Orono, ME 04469, USA
[b] Corning School of Ocean Studies, Maine Maritime Academy, Castine, ME 04420, USA
[c] Schoodic Institute at Acadia National Park, Winter Harbor, ME 04693, USA

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ABSTRACT

As the value of ecosystem-based management (EBM) approaches is increasingly recognized in marine ecosystems, it is critical that the impacts of resource harvest are assessed at various spatial scales. This is particularly true for habitat-forming resources, such as wild seaweeds, that act as foundation species by physically structuring ecosystems. The impacts of spatially heterogeneous harvest may change with scale, and have different management implications based on the ecosystem process or organism under consideration. *Ascophyllum nodosum* (hereafter rockweed) is a canopy-forming fucoid seaweed endemic to rocky coastlines in the North Atlantic Ocean that has been harvested for centuries. We conducted a Before-After Control-Impact study of commercial rockweed harvest at 38 sites across the coast of Maine (USA) from 2018 to 2020 in an effort to understand impact and one-year recovery of two rockweed bed structural characteristics, height and biomass, at a scale similar to a single harvest event. Our results indicate that rockweed harvest is spatially heterogeneous at the scale of the rockweed bed, and as a result, the effect sizes of harvest at this scale are smaller than those reported in previous studies that assessed smaller spatial scales. Mean rockweed biomass recovered to pre-harvest values after one year of recovery, but mean rockweed height remained lower at impacted sites. While post-harvest recovery was generally high in our study, sites that experienced higher intensities of harvest were less likely to fully recover height or biomass one year post-harvest. Our findings provide resource managers with a bed-scale perspective that can inform EBM approaches, particularly for population-level management of harvested resources and impacts of harvest on highly mobile organisms—such as birds and fish—that interact with these ecosystems at larger spatial scales.

1. Introduction

The harvest and recovery of seaweeds (macroalgae) has been studied widely across littoral zones and latitudes (Keser et al., 1981; Mafra Jr. and Cunha, 2006; Ulaski et al., 2020; Westermeier et al., 2019). There is high interest in seaweeds' response to harvest given their ecological role as foundation species (Dudgeon and Petraitis, 2005; Schmidt et al., 2011) and economic value for coastal communities (Rebours et al., 2014). Many seaweed species exhibit relatively fast growth rates (Mafra Jr. and Cunha, 2006; Reed et al., 2008), and the ability of some to recover biomass a few years after harvest is often highlighted in examples of sustainable fisheries (e.g., Marquez et al., 2014; Vea and Ask, 2011). However, there has been a paradigm shift toward ecosystem-based management (EBM) in recent decades—particularly in marine ecosystems—as resource managers recognize the importance of maintaining not only the population sizes of targeted resources, but also trophic interactions throughout associated food webs (Arkema et al., 2006; Pikitch et al., 2004).

Assessing the food-web impacts of commercial seaweed harvest requires that the scale of inquiry overlaps with the scales of both human harvest and the food web itself. The proportion of harvested individuals can change across spatial scales and result in variable impacts to habitat quality depending on the home range size and movement type of the organism under consideration (Grindal and Brigham, 1999; Leonard et al., 2008). Along many North Atlantic rocky intertidal zones, *Ascophyllum nodosum* (hereafter rockweed)—a canopy-forming fucoid

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* Corresponding author at: School of Biology & Ecology, University of Maine, 5751 Murray Hall, Orono, ME 04469, USA.
E-mail address: edwin.johnston@maine.edu (E.M. Johnston).

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seaweed—dominates the intertidal seaweed assemblage (Guiry and Morrison, 2013; Vadas et al., 2004). Rockweed has experienced a rise in global harvest over the past several decades and, as a result, there have been concerns about the ecological sustainability of harvesting practices (Lotze et al., 2019; Seeley and Schlesinger, 2012). Some jurisdictions report rockweed harvest by total landed weight or percent biomass removed across a landscape-scale area on the order of tens of square kilometers (i.e., sector; Ugarte and Sharp, 2012), yet these metrics lack context at the site-level scale over which a single harvest event occurs and some highly mobile organisms—such as birds and fish—utilize the ecosystem. Furthermore, impacts associated with small, intensely harvested patches (e.g., several m^2; Walder, 2015) may be different than those associated with rockweed beds that experience spatially heterogeneous harvest typical of commercial practices (DFO, 1999). Quantifying harvest impacts at the harvest-site scale (i.e., hundreds to thousands of square meters) will allow EBM approaches to simultaneously assess population-level management of the harvested resource and the impacts of commercial harvest on mobile organisms that interact with these ecosystems at relatively large spatial scales.

In addition to assessing harvest impacts at different spatial scales, resource managers must consider the representativeness of research protocols to commercial harvest in their jurisdiction. For instance, some studies use harvest intensities that cut rockweed fronds below the legal harvest height in the area of study (Keser et al., 1981; Black and Miller, 1991; Fegley, 2001). Studies may also create uniformly harvested treatment plots with hand shears that are not typical of patchy commercial harvest (Keser et al., 1981; Fegley, 2001; Walder, 2015). Recovery thresholds may be crossed at these high harvest intensities, but species may show greater resilience at lower harvest intensities (Keser et al., 1981). As a result, harvest regulations informed by research that lacks representativeness to commercial practices can lead to uncertainty in the outcomes of management decisions.

Our objective was to design an experiment to assess the effects of commercial rockweed harvest by measuring impact and recovery at the same spatial scale as the harvest. We conducted a Before-After Control-Impact (BACI) experiment using commercial rockweed harvest practices at 38 sites across the coast of Maine (USA; Fig. 1). To assess impact and recovery, we measured mean bed height and biomass during three time periods: pre-harvest (2018), harvested (2019), and one year post-harvest (2020). Given the large site sizes in our study and the limitations of sampling their full spatial extent, we use a two-part approach in our analysis. First, we tested whether our sampling methodology detected harvest at impact sites relative to control sites. Second—contingent on detecting harvest—we quantified the impact and recovery of rockweed height and biomass at the rockweed bed scale. We hypothesized that harvest impacts to both rockweed characteristics will be spatially heterogeneous at a site, resulting in harvest impacts that are detectable at the site scale, but of smaller effect size than those reported in previous studies with smaller treatment plot sizes. Additionally, we hypothesized that sites with greater harvest intensity (i.e., biomass loss) will show less recovery one year later. We define recovery as a return to pre-harvest baseline values in height and biomass. While this approach defines impact and recovery strictly by these two morphological characteristics of the target resource, and does not consider any direct or indirect impacts on other species in the ecosystem, our study provides a harvest-scale perspective that can inform EBM recommendations in rockweed ecosystems.

2. Methods

2.1. Study design

The BACI study design (Stewart-Oaten et al., 1986) is commonly used to assess the impacts of disturbance, and has been frequently used to assess the impacts of rockweed harvest (e.g., Kay, 2015; Kelly et al., 2001; Trott and Larsen, 2012; Ugarte et al., 2006; Walder, 2015). BACI

