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RESEARCH

Sustainable management of *Fucus* beds – testing of UAV-assisted biomass mapping and evaluation of re-growth after harvest at individual and population level

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Abstract

Experimental harvests of *Fucus* beds were conducted at three sites in central Denmark applying four harvest treatments: apical tip harvest, full harvest, thinning harvest (full harvest of one third), and control (no harvest) to 1) determine correlations between *Fucus* areal cover and biomass harvest potential, and 2) examine effects of harvest treatment on biomass yield and recovery capacity. The study examined recovery capacity at individual algae scale through the capacity for generating new shoots and/or biomass regrowth, and at population scale using unoccupied aerial vehicles (UAVs) to estimate areal cover recovery. The results indicated significant variability in harvest yields and recovery responses, where full harvest provided the highest but variable yields, ranging from 0.33 to 5.85 kg FW m^{-2}. The full harvest also had the highest impact on individual algae biomass and population scale areal cover with observable slower recovery capacity compared to other harvest treatments. For the full harvest treatment, UAV-based assessments showed areal cover recovery six months post-harvest, whereas individual algae had not fully recovered one year after full harvest. The use of UAVs proved useful for monitoring the areal cover of *Fucus* beds, but less reliable in estimating the standing stock biomass. Future studies should focus on refining UAV-based methodologies to enhance accuracy and reliability in estimating areal cover and standing stock, and on large scale, long-term harvest impacts.

Keywords *Fucus* spp. · Phaeophyceae · UAV imaging · Sustainable resource management · Biomass composition · Heavy metals

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Introduction

Species of the brown macroalgae genus *Fucus* (Ochrophyta, Fucales, Phaeophyceae) are widespread in the littoral zone globally (Guiry and Guiry 2022). *Fucus* species are perennial and provide several ecosystem services (Heckwolf et al. 2021), and while the ecological importance of these species is increasingly emphasized, the existence of *Fucus* species is increasingly threatened by human activities (Kautsky et al. 1986).

There is a commercial interest in procuring biomass from *Fucus* species due to its multitude of uses spanning from food and agricultural purposes to the extraction of high value bioactives with applications in the nutraceutical, cosmetic and pharmaceutical industries (Catarino et al. 2018).

The demand for seaweed biomass can be met by either wild harvest, cultivation, or both. Whilst seaweed cultivation is an emerging and potential future sector in Europe (Araújo et al. 2021), the present European seaweed industry is still in its infancy contributing with less than 1% of the global seaweed production volume, and with a biomass supply that is 98% based on wild harvest (Araújo et al. 2021; FAO 2022). Seaweed harvesting methods span widely from small-scale hand harvesting to more efficient methods using boats, divers or raking instruments and finally to large-scale mechanical harvest methods (Mac Monagail et al. 2017). No commercial *Fucus* cultivation industry currently exists despite cultivation efforts and attempts to control the *Fucus* life cycle (Moss 1967; Fulcher and McCully 1969; McLachlan et al. 1971; Meichssner et al. 2020; 2021). In Europe, 37 companies are engaged in the harvest of fucoid species from wild stocks, but the harvested biomass volumes are not reported (Araújo et al. 2021).

The need for sustainable management strategies of wild seaweed resources is vital to prevent over-exploitation of coastal seaweed ecosystems and to secure their continued persistence over time, both with regards to the seaweed resource itself and all its associated ecosystems services (Rebours et al. 2014; Mac Monagail et al. 2017; Heckwolf et al. 2021). In contrast to other marine habitats such as seagrass meadows and boulder reefs however, only little is mentioned in international environmental governance regarding the protection of seaweed forests (Valckenaere et al. 2023).

When focusing only on wild sources of brown seaweeds, several countries, including Chile, Japan, South Africa, New Zealand, Ireland, Iceland, Scotland, Canada, United States, France, and Norway, have implemented harvesting regulations and/or management plans, albeit at varying degrees of comprehensiveness (Mac Monagail et al. 2017; Lotze et al. 2019; Camarena-Gómez et al. 2022). In some countries, the harvest of specific species is even prohibited, such as in Germany, where *Fucus vesiculosus* and *Fucus serratus* are categorized as threatened (vulnerable) species (Schories et al. 2013). In contrast, Denmark lacks any basis for sustainable or ecosystem-based management of wild seaweed resources and currently very limited harvesting regulations are in place (Anker et al. 2024).