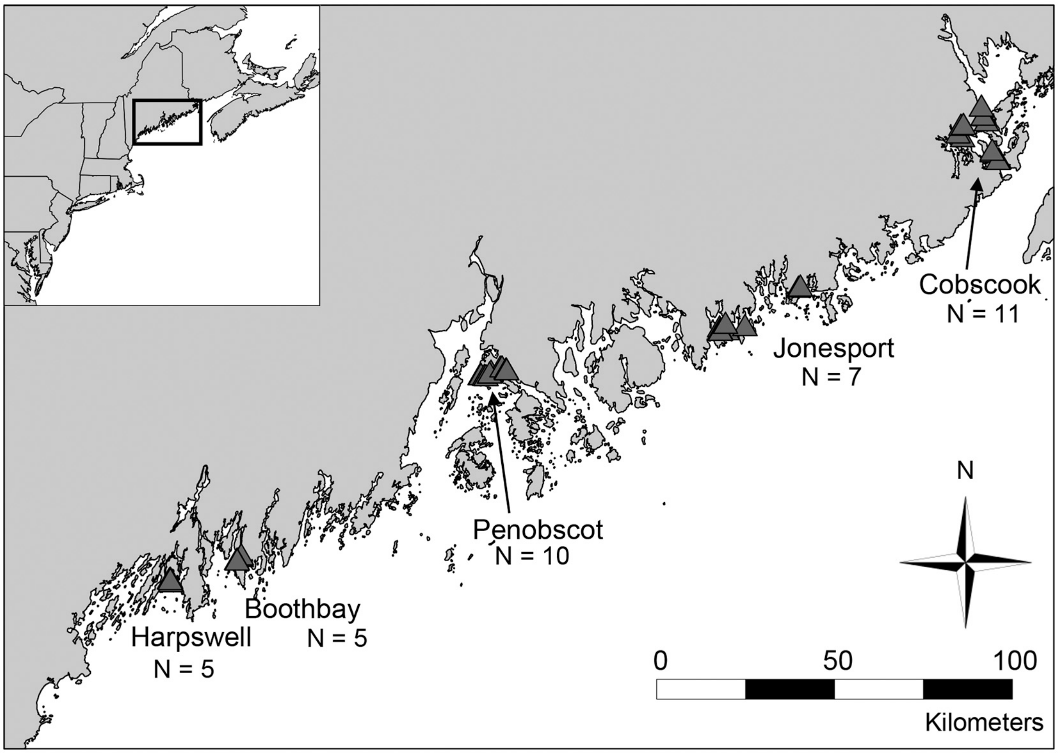

Fig. 1. The Before-After Control-Impact (BACI) experiment conducted at 38 sites across five regions. Regional treatment totals were as follows: Harpswell 2 control, 3 impact; Boothbay 2 control, 3 impact; Penobscot 4 control, 6 impact; Jonesport 4 control, 3 impact; Cobscook 7 control, 4 impact. Treatments are not visually differentiated due to high symbol overlap at the current scale. Harpswell and Boothbay were combined into a single "Midcoast" region during analyses to better balance sample sizes across regions.

experiments allow for strong causal inference—spatial replication (control vs. impact) separates the effects of natural environmental variation and experimental treatment, while temporal replication (before vs. after) assesses whether post-disturbance differences between control and impact groups were present pre-disturbance. We used a repeated-measures BACI design (Green, 1993) with rockweed surveys at each site before harvest (August–October 2018), immediately after harvest (August–December 2019), and one year after harvest (August–November 2020). Our annual survey window was informed by typical harvest schedules and avoided biomass assessment during the late spring reproduction of rockweed when reproductive receptacles can increase seaweed weight considerably (Vadas et al., 2004).

2.2. *Site selection and rockweed harvest*

One of our primary objectives was to maximize the representativeness of rockweed harvest to commercial practices in our region (Maine). Therefore, we worked with several rockweed harvest companies—Acadian Seaplants ($N = 28$ sites), North American Kelp ($N = 5$ sites), and Source Incorporated (N = 5 sites)—and private landowners to establish 38 sites along the Maine coast. Based on their own criteria, each company defined their geographic boundaries of harvestable shoreline within which research sites could be established, resulting in five study regions—Harpswell, Boothbay, Penobscot, Jonesport, and Cobscook (Fig. 1). We initially began the study with another company using knife-harvesting in the mid-coast region, but after initial efforts resulted in only two viable sites (one treatment, one control) we did not have enough replication to control for either regional or harvest method differences and these two sites were removed from the study. Within each company boundary, we used Google Earth satellite imagery to identify potential sites that a) were non-cliff rocky intertidal habitat and b) had extensive rockweed beds suitable for commercial-scale harvest. Additionally, we worked with harvesters to select candidate sites that were not harvested within at least the past three years. Sites were located either on the mainland or near-shore islands to ensure harvest and survey accessibility. Typical substrata included bedrock and boulders.

From the pool of candidate sites, we first selected sites for which we received landowner permission to access the intertidal. We next selected sites until we reached the maximum number of sites a company could harvest given their anticipated availability of harvesters and equipment, or until our pool of candidate sites was exhausted. While harvest companies defined the candidate patch boundaries—providing direct application to industrial practices—we assigned treatment type (control or impact) to each site. Landowner permissions to harvest rockweed prevented a fully spatially random treatment assignment, but we ensured that there was a spatial mixture of control ($N = 19$) and impact (N = 19) sites within each of the five predefined regions. In addition, we attempted to ensure that there was no geomorphological bias between treatment type (e.g., a mixture of coastline features such as points, coves, etc.). Sites were vertically bounded by the high and low tide lines, and measured 100 m horizontally (parallel to the shoreline), a size representative of the scale at which commercial harvesters operate (A. Feibel, personal communication). We define a rockweed bed at the scale of the harvest event in this study (i.e., a study site), but we recognize that these beds are often part of larger ecologically contiguous units.

Control sites were unharvested throughout our study, and all impact sites were harvested once between June and November 2019 by commercial harvesters under current Maine regulations (40.6 cm minimum cutting height). We provided companies with Global Positioning System (GPS) coordinates of site boundaries, and instructed companies to harvest as they would during commercial operations. Rockweed harvest occurred by two methods: mechanical harvester vessel ($N = 13$) and hand rake ($N = 6$; see Rockweed Plan Development Team et al., 2014 for details on each method). We personally observed multiple site harvests with each company ($N = 7$) to confirm that their practices aligned with typical harvest practices. In addition, harvest companies reported total seaweed harvest landings from our study sites when possible.

2.3. *Rockweed height and biomass assessment*

Rockweed height and biomass assessment allowed us to measure variation in both harvest intensity (at our impact sites) and in natural sources of variation (at all sites), such as rockweed growth and frond breakage due to storms. We conducted rockweed assessments once per site during each time period—pre-harvest (2018), harvested (2019), and one year post-harvest (2020). Our methodology was adapted from the Maine Department of Marine Resources' Fishery Management Plan for Rockweed (Rockweed Plan Development Team et al., 2014). During low tide, we haphazardly placed two 10-m transects in separate areas of the rockweed bed ($>$ 20 m apart), parallel to the shoreline. Transects were placed left- and right-of-center at a middle tidal height, which is the most productive zone for rockweed and where most harvest takes place (Stengel and Dring, 1997; A. Feibel, personal communication). We marked transect locations with Garmin GPS handheld units and placed each transect in the same location during each survey year (GPS manufacturer reported error of $\leq$3 m).

Along each 10-m transect, five 0.5 × 0.5 m quadrats (0.25 m^2) were sampled every two meters, placed along alternating sides of the transect. At each quadrat, we used a three-step process to assess rockweed structural characteristics. First, we counted the number of holdfasts (the part of the rockweed individual that attaches to the substrate). Holdfasts, and therefore rockweed individuals, were considered separate if they were $>$ 0.5 cm apart (Kay et al., 2016). Our surveys included holdfast count to allow us to assess variation in rockweed density between time periods.

Second, we haphazardly selected three rockweed individuals and measured their length from the holdfast to the tip of the longest frond. If the longest frond significantly overestimated canopy height (e.g., a single outlier frond), we measured the length of the tallest frond in the group that represented the top of the canopy. Our haphazard selection of rockweed individuals could have been biased toward longer algae that were more conspicuous, which would result in mean height values more representative of canopy structure than all individuals within a site. However, we would not expect this potential bias to change across treatments or time periods (i.e., affect inferences in our study).

Third, we placed all rockweed from holdfasts within the quadrat into a mesh bag and weighed it with a spring scale. We left several inches between the holdfast and the bottom of the cinched mesh bag to allow slack for weighing and to prevent damage to the rockweed individuals. Small individuals that had holdfasts $<$2 cm in diameter with fronds that did not exceed 30 cm were excluded from rockweed surveys. All sampling was non-destructive in an effort to isolate changes in rockweed characteristics to either natural variation or harvest, and not from sampling methods.

Commercial rockweed harvest is not homogeneous across the bed and leads to variation in local biomass removal (Rangeley and Davies, 2000; Ugarte et al., 2006). The primary objective of our sampling methodology was to estimate height and biomass at the site scale. We did not ensure that there was perfect spatial overlap between harvest and either our quadrats or our transects, and harvesters were unaware of the location of sampling within each site. We expected that conventional commercial practices would result in a spatially heterogeneous harvest that would only partially overlap with our precise sample locations, and thus our measurements would provide us with a representative assessment of harvest impact at the site, but not the holdfast, scale. Importantly, our design was not intended to precisely estimate biomass removed from the site, but to capture typical within-site variability. This approach allowed us to estimate average changes in height and biomass across a given site, and to provide an informative, unbiased average of harvest impact across our 19 impact sites, incorporating both among- and within-site variation.

2.4. Statistical analysis

All statistical analyses were performed in program R version 4.1.2 (R Core Team, 2021). Regional differences in pre-harvest rockweed height and biomass were analyzed using linear mixed models (LMMs) in the lme4 package (Bates et al., 2015). We included region as a fixed effect and site, transect, and quadrat as hierarchical sets of nested random effects to account for spatial non-independence.

Tests of the impacts of rockweed harvest on height and biomass were divided into three separate analyses. Transects and sites were the experimental units in these analyses and we therefore calculated mean height and biomass values over five and ten quadrats, respectively, at each site. First, we assessed whether our sampling methodology detected rockweed harvest at impact sites relative to control sites. We performed contingency χ^2 analyses to examine the relationship between treatment type and the number of transects at a site that declined in mean rockweed height and biomass between the pre-harvested and harvested time periods. Second, we tested the impact of rockweed harvest across all study sites with LMMs that had two main effects and their interaction: treatment (control or impact) and time period (pre-harvest, harvested, one year post-harvest). To quantify the impact of harvest, we calculated standardized and unstandardized effect sizes, respectively,

$$ln\left(\frac{\bar{X}_{\text{Harv,I}}}{\bar{X}_{\text{Harv,C}}}\right)-ln\left(\frac{\bar{X}_{\text{Pre,I}}}{\bar{X}_{\text{Pre,C}}}\right) \tag{1}$$

$$\left(\bar{X}_{\text{Harv,I}}-\bar{X}_{\text{Pre,I}}\right)-\left(\bar{X}_{\text{Harv,C}}-\bar{X}_{\text{Pre,C}}\right) \tag{2}$$

where $\bar{X}_{ij}$ equals the estimated marginal mean $\bar{X}$ during time period i (Pre = pre-harvest, Harv = harvested) at sites with treatment type j (I = impact, C = control; Rosenberg et al., 2013). Reporting both metrics allowed us to make comparisons with other studies (standardized) while also providing context within the current study (unstandardized). For each effect size, we calculated reduced bias-corrected bootstrap 95% confidence intervals (Tibbe and Montoya, 2022). Third, we tested whether the impact of rockweed harvest varied by study region with LMMs that included a three-way interaction between treatment, time period, and region.

In the LMMs for all three analyses, we included a random effect of site nested within region in order to account for repeated sampling at sites grouped by region. Models were assessed for homoscedasticity using plots of model residuals versus fitted values and for normality using Q-Q plots. Kenward-Roger approximations for degrees of freedom were used to calculate *P* values using the lmerTest package (Kuznetsova et al., 2017). One degree of freedom planned contrasts were used to investigate specific hypotheses using the emmeans package (Lenth et al., 2020). Throughout the analyses we combined Harpswell ($N = 5$ sites) and Boothbay (N = 5 sites)—which are geographically proximate—into a single "Midcoast" region in order to better balance sample sizes across regions.

We also examined the relationship between harvest intensity—measured as the change in mean rockweed biomass at a site over the first time interval (pre-harvest to harvested)—and the a) amount of post-harvest growth and b) recovery of each rockweed characteristic. Post-harvest growth was defined as the absolute amount of change in either height or biomass during the second time interval (harvested to one year post-harvest), while recovery was defined as the percent of the baseline (pre-harvest) value observed at the end of our study (one year post-harvest). We used linear regressions with a single explanatory variable (harvest intensity) to assess these relationships.

During preliminary analyses, we removed four statistical outliers (i.e., ≥ 3 SD from the mean) from final analyses (Fig. S1). First, we removed the biomass value from one quadrat and the height value from one alga that were 6.73 kg 0.25 m^{-2} heavier and 68 cm longer than the next highest values, respectively. Second, we removed one Jonesport impact site with a mean biomass value 4.1 SD above the mean in the pre-harvest time period. The site with the next most extreme biomass value in the first time period was 1.6 SD away from the mean. We also removed one Cobscook impact site where we recorded 373% more holdfasts between the pre-harvest and harvested time periods, which corresponded to a 166% increase in biomass. This change in holdfasts was 6.1 SD above the mean, with the next most extreme value 2.1 SD away from the mean. Each of these decisions was motivated by the fact that our transects were unlikely to measure the exact same rockweed individuals during each time period, and, therefore, it was important that we identified extreme sampling outliers that resulted from our sampling design.

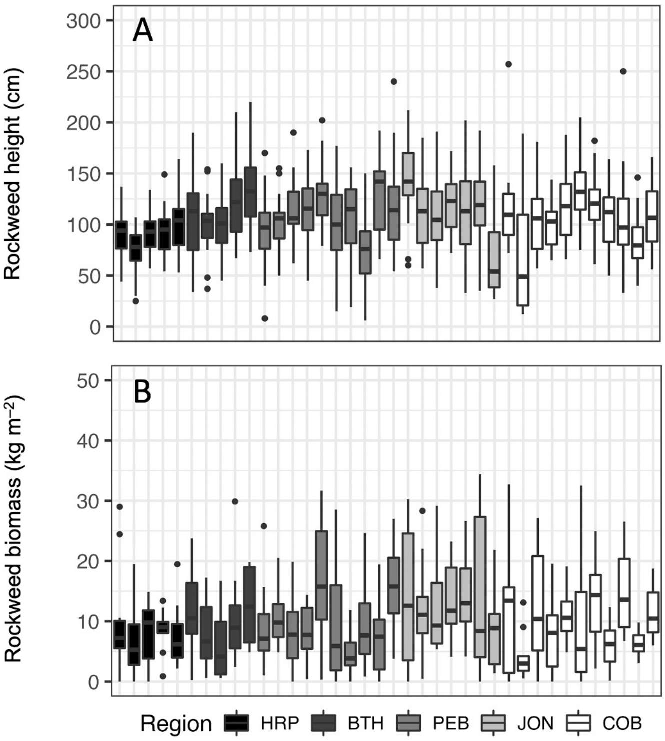

Fig. 2. Regional comparisons of (A) mean rockweed height and (B) biomass at 38 sites across five regions. For each site, boxplots are comprised of 30 values for height and 10 values for biomass. All differences between region group means are non-significant (α = 0.05) for both rockweed characteristics. Only surveys from the pre-harvest time period at control and impact sites are included. Regional abbreviations are as follows: HRP = Harpswell, BTH = Boothbay, PEB = Penobscot, JON = Jonesport, and COB = Cobscook.

3. Results

Mean holdfast count increased slightly at each consecutive time period, but the treatment *x* time period interaction was not statistically significant ($F_{2,72} = 0.37$, $P = 0.69$), indicating that changes in rockweed densities would not impact the inferences in our study. In addition, there was no statistically significant effect of harvest observation on the change in rockweed biomass between the pre-harvest and harvested time periods ($F_{1,17} = 1.78$, $P = 0.20$).

3.1. Pre-harvest: regional comparison

Mean rockweed height and biomass were relatively homogeneous across the coast of Maine. Thirty-eight out of 114 rockweed assessments occurred in 2018 before harvest, providing a coastwide comparison of rockweed characteristics exclusive of the short-term impacts of rockweed harvest. Given that commercial-scale rockweed harvest has occurred in Maine since the 1970s, inherent in our regional 'unharvested' comparisons are variable harvest histories across the coast.

Table 1
Contingency tables assessing the relationship between treatment and changes in rockweed height and biomass between the pre-harvest and harvested time periods.