The spatial distribution of seaweed beds is traditionally monitored using different techniques, ranging from in-water methods involving diver observations, photos, and/or video recordings, to air- and space-borne remote sensing methods involving aircraft or satellite-based technologies (Lønborg et al. 2022). While in-water methods provide data of very high spatial resolution, they are often highly limited in spatial extent, time-consuming, and labor- intensive. Traditional air- and space-borne remote sensing techniques, on the other hand, can map large areas at a lower cost per unit area (Klemas 2015), but they are often lacking the spatial resolution or specificity required to solve specific monitoring tasks. In recent years, unoccupied aerial vehicles (UAVs) have received attention due to their potential of bridging between the survey methods by performing monitoring tasks with a high spatial and temporal resolution over relatively large areas in a cost- and time-effective way (Rossiter et al. 2020a, b; Svane et al. 2021; Diruit et al. 2022; Borges et al. 2023; Lewis et al. 2023).

Few studies exist on the effects of harvesting of *Fucus* beds (Knight and Parke 1950; Keser et al. 1981; Creed et al. 1996), whereas several studies exist on the effect of harvest of other fucoid species such as *Ascophyllum nodosum* (Boaden and Dring 1980; Ingólfsson and Hawkins 2008; Seeley and Schlesinger 2012; Gendron et al. 2018; Lauzon-Guay et al. 2021).

Obviously, canopy height and standing stock biomass are negatively affected for both species when harvested by cutting, but both species can recover from annual harvest events, albeit with a faster regrowth of *F. vesiculosus* than of *A. nodosum* (Keser et al. 1981). Harvesting methods often involve cutting of all individuals within a larger area at a certain height above the substrate (Keser et al. 1981) or by harvesting a fraction of the standing individuals in a certain area (Creed et al. 1996). Whilst harvest strategy impacts the recovery of the individuals, populations, and associated ecosystems (Stagnol et al. 2013), it may also have an impact on the quality of the harvested biomass as observed in *F. vesiculosos* where concentrations of iron and cupper was shown to correlate with tissue age (at clean sites) (Stengel et al. 2005) and in *F. spiralis,* where non-reproductive thallus was shown to accumulate higher concentrations of heavy metals than receptacles (Munda 1986).

This study aimed for providing inputs for future management of *Fucus* beds, by 1) testing the hypotheses that 1) UAVs and image analysis can provide a method of mapping of *Fucus* areal cover, 2) *Fucus* biomass standing stock (harvest potential and biomass recovery) can be estimated via UAV estimates of *Fucus* areal cover, 3) the biomass from full harvest as compared to tips harvest would have a higher content of heavy metals due to a higher ratio of old to new tissue, and finally 4) that the most intense harvest method (full harvest) will result in the lowest recovery capacity, at individual as well as population scale. Four different harvest treatments were applied: tips harvest, thinning harvest, full harvest and a control with no harvest.

Materials & methods

Study and site description

This study combined data from two independent Danish research projects, Tang.nu and VildTang. Three sites, all subjected to commercial harvest of *Fucus* spp. were included in the two projects. Tang.nu included two sites in Aarhus Bay: Begtrup Vig (56°16'N 10°52'E) and Knebel Vig (56°13'N 10°28'E). VildTang included Knebel Vig (56°13'N 10°28'E) and Isefjorden (55°49'N 11°43'E) (Fig. 1). In Knebel Vig, there was no spatial overlap between the harvest activities of the two projects. The sites are in the following referred to as 'Begtrup', 'Knebel' and 'Isefjorden'.

Both projects investigated the use of UAVs for estimating the areal cover of *Fucus* beds and the potential for predicting the *Fucus* biomass harvest potential through correlations between the *Fucus* areal cover and harvested biomass from different harvest treatments. Further, the projects investigated the recovery potential of specific individuals of *F. vesiculosus* exposed to the different harvest treatments. In both projects, the individual recovery was assessed as the capacity to generate new shoots by measuring shoot numbers and lengths.

Further, in the VildTang project, individual algae biomass recovery was also measured by weighing, and the population (plot scale) recovery capacity was investigated by estimating the areal cover recovery following the different harvest treatments.

Harvest treatments and plot design

In both projects, similar harvest treatments were applied for both scales of investigation (individual and plots) (Fig. 2, bottom left): 1) full harvest: harvesting all individuals leaving only the proximal 10 cm of the frondage 2) thinning harvest: full harvest of approx. every third individual leaving the remaining two thirds of the individuals in an area

Fig. 1 Map of Denmark with the enlarged section showing the central part of Denmark. The red dots indicate the three study sites; Knebel Vig (Knebel), Begtrup vig (Begtrup) and Isefjorden

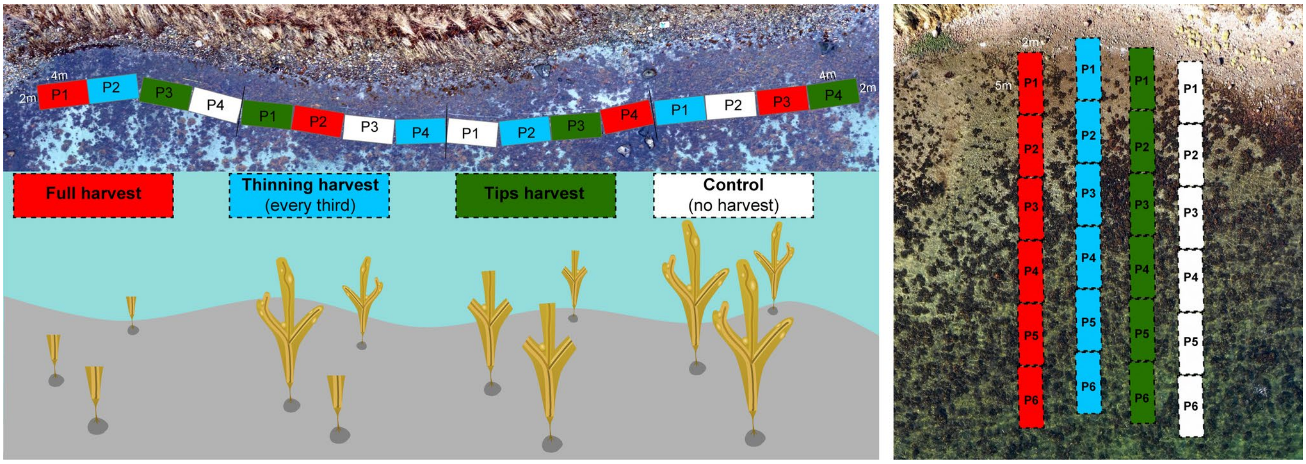


Fig. 2 Visualization of the harvest treatments and arrangement of harvest plots. **Bottom left**: the four different harvest treatments applied at both individual scale and plot scale: Full harvest (harvest of all individuals, only leaving the proximal 10 cm) in red. Thinning harvest (harvest of one third of all individuals, only leaving the proximal 10 cm, while leaving the remaining two thirds untouched) in blue. Tips harvest (harvest of all individuals at the apical tips) in green, and control (no harvest) in white. **Top left**: Experimental plots arranged in parallel to the coastline (Knebel 2020-22 + Isefjorden). **Right**: Experimental plots arranged perpendicular to the coastline (Begtrup 2018-19 + Begtrup and Knebel 2019)

untouched, 3) tips harvest: harvesting the apical tips (equivalent to the distal third) of all individuals, and 4) no harvest (control).

The first project (Tang.nu) included two campaigns, one in Begtrup in 2018 which investigated individual harvest responses only, and one conducted in both Knebel and Begtrup in 2019, investigating both individual and plot scale harvest responses. Here the experimental plots (2x5 m, 10 m^2) were located within four transects (2 m wide) which were arranged perpendicular to the coastline, one transect for each treatment (Fig. 2, right). This meant that all plots within the same transect received the same harvest treatment, hereby lamentably confounding the effect of transect and harvest treatment. At both locations however, the transects were arranged in areas with an overall homogenous substrate, depth profile and *Fucus* cover, which to some extent mitigated, but not eliminated, this confounding. The transects were set from the first occurrence of *F. vesiculosus* around the high tide level and stretching 30 m out in Begtrup (six 2x5 m plots) and 35 m out in Knebel (seven 2x5 m plots), resulting in a total of 24 and 28 experimental plots, respectively.