Rockweed Characteristic			
Treatment	Number of Transects With Mean Decline in Rockweed Characteristic (Pre-harvest to Harvested)		
Height			
	Zero	One	Two
Control	11	4	4
Impact	4	8	7
		X^2	5.42
		df	2
		P	0.07
Biomass			
	Zero	One	Two
Control	7	11	1
Impact	5	6	8
		X^2	7.25
		df	2
		P	0.03

Mean rockweed height did not differ significantly between regions, with means (± SE) ranging from 89.6 ± 8.0 cm (Harpswell) to 113.5 ± 8.0 cm (Boothbay) ($F_{4,32.89} = 1.45$, $P = 0.24$; Fig. 2A). Similarly, mean rockweed biomass was not significantly different between regions, with means (± SE) ranging from 8.3 ± 1.4 kg m^{-2} (Harpswell) to 12.7 ± 1.1 kg m^{-2} (Jonesport) ($F_{4,33} = 1.26$, $P = 0.31$; Fig. 2B). The variances of nested random effects indicate that within-group variation in rockweed height increases monotonically from the quadrat to site spatial scale, while for biomass the smallest variation occurs at the site scale (Table S1).

3.2. Pre-harvest to harvested: impact of harvest

Across several analyses assessing the impacts of harvest—described below—there was marginal statistical support for an effect of treatment ($0.10 > P > 0.01$). The effect of treatment on the number of transects that declined in mean rockweed height or biomass between the pre-harvest and harvested time periods was near the alpha level (0.05) in our study for both height ($\chi^2 = 5.42$, $P = 0.07$) and biomass ($\chi^2 = 7.25$, $P = 0.03$). For each bed characteristic, both transects declined more often at impact sites (height: $N = 7$ impact and 4 control; biomass: $N = 8$ impact and 1 control), while neither transect declined more often at control sites (height: $N = 4$ impact and 11 control; biomass: N = 5 impact and 7 control). The spatially heterogeneous patterns of commercial harvest and natural disturbance were apparent (Fig. S3), with only one transect declining in mean height and biomass at several control and impact sites (Table 1).

The treatment *x* time period interaction was close to the alpha level in our study for both mean height ($F_{2,\ 72} = 2.63$, $P = 0.08$) and biomass ($F_{2,\ 72} = 3.25$, $P = 0.04$; Table 2). Planned contrasts indicated marginal support for greater declines in mean height and biomass at impact sites than control sites (height, $t_{1,\ 72} = -1.91$, $P = 0.06$; biomass, $t_{1,\ 72} = -2.21$, $P = 0.03$; Table 2, Fig. 3). The standardized effect size of harvest on mean biomass (−0.28, 95% CI = −0.58 to 0.003) was more than double the effect size on mean height (−0.11, 95% CI = −0.25 to 0.04; Table 3). These magnitudes of impact equated to unstandardized effect sizes of −11.9 cm (95% CI = −27.3 to 3.8 cm) for height and − 2.97 kg m^{-2} (95% CI = −6.03 to 0.08 kg m^{-2}) for biomass. For both rockweed

Table 2
Results from the linear mixed-effects models testing the impact of rockweed harvest on rockweed height and biomass at the scale of the rockweed bed. The significance levels ($P \leq 0.05$ in bold) are calculated from *F*-statistics of type III hypothesis tests, based on Kenward–Roger approximations for degrees of freedom. Marginal R^2 considers only the variance of the fixed effects, while conditional R^2 considers the variance of both fixed and random effects. The planned contrasts represent the effect of treatment on (top to bottom) harvest impacts, post-harvest growth, and one-year recovery, respectively. Abbreviations are as follows: Pre = Pre-harvest, Harv = Harvested, Yr Post = One Year Post-harvest, I = Impact, and C = Control.

Rockweed characteristic	Source of variation					
Height	*Fixed effect*	Variance	SD	*df*	*F*	*P*
	Treatment			1, 35.04	0.44	0.51
	Time Period			2, 72	1.39	0.25
	Treatment *x* Time Period			2, 72	2.63	0.08
	Random effect					
	Region	6.53	2.56			
	Region(Site)	125.61	11.21			
	Residual	185.80	13.63			
	Planned contrast	Estimate	SE	*df*	*t*	*P*
$(\bar{X}_{Harv,\ I} - \bar{X}_{Pre,\ I}) \neq (\bar{X}_{Harv,\ C} - \bar{X}_{Pre,\ C})$		−11.93	6.25	1, 72	−1.91	0.06
$(\bar{X}_{Yr\ Post,\ I} - \bar{X}_{Harv,\ I}) \neq (\bar{X}_{Yr\ Post,\ C} - \bar{X}_{Harv,\ C})$		−0.91	6.25	1, 72	−0.15	0.88
$(\bar{X}_{Yr\ Post,\ I} - \bar{X}_{Pre,\ I}) \neq (\bar{X}_{Yr\ Post,\ C} - \bar{X}_{Pre,\ C})$		−12.84	6.25	1, 72	−2.05	**0.04**
	Marginal R^2: 0.05, Conditional R^2: 0.44					
Biomass	*Fixed effect*	Variance	SD	*df*	*F*	*P*
	Treatment			1, 34.26	0.22	0.64
	Time Period			2, 72	6.82	**0.002**
	Treatment *x* Time Period			2, 72	3.25	**0.04**
	Random effect					
	Region	0.81	0.90			
	Region(Site)	3.12	1.77			
	Residual	8.62	2.94			
	Planned contrast	Estimate	SE	*df*	*t*	*P*
$(\bar{X}_{Harv,\ I} - \bar{X}_{Pre,\ I}) \neq (\bar{X}_{Harv,\ C} - \bar{X}_{Pre,\ C})$		−2.98	1.35	1, 72	−2.21	**0.03**
$(\bar{X}_{Yr\ Post,\ I} - \bar{X}_{Harv,\ I}) \neq (\bar{X}_{Yr\ Post,\ C} - \bar{X}_{Harv,\ C})$		2.97	1.35	1, 72	2.21	**0.03**
$(\bar{X}_{Yr\ Post,\ I} - \bar{X}_{Pre,\ I}) \neq (\bar{X}_{Yr\ Post,\ C} - \bar{X}_{Pre,\ C})$		−0.004	1.35	1, 72	−0.003	1.00
	Marginal R^2: 0.11, Conditional R^2: 0.39					