The second project (VildTang) included two campaigns, one in Knebel (2020-22) and one in Isefjorden (2021-22). During both campaigns, both individual and plot scale harvest responses were investigated. Here the experimental plots (2x4 m, 8 m^2) were arranged in parallel to the coastline at the depth of the apparent maximum *F. vesiculosus* coverage in order not to confound the effects of transect and harvest treatment (Fig. 2, top left).

Fucus harvest and recovery capacity

The *Fucus* recovery capacity in response to the different harvest treatments was investigated at both individual and plot scale (for a full overview of activities, see Table 1). The plot scale recovery capacity was investigated by assessing the surface area cover (%) recovery of the population within each experimental plot. The individual scale recovery capacity was investigated by examining new proliferating shoots (counting numbers and measuring lengths) of randomly selected and labelled *F. vesiculosus* individuals. All shoots were grouped according to their origin at either the holdfast, the stem or the cut induced by the harvest treatment (or other natural means of weathering). In the VildTang project, the biomass recovery capacity was also recorded, measured as the fresh weight (FW) of the labelled *F. vesiculosus* individuals.

During the Tang.nu project, plot scale harvests were carried out to quantify the exact harvest biomass yields (kg FW). The UAV-based estimates of *Fucus* areal cover (%) were carried out for each plot immediately before and after harvest. Further, two individual scale harvest experiments were carried out. Here, the recovery capacity was investigated by counting the numbers of new proliferating shoots and measuring their lengths at the end of each experiment.

During the VildTang project, combined individual and plot scale harvest campaigns were carried out in Knebel and Isefjorden. The campaigns were initiated by labelling individuals and performing harvest treatments at both scales. Harvest yields were quantified (kg FW) and UAV-based

Table 1 Overview of all harvest and UAV activities in the two projects. Types of activities: Harvest (H), Unmanned aerial vehicle imaging (UAV), Visual inspection of areal cover (%) (V), Weighing of individuals (W), Counting and measuring of shoots (C). Project T (Tang.nu.) & Project V (VildTang)

Scale	Project	Year	2018	2019			2020			2021				2022	
		Month	11	4	9	11	5	8	11	3	5	9	11	3	5
Plot	T	Begtrup	H+UAV												
	T	Knebel, Begtrup		H+ UAV											
	V	Knebel					H+V	UAV	UAV	UAV	UAV	UAV		UAV	
	V	Isefjorden								H+UAV	UAV	UAV	UAV		H+UAV
	V	Knebel							H+V+UAV	H+V+ UAV		H+V+ UAV			
	V	Isefjorden								H+V+UAV	H+V+ UAV	H+V+ UAV			
Individual	T	Begtrup	C	C											
	T	Knebel, Begtrup			C	C									
	V	Knebel					W+C	W+C	W+C	W+C	W+C		W+C	W+C	
	V	Isefjorden								W+C	W+C	W+C	W+C		W+C

estimates of areal cover (%) before and after harvest were carried out. However, due to Covid-19 restrictions at the initiation of the Knebel campaign, the areal cover (%) before and after harvest treatments could not be estimated by UAV, and was instead estimated by two independent experts visually estimating the *Fucus* cover of each designated experimental plot by walking through the plots and visually estimating the areal cover of the 2x4 m (8 m^2) plots, marked by concrete tiles. Following, UAV-based estimates of *Fucus* cover (%) were made at regular intervals at both sites to follow the plot scale recovery capacity. The individual scale harvest recovery capacity was investigated by recovering the labelled individuals, counting the numbers of new proliferating shoots, measuring shoot lengths and weighing the biomass at regular intervals (Table 1).

Additionally, 81 small-scale 'calibration' plots were included in the VildTang project to also estimate the biomass recovery. All experimental plots (n=16) in Isefjorden were exposed to the full harvest treatment at the end of the campaign. Hereby, the initial harvest yields could be compared to the final area-specific biomass yield in each plots after a whole growth season.

Plot scale correlations between harvested biomass and UAV based estimates of areal cover

Harvested biomass

The drained biomass (kg FW) harvested from each plot was weighed prior to transportation to the laboratory for drying and further handling. In the Tang.nu project, the biomass was pooled for all fucoid species present, i.e. *F. vesiculosus, F. serratus* and *F. spiralis.* In the VildTang project, the harvested biomass was almost entirely *F. vesiculosus* and the few individuals of other fucoid species were selectively excluded.

UAV methodology

Two different unoccupied aerial vehicles (UAVs) and flight missing planning softwares were used in the two different projects:

In the Tang.nu project, a consumer grade low weight quadcopter of the type DJI Mavic 2 Pro was used. This UAV has a 20 million effective pixels 1-1/2.3-inch CMOS sensor-equipped RGB-camera with an 78.8° field of view at 28 mm aperture (35 mm format equivalent). The flight mission planning software DJI Ground Station Pro was used in the Tang.nu project to plan and execute the flights with a flight speed of 3 m s^{-1}, a flight altitude of 20 m and an image front and side overlap of 80%, corresponding to a Ground Sample Distance (GSD) of 5.5 mm and single image dimensions of 30x20 m.

In the VildTang project, the UAV platform used was a consumer grade low weight quadcopter of the type DJI Phantom 4 Pro. The payload of this UAV is a 20 million effective pixels 1-inch CMOS sensor-equipped RGB-camera with an 84° field of view at an 8.8 mm/24 mm and f. 2.8–11 aperture. The flight mission planning software UgCS ver. 4.7.685 was used to plan and execute the flights conducted, with a flight speed of 3 m s^{-1}, a flight altitude of 30 m and an image front and side overlap of 75%, corresponding to 8.22 mm GSD and single image dimensions of 45x30 m.

Image processing and analysis workflows were identical in both projects. Single-image-georeferenced orthomosaics were created for each flight date using Agisoft Metashape Professional ver. 1.7.4. A pixel-based maximum likelihood classification was performed in ArcGIS Pro 2.9.2 on the red, green and blue bands of the orthomosaic to create a classified raster as output. For each classification, 10 circular training samples with a diameter of 1 m were selected from the created orthomosaic for each of the two classes of *Fucus* and substrate based on expert knowledge. Areal cover (m^2) of *Fucus* within the plots was determined based on the output raster and used with plot size (m^2) to calculate *Fucus* cover (%).

To assess the accuracy of the classified raster outputs, the producer accuracy, user accuracy, and overall accuracy were calculated in a confusion error matrix based on 100 validation points attributed to each class (Supplementary Table 1). The validation points were selected by stratified random sampling from the obtained images and adjacent to the experimental plots while excluding areas used for training. Validation points were attributed to the classes *Fucus* spp. and substrate based on expert knowledge. The accuracy assessment was performed with the ArcGIS Pro built-in accuracy assessment tool in the Spatial Analyst toolbox. For an overview of UAV activities, see Table 1.

Calibration plots

In the VildTang project, 81 extra small-scale plots in areas outside the experimental transects were included to add more data on the correlation between *Fucus* cover (%) and harvest yield (kg FW), whilst also allowing for a comparison of the UAV-based and visual techniques for *Fucus* cover (%) estimates. These 'calibration plots' were defined by randomly distributing sinking rings with an area of 0.8 m^2 in the areas adjacent to the larger experimental plots in *Fucus* beds of varying apparent coverage. Within the rings, the *Fucus* area cover was assessed both by UAV and visual expert assessment. Following the *Fucus* cover estimates, the full harvest treatment was applied for all calibration plots (n=81) and the drained biomass was weighed (kg FW). The 81 calibration plots were distributed in time and space, with 45 of the calibration plots in Knebel and 36 in Isefjorden, and with 27 assessed during spring (March-May) and 54 during late summer/autumn (August-November).

Individual scale estimates of re-growth

Randomly selected *F. vesiculosus* individuals were exposed to one of the four different harvest treatments previously described. The individuals were labeled using numbered (HellermanTyton, PVC cable markers) cable ties (Branford, nylon cable ties or similar) and following placed back into the field site at the similarly treated plots. In the Tang.nu project, all labeled individuals exposed to the harvest treatments (n=10 for each of the four harvest treatments) were naturally attached to a sizeable rock for a total of 40 individuals. In the VildTang project, the labeled individuals exposed to the harvest treatments (n=9 for each harvest treatment) were artificially attached to concrete tiles using rope, in sets of three individuals per tile, for a total of 36 individuals. This was to include their weight as a recovery response parameter, as they could be removed from the rope, weighed and reattached.