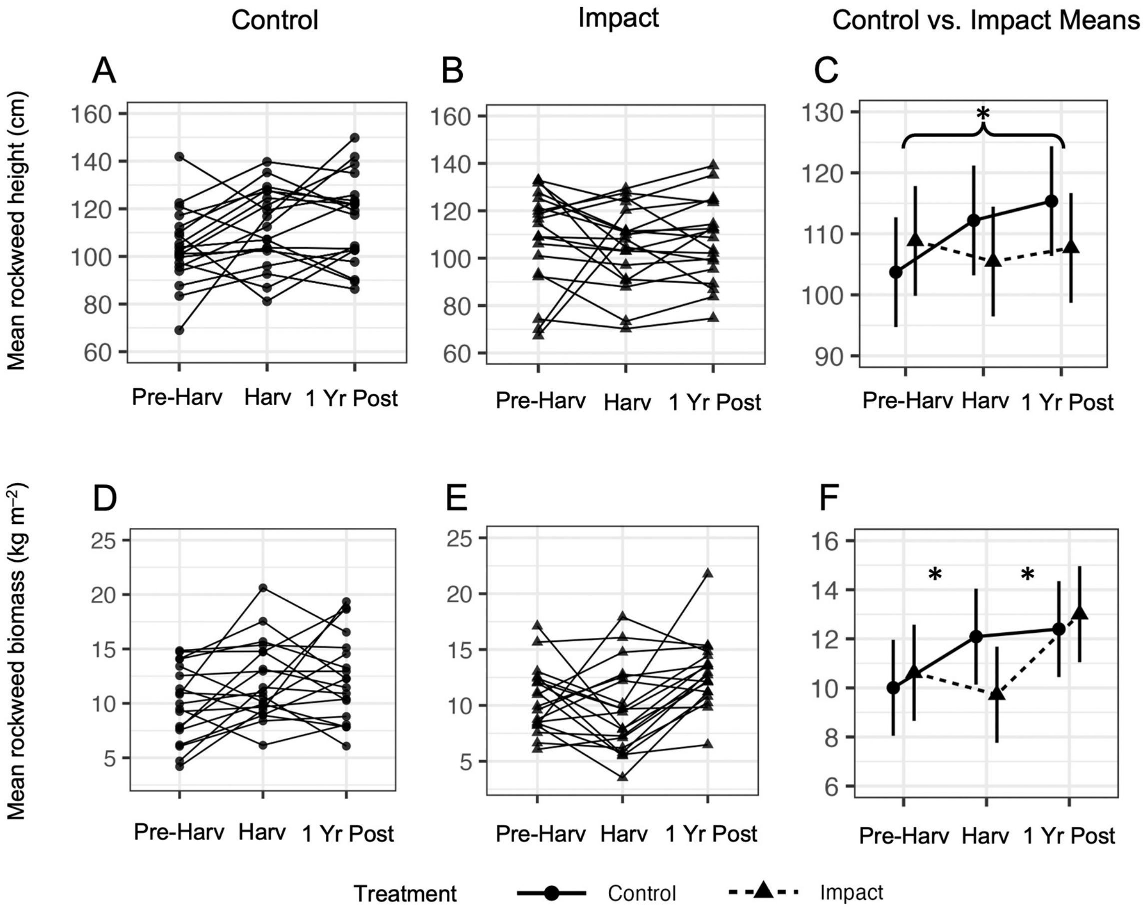

Fig. 3. Change in mean rockweed height and biomass across three time periods. Each point in panels A, B, D, and E represents a mean site value, and a line connects a given site through time. Error bars for each point are not shown in these plots to aid visual clarity. In panels C and F, points represent treatment means ±95% confidence intervals. Asterisks indicate statistically significantly differences ($\alpha = 0.05$) in the change in height or biomass between treatments for a given time interval. Pre-Harv = Pre-harvest, Harv = Harvested, and 1 Yr Post = One Year Post-Harvest.

characteristics, the mean increase at control sites (height = 8.5 cm, biomass = 2.08 kg m^{-2}) contributed more than the mean decrease at impact sites (height = −3.4 cm, biomass = −0.89 kg m^{-2}) toward the effect sizes. Lastly, the impact of harvest varied by region for both rockweed characteristics (Fig. 4). Midcoast was the only region to experience statistically significant declines in rockweed height or biomass following harvest (height, $t_{1,\,60} = -2.26$, $P = 0.03$; biomass, $t_{1,\,60} = -3.03$, $P = 0.004$; Table S2, Fig. S2).

3.3. Harvested to one year post-harvest: regrowth after harvest

Mean rockweed height increased slightly during the post-harvest interval at both control and impact sites (3.2 and 2.2 cm, respectively; $t_{1,72} = -0.15$, $P = 0.88$; Fig. 3C). In contrast to height, the post-harvest increase in mean rockweed biomass was significantly greater at impact sites than at control sites (3.28 and 0.31 kg m^{-2}, respectively; $t_{1,72} = 2.21$, $P = 0.03$; Fig. 3F). As a result, the standardized effect size of harvest on regrowth was higher for biomass (0.27, 95% CI = −0.003 to 0.55) than for height (−0.007, 95% CI = −0.15 to 0.13).

Across regions, post-harvest changes in mean height were small and there were no statistically significant effects of treatment. Increases in biomass were greater at impact sites than at control sites in all four regions, but none of these treatment differences were statistically significant (Midcoast: $t_{1,60} = 1.12$, $P = 0.27$, Penobscot: $t_{1,60} = 1.17$, $P = 0.25$, Jonesport: $t_{1,60} = 0.47$, $P = 0.64$, Cobscook: $t_{1,60} = 1.50$, $P = 0.14$; Fig. 4).

3.4. Pre-harvest to one year post-harvest: recovery from harvest

At the end of the study, mean height (± SE) at impact sites (107.7 ± 4.3 cm) remained below mean height at control sites (115.4 ± 4.3 cm), indicating a lack of recovery to pre-harvest values ($t_{1,\,72} = -2.05$, $P = 0.04$; Fig. 3C). Less than half of the impact sites (9/19 = 47%) showed complete recovery in rockweed height (range: 67.1–177.9%; mean ± SD: 102.5 ± 27.8%), but most of the sites that exhibited partial recovery (7/10 = 70%) were within 80% of original height values. In contrast to height, biomass exhibited a complete recovery on average across all sites ($t_{1,\,72} = -0.003$, $P = 1.00$; Fig. 3F). Furthermore, the majority of impact sites (14/19 = 74%) showed complete recovery in rockweed biomass and many sites exceeded pre-harvest values (range: 51.6–201.1%; mean ± SD: 130.5 ± 38.8%).

Recovery varied across regions for both rockweed characteristics. In Midcoast, mean height at impact sites remained lower than at control sites after one year of recovery ($t_{1,\,60} = -3.20$, $P = 0.002$; Fig. 4A). Mean biomass also remained lower at impact sites in this region, but there was less statistical support for a difference between treatments ($t_{1,\,60} = -1.92$, $P = 0.06$; Fig. 4B). In the other three regions (Penobscot, Jonesport, and Cobscook), there were no statistically significant effects of treatment on recovery for either rockweed characteristic (Table S2).

3.5. Harvest intensity gradient

There was no effect of harvest intensity—defined as the change in mean rockweed biomass between pre-harvest and harvested time

Table 3
Review of studies assessing the impact of rockweed harvest on rockweed height and biomass. Standardized and unstandardized effect sizes are calculated when possible (formulas provided in table note), and main results are provided otherwise. Some effect sizes were calculated from study figures with ImageJ. Studies with complete rockweed removal as the main treatment were not considered. In the Harv. Type column, C = commercial harvest and R = researcher harvest. Sites are defined as separate rockweed beds, while plots are defined as the spatial extent at which each treatment was applied. In cases when a full rockweed bed represents a treatment (e.g., this study), sites and plots are equal. Regional regulations (minimum cutting height) are provided for studies for which we were able to calculate an effect size.

Study	Region	Harv. Type	Sites	Treatments	Total Trtmnt. Plots Per Site	Plot Size	Rockweed Character-istic	Standardized BACI Effect Size (95% CI)	Unstandardized BACI Effect Size (95% CI)	Length of Recovery Data
Johnston et al. 2023 (this study)	Maine (USA)	C	38	Unharvested, commercial harvest (40.6 cm min. cut)	1	Mean ± SD = 3866 ± 3003 m^2	Height Biomass	−0.11 (−0.25, 0.04) −0.28 (−0.58, 0.003)	−11.9 cm (−27.3, 3.8) −2.97 kg m^{-2} (−6.03, 0.08)	1 year
Kay, 2015	Nova Scotia (Canada)	C	1	Unharvested, commercial harvest (12.7 cm min. cut)	2	3750 m^2	Height Biomass	−0.20 −0.29	−22 cm −3.3 kg m^{-2}	4 weeks
Walder, 2015	New Brunswick (Canada), Maine	R	3	Unharvested, 40.6 cm	18, 30, 40	4 m^2	Height Biomass	−1.04 –	−89.7 cm –	3 Months
Ugarte et al., 2006	New Brunswick	C	1	Unharvested, commercial harvest (12.7 cm min. cut)	5	64 m^2	Height Biomass	−0.21 −0.52	−13.8 cm −5.36 kg m^{-2}	2 years
Kelly et al., 2001	Ireland	C	2	Unharvested, mechanical harvest, hand harvest (no min. cutting height)	3	50 m x intertidal width	Height Biomass	Hand: −1.42 Mechanical: −0.58 –	Hand: −63.7 cm Mechanical: −40.8 cm –	11–17 months
							Main Results If Unable to Calculate Effect Sizes			
Lauzon-Guay et al., 2021	New Brunswick, Nova Scotia	C	NB = 21 sectors, NS = 39 sectors.	Unharvested (4 NB sectors sampled at end of study only), commercial harvest	1	Rockweed bed (sizes unknown)	No significant decrease in rockweed biomass in NB or NS harvest sectors over 25 years, but biomass in unharvested NB sectors was 7% higher than in harvested sectors at end of study. Average rockweed height decreased by 7.8 cm in NS and increased by 13.8 cm in NB. Rockweed height in unharvested NB sectors was similar to values in harvested sectors.			Repeated harvesting across 25 years. Harvest intervals unknown.
Gendron et al., 2018	Quebec (Canada)	R	1	15 cm, 30 cm	10	25 m^2	Three-year recovery period maximizes harvested biomass. 15-cm cutting height often provided higher biomass yields than the 30-cm cutting height, especially at longer recovery periods.			1,2,3,4, or 5 year recovery intervals studied over 28 years of repeated harvesting
Phillippi et al., 2014	Maine	R, C	2	Unharvested, 20.3 cm (hand shears), 40.6 cm (hand shears); commercial harvest	54 (hand shears); 2 (comm. harvest)	4 m^2 (hand shears); 60 m x intertidal width	No data provided on rockweed harvest. Results focus on macroinvertebrate responses to harvest.			None
Trott and Larsen, 2012	Maine	C	1	Unharvested, commercial harvest	2	~683 m^2	No difference in average biomass between control and impact plots two months post-harvest.			Two months
Blinn et al., 2008	New Brunswick	C	12 (year 1), 8 (year 2)	Unharvested, commercial harvest	1	Rockweed bed (sizes unknown)	No pre-harvest data. No significant difference in rockweed density or height between unharvested and harvested sites.			None
Sutherland, 2005	New Brunswick	C	43 across six sectors	Commercial harvest	1	Rockweed bed (sizes unknown)	Assessed rockweed beds in six harvest sectors. Compared to an earlier study of the same beds (Smith 2000), average rockweed bed height and biomass were lower in half of the sectors.			None
Hamilton and Nudds, 2003	New Brunswick	R	1	Unharvested, 50% biomass removal	12	24.5 m^2	No data provided on impact of rockweed harvest. Rockweed volume recovered one year post-harvest, while height did not.			1 year
Fegley, 2001	Maine	R	4	Unharvested, 18 cm, 36 cm	9	25 m^2	88% biomass recovery two years post-harvest for 36 cm treatment. 12.3 cm average growth in first year post-harvest for 36 cm treatment vs. 11.9 cm average growth for control.			2 years