The individual harvest response measurements consisted of counts (number of shoots per individual) and length (mm per shoot) measurements of new proliferating shoots. These shoots were grouped by their origin from either holdfast, stem or the cut caused by the harvest treatment (or cuts otherwise induced by wave action and other natural means of weathering) to follow the physiological response. In the Tang.nu project, these counts were carried out several months after the harvest treatments, whereas in the VildTang project, these counts were carried out at regular intervals. In the VildTang project, the individuals were untied from the tile, dry-blotted and weighed (g FW) to follow changes in individual standing stock biomass. These weight measurements were conducted before and after harvest treatment and at regular intervals. For an overview see Table 1.

Fucus biomass composition

For *F. vesiculosus*, biomass composition analyses were conducted on plot harvest samples to determine possible differences in biomass quality due to harvest treatments or harvest timing (seasonality). No biomass analyses were conducted on the individually treated and labelled specimens. Three independent biological replicate samples were analysed per harvest treatment for the campaigns included.

Dry matter, ash, carbon, nitrogen and phosphorus

The biomass dry matter (DM) content, ash content and tissue concentrations of carbon (C), nitrogen (N) and phosphorus (P) was determined as in Boderskov et al. (2023).

Heavy metals

For arsenic, cadmium, mercury and lead analyses, aliquots of 2–300 mg dry seaweed powder were digested in 4 mL Milli-Q water/4 mL Merck Suprapure HNO_3 mixtures in an Anton Paar Multiwave 7000 microwave oven (220°C: 30 min). Series of procedural blanks, duplicates, and replicates of the Certified Reference Material (CRM) (NIST 3232 Kelp Powder (*Thallus laminariae*)) were prepared along with the samples for analytical quality assessment and control. Digestion solutions were subsequently diluted with Milli-Q water, weighted, and analyzed using either an Agilent 7900 Inductively Coupled Plasma Mass Spectrometer (ICP- MS) or an iCAPq ICP-MS (Thermo Fischer, Germany).

Iodine

For iodine analyses, a modified version of the EN 15111:2007 method (EN 15111:2007) was applied. In short, aliquots of 150–200 mg seaweed powder were transferred to pre-weighed 50 mL polypropylene centrifuge tubes. Series of procedural blanks, duplicates, and replicates of CRM NIST 3232 Kelp Powder (*Thallus laminariae*) were prepared for analytical quality assessment and control. Five mL of Milli-Q water was added to each tube and the solutions thoroughly mixed. One mL of 25% tetramethylammonium hydroxide (TMAH) was added, the solutions mixed carefully, and the tubes closed with a lid. The samples were heated at 90±3˚C for 3 h. After 1.5 h the tubes were briefly taken out and mixed to ensure that no material stuck to the bottom. After cooling, the samples were diluted to approximately 50 mL with 0.5% TMAH, mixed again, and weighted. A 5 mL aliquot of each sample was transferred to centrifuge tubes, centrifuged for 5 min, and the supernatant diluted with 0.5% TMAH to an iodine concentration below 100 μg L^{-1}. The solutions were finally analyzed for iodine using an iCAPq ICP-MS with tellurium as internal standard.

Statistics

Effect of harvest treatments on plot harvest yields across all locations and surveys were tested using a Kruskal-Wallis test due to lack of normality and homogeneity of variance in data. A linear mixed model (LME) ANOVA was used to test differences in areal cover (%) with treatment, date and their interaction as fixed effects, and with the different plot replicates as a random effect for Knebel 2020–2022 and Isefjorden which included repeated measurements. A regular two-way ANOVA was used to test for differences in areal cover (%) before and after harvest treatment in Begtrup and Knebel 2019, with log transformation of the areal cover (%) in Begtrup to achieve normality and homogeneity of variance. Individual level or single algae measurements of the different harvest treatment responses, shoot and biomass development were not treated statistically. For all data sets, a normal distribution of data was tested using a Shapiro-Wilk test and a homogenous variance in data was tested using Bartlett's test, both supported by diagnostics plots. Post-hoc analyses of statistically significant effects were conducted using applicable pairwise comparisons (Bonferroni and Tukey's). Unless specifically mentioned, all data are presented as mean values ± 1 SE and all statistical testing use a significance level of 0.05 and a trend level of 0.1. All data analyses were conducted in R (R Core Team 2021). For statistics summary