(*continued on next page*)

Table 3 (*continued*)

Study	Region	Harv. Type	Sites	Treatments	Total Trtmnt. Plots Per Site	Plot Size	Rockweed Characteristic	Standardized BACI Effect Size (95% CI)	Unstandardized BACI Effect Size (95% CI)	Length of Recovery Data
Lazo and Chapman, 1996	Nova Scotia	R	1	Unharvested, low intensity (15 min.), medium intensity (30 min.), high intensity (45 min.)	21	336 m^2	18% (SD = 5), 60% (SD = 19) and 70% (SD = 18) of the stand biomass was removed in the low-, medium-, and high-intensity treatments. Post-harvest growth was higher in harvested than unharvested plots.			2 years
Ang et al., 1993	Nova Scotia	C	1	Unharvested, commercial harvest	6	400 m^2	Localized biomass loss of 80% after harvest. Results focus on the effect of harvest on rockweed size structure and mortality.			None
Keser et al., 1981	Maine	R	10	Complete removal, 15 cm, 25 cm	3	5 m x intertidal width	Weighed harvested biomass rather than biomass of remaining algae. 15 cm and 25 cm yields were highest on the first harvest and declined with successive harvests.			3 years
Boaden and Dring, 1980	Northern Ireland	C	1	Unharvested, 10-15 cm	2	~1000 m^2	Rockweed internodal length and lateral branching increased after harvest, but provided 20% less shore cover than in the uncut area.			3 years
Baardseth, 1970	Norway	C	1	Commercial harvest	1	809 m^2	Variable recovery (55% to >100%) of beds, measured as harvest yield, three years after harvest			3 years

Note: Standardized effect sizes = $\ln\left(\frac{\bar{X}_{Harv,I}}{\bar{X}_{Harv,C}}\right) - \ln\left(\frac{\bar{X}_{Pre,I}}{\bar{X}_{Pre,C}}\right)$. Unstandardized effect sizes = $(\bar{X}_{Harv,\ I} - \bar{X}_{Pre,\ I}) - (\bar{X}_{Harv,\ C} - \bar{X}_{Pre,\ C})$. $\bar{X}_{i,\ j}$ represents the mean height or biomass value during the *i*th time period (Pre = Pre-harvest, Harv = Harvested) at sites with *j* treatment type (I = impact, C = control). We were not able to calculate effect size 95% confidence intervals for studies other than our own due to data limitations.

periods—on the post-harvest growth of rockweed height ($P = 0.74$, $R^2 = 0.007$; Fig. 5A). In contrast, there was a positive effect of biomass change on height recovery ($P = 0.006$, $R^2 = 0.36$; Fig. 5B). In other words, sites that experienced greater harvest intensities were less likely to return to pre-harvest values of rockweed height by the end of the study. Unlike height, post-harvest growth of biomass tended to be higher at sites that experienced higher harvest intensities ($P = 0.01$, $R^2 = 0.33$; Fig. 5C). However, there was also a positive effect of biomass change on biomass recovery ($P = 0.006$, $R^2 = 0.37$; Fig. 5D), indicating that sites that experienced greater harvest intensities were less likely to return to pre-harvest values of rockweed biomass after one year of recovery.

4. Discussion

We conducted a Before-After Control-Impact study with commercially harvested rockweed beds at 38 sites across five regions in Maine to

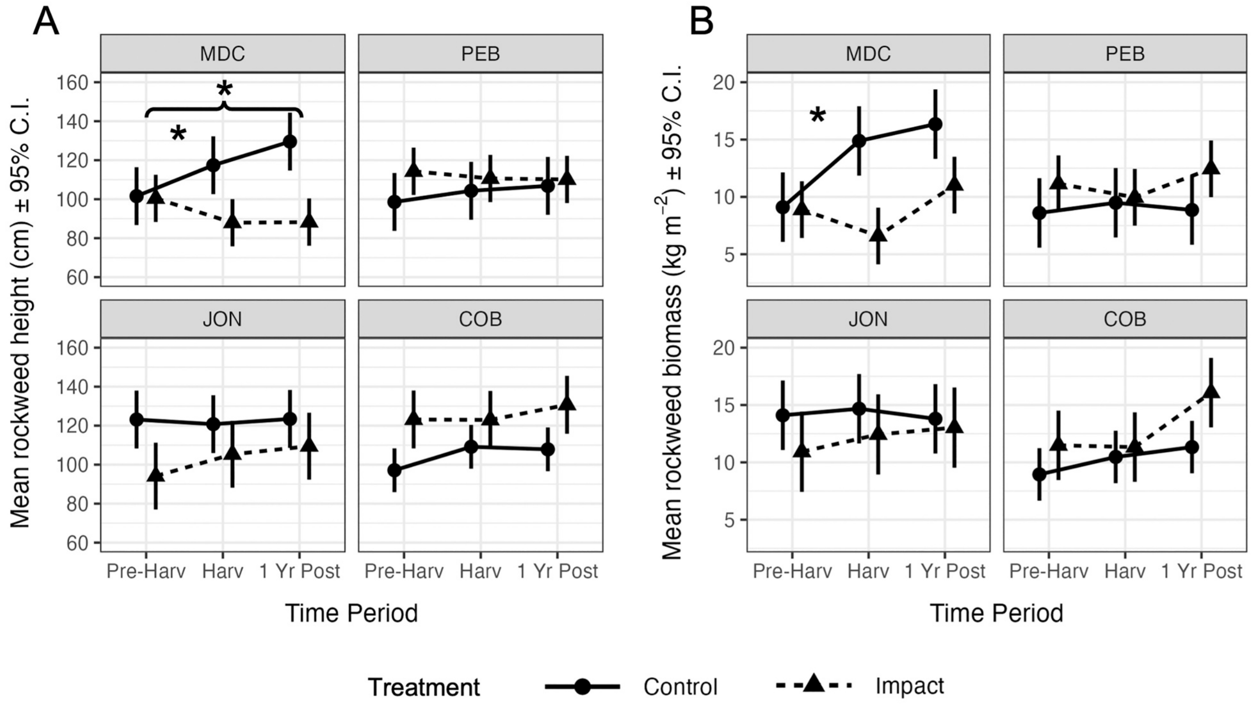

Fig. 4. Change in mean (A) rockweed height and (B) biomass across three time periods in each study region. Asterisks indicate statistically significantly differences ($\alpha = 0.05$) in the change in height or biomass between treatments for a given time interval. Abbreviations are as follows: Pre-Harv = Pre-harvest, Harv = Harvested, 1 Yr Post = One Year Post-harvest, MDC = Midcoast, PEB = Penobscot, JON = Jonesport, and COB = Cobscook.

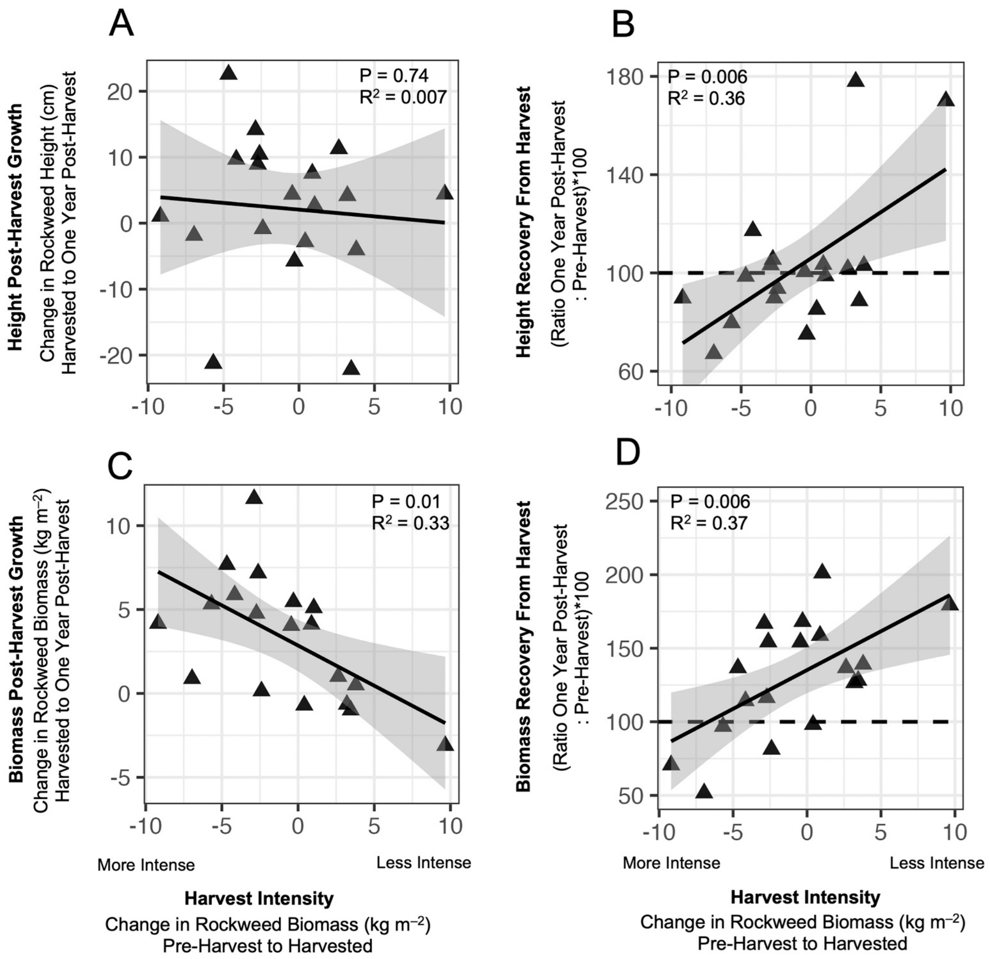

Fig. 5. Post-harvest growth rate and one-year recovery of rockweed height (A, B) and biomass (C, D) across a gradient of harvest intensity. Only impact sites are displayed. Dashed horizontal lines in panels B and D indicate 100% recovery to pre-harvest values. The gray shading around the regression lines represents the 95% confidence interval.

quantify the bed-scale impact and short-term (i.e., one year) recovery from rockweed harvest. Our findings support our prediction that harvest impacts are spatially heterogeneous at the scale of the rockweed bed, resulting in declines in mean rockweed height and biomass that were relatively small in their effect sizes relative to the effects on the most impacted rockweed individuals. These trends varied by region, with impacts most pronounced in Midcoast. Both rockweed bed characteristics increased during the year following harvest; however, there was no effect of treatment on the post-harvest growth in height, while there was a greater increase in post-harvest biomass at impact sites than control sites. Sites that experienced greater harvest intensities had lower recovery of height and biomass after one year, but overall, recovery was greater than we expected, with many impact sites showing >80% recovery in height and biomass. These findings highlight the ability of rockweed beds to initiate recovery soon after harvest. Lastly, the statistical support for an effect of treatment in several of our analyses was marginal ($0.10 > P > 0.01$) due to high between-site variation among treatments in our study.

4.1. Pre-harvest: regional comparison

Across a large portion of the Maine coast, mean rockweed height and biomass were relatively homogeneous. While there was high inter-site variation within regions, our results indicate that any regional differences in rockweed harvest histories or environmental conditions have not led to significant landscape-scale differences in rockweed bed height or biomass among our study sites that span the coast of Maine. Furthermore, the range of mean site biomass values in our study (3.53–21.76 kg m^{-2}) did not differ markedly from previous assessments of rockweed biomass in Maine (Rockweed Plan Development Team et al., 2014; see their Table 2).

Variance in rockweed height and biomass increased monotonically across hierarchical spatial scales, but in opposite directions for the two characteristics. For biomass, variance was larger within transects than within sites, but this phenomenon may have been a methodological outcome rather than a biological one. While transects were typically in areas where rockweed fully covered the substrate, we only weighed algae with holdfasts inside the quadrat. Quadrats that contained no holdfasts had biomass values of zero, which contributed to high variance in some transects. In contrast, measuring height was predicated on rockweed presence and mean values were not expressed in areal units. Variance in height within quadrats was less than half of the variance within transects and sites. This may be due in part to patterns of disturbance—natural or anthropogenic—that create variation in height at similar spatial scales to some of our sampling scales (e.g., transect, site), but not others (quadrat).

4.2. Pre-harvest to harvested: impact of harvest

The bed-scale impact of rockweed harvest on biomass was roughly twofold greater than on height. These findings are similar to other studies of commercial rockweed harvest in the western North Atlantic (Kay, 2015; Ugarte et al., 2006; Table 3). Taller rockweed individuals tend to have a greater proportion of their biomass in the upper canopy compared to smaller individuals (Ugarte et al., 2006), and as a result, the proportion of a mature individual's biomass and height lost during harvest may not be equal. The effects of differential harvest impacts on height and biomass for other species within the associated food web are likely taxa-specific. For instance, canopy height may be a more important bed characteristic for the youngest class of Common Eider (*Somateria mollissima*) ducklings that feed in rockweed habitats by dabbling in floating canopies at higher tides (Hamilton, 2001). Conversely, some macroinvertebrates such as isopods forage on rockweed epiphytes (Pavia et al., 1999) and may be most impacted by reductions in the surface area (i.e., biomass) of rockweed beds. Height and biomass may also provide different roles in modifying abiotic conditions in rockweed habitats. For instance, average air temperatures along the Maine coast are increasing (Maine Climate Office, 2022) and rockweed's ability to provide thermal refugia during low tide may be differentially impacted by reductions in height versus biomass.

The effect sizes of harvest on both height and biomass were lower in our study than in other studies for which we could calculate effect sizes (Table 3). Small, researcher-harvested plots (Walder, 2015) and locations with no minimum cutting heights (Kelly et al., 2001) unsurprisingly exhibited the largest effect sizes (only height assessed in both studies). Furthermore, minimum cutting height in Atlantic Canada (12.7 cm) is considerably shorter than in Maine (40.7 cm) and may explain some of the larger effect sizes in other studies (Kay, 2015; Ugarte et al., 2006). However, the effect size of harvest on biomass in our study (−0.28) was very close to the value (−0.29) in the only other study to conduct commercial harvest at the scale of the rockweed bed for which we could calculate effect sizes (Kay, 2015). Even though these studies occurred in locations with different minimum cutting heights, harvesters cannot precisely control the cutting height of algae at higher tides (Ugarte et al., 2006), and the exploitation rates may have been similar among comparable harvest efforts. Future rockweed harvest studies should provide data that allow for the calculation of effect sizes, which will enable managers to assess whether −0.3 is a typical effect size of harvest on biomass across regions and harvest methods.

The impact of rockweed harvest on both bed characteristics was variable across our four study regions. The southernmost region (Midcoast) was the only region to exhibit statistically significant declines in height or biomass among impact sites. Standardized effect sizes were roughly threefold stronger for both characteristics in this region (height: -0.28 [95% CI = −0.54 to −0.02]; biomass: -0.78 [95% CI = −1.16 to −0.41]) than for our study-wide estimates (Table 3). This region contained only mechanical harvest—while the other regions contained a mixture of mechanical and hand harvest—but it also was the only region harvested by two of the harvesting companies. These possible explanatory factors were not fully crossed in our study design and we therefore are unable to speculate as to whether the observed regional differences in harvest impacts were due in larger part to harvest method or company. The main objective of our study was to assess the average impact of harvest protocols presently operating in Maine. However, this result highlights the importance of monitoring a harvested resource across the full spatial scale of exploitation.

Lastly, we acknowledge the limitations of our sampling design given the fact that there were several impact sites that increased in mean height ($N = 5$) and biomass ($N = 8$) between the pre-harvest and harvested time periods. This is likely due to a lack of spatial overlap between transects and harvest at these sites. Despite this limitation, our study had high replication among each treatment (19 impact and 19 control sites), and we believe that treatment means (Fig. 3C and F) are informative of an average impact of harvest at the scale of the rockweed bed. It would be valuable to sample a small number of commercially harvested sites extensively (e.g., nine 10-m transects equally stratified by tidal height) and compare the estimates of impact (i.e., effect sizes) and associated confidence intervals to those obtained using our sampling methodology at the same sites. These data can test the ability of our methods to serve as a valid index of the average bed-scale impacts of rockweed harvest across a large number of sites.

4.3. Harvested to one year post-harvest: regrowth after harvest

One year after harvest, there was an effect of treatment on the post-harvest growth of rockweed biomass, but not height, indicating that the two rockweed characteristics responded differently immediately after harvest. These findings are generally congruent with results from other harvest studies that have evaluated rockweed height and biomass growth over comparable post-harvest intervals (Fegley, 2001; Ugarte et al., 2006). Mature, unharvested rockweed individuals tend to have a bimodal distribution of frond lengths, with a few large fronds that form the canopy and high densities of small, suppressed fronds that grow slowly due to low sub-canopy irradiance levels (Ang et al., 1996; Cousens, 1985). Rockweed canopies float on the surface of the water during higher tides and are the portion of the algae typically harvested (Ugarte et al., 2006). A common hypothesis is that rockweed harvest results in reduced canopies that allow growth of suppressed shoots due to increased light exposure (Baardseth, 1970; Cousens, 1985; Ugarte et al., 2006; Vadas and Wright, 1986). Furthermore, harvest can lead to increased lateral branching during regrowth that increases total biomass relative to canopy height (Boaden and Dring, 1980). While our study lacks data on the mechanistic underpinnings of these processes, our results support the idea that a significant proportion of post-harvest growth occurs below frond apices in the canopy. This likely explains why there was greater growth of biomass (weighing whole alga) than height (a maximal value) after harvest at impact sites. Our results might suggest that individual rockweed morphology becomes more dense during short-term recovery (Fegley, 2006), but we cannot definitively conclude this given that we compared site-level averages in height and biomass rather than explicitly measuring the morphological change of marked individuals.

Regional variation in post-harvest biomass growth was largely related to the magnitude of initial declines after harvest. This is apparent in the V-shaped trends at impact sites in the Midcoast and Penobscot regions (Fig. 4B). However, biomass increased considerably in Cobscook during the recovery interval, despite weak initial declines from harvest. Site-level data reveal that declines and gains in biomass between the pre-harvest and harvested time periods resulted in little average change in the region, but post-harvest gains at the two sites that lost biomass were particularly high (Fig. S2).

4.4. Pre-harvest to one year post-harvest: recovery from harvest

One year post-harvest, mean rockweed biomass fully recovered at impact sites relative to control sites, while mean height remained lower at impact sites. The ability of rockweed to recover a large proportion (> 80%) of its biomass soon after harvest, and even exceed initial values in some instances, has been observed widely across regions and harvest protocols (Baardseth, 1970; Fegley, 2001; Gendron et al., 2018; Hamilton and Nudds, 2003; Trott and Larsen, 2012; Ugarte et al., 2006). Despite greater biomass growth at sites with higher harvest intensities, it is important to note that the likelihood of complete height and biomass recovery after one year was lower at these more disturbed sites. As a result, if the goal is to maintain tall algal canopies, resource managers may need to allow longer recovery intervals at sites with higher harvest intensities, even in the presence of higher rates of biomass growth.

While rockweed height may not recover at the same rate as biomass, it is important to consider the ecological implications of a) the difference in height observed at the end of the study (control: 115.4 ± 4.3 cm, impact: 107.7 cm ± 4.3) and b) potential changes in the height-biomass relationship in harvested rockweed beds. Ultimately, resource managers must consider thresholds of 'recovery' that vary by resource stakeholder. For instance, rockweed harvesters or blue carbon initiatives may be most interested in the total biomass of a bed, while wildlife managers may focus on retaining bed characteristics (e.g., clump density) that benefit another taxon of interest.

Another critical factor to consider in rockweed management is the recovery interval between repeated harvests. Our study was extensive in spatial scale, but it was limited in temporal scale. It is unclear how observed trends would change in years two and three of recovery, and whether biomass at impact sites would continue to increase at a faster rate than height. We recognize that resource managers must think about harvest intervals and recovery of the resource at multi-year and decadal scales (e.g., Gendron et al., 2018; Lauzon-Guay et al., 2021). While we cannot say with certainty that the magnitude of rockweed harvest observed in this study is sustainable across repeated harvests and shifting environmental conditions, our data suggest that recovery, especially in biomass, can occur within a single year at the bed-scale using current commercial methods.

4.5. Conclusions

As ecosystem-based management (EBM) approaches become more widely adopted in marine ecosystems, it is important to consider management at several spatial scales. For instance, commercial rockweed harvesting in regions of Maine and Atlantic Canada is regulated at the scale of the individual alga (40.6 cm and 12.7 cm minimum cutting heights, respectively) and at the scale of the sector (17% annual biomass removal). Examining rockweed harvest impacts and growth rates in the patches of highest harvest intensity is critical for understanding how the target resource responds to disturbance. However, when harvest is spatially heterogeneous at the bed scale—as is the case with commercial rockweed harvest—quantifying harvest impacts at larger spatial scales can benefit resource management in EBM frameworks.

Our findings indicate that the impact of commercial rockweed harvest on two common bed characteristics (height and biomass) is smaller at the scale of the rockweed bed than at smaller scales that do not capture the spatial heterogeneity of harvest impacts. This study represents an initial step toward making EBM recommendations in these ecosystems, and the applicability of this perspective depends on the spatial scale at which resource managers target their actions. Highly mobile organisms such as birds and fish may utilize rockweed habitats at the bed scale or larger and respond to bed averages more closely than smaller scale impact estimates. Mobile macroinvertebrates, on the other hand, may relocate within beds to areas of either the highest or lowest harvest impacts, with potentially little changes in their abundance at the bed scale within some ranges of spatial heterogeneity. Further research is needed to understand the implications of our findings for other members of rockweed ecosystems, but our findings underscore the importance of taking bed-scale impacts into consideration. Future harvest impact studies should include recovery data of sufficient duration (e.g., 1–3 years) and prior harvest history whenever possible to understand how the various components of these ecosystems respond after repeated commercial harvest.

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CRediT authorship contribution statement

Elliot M. Johnston: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Visualization. **Hannah N. Mittelstaedt:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Laura A. Braun:** Investigation, Writing – review & editing. **Jessica F. Muhlin:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Brian J. Olsen:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition. **Hannah M. Webber:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Amanda J. Klemmer:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets and R code produced by this research are publicly available at: https://datadryad.org/stash/dataset/doi:10.5061/dryad.gmsbcc2s8

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2023.151869.

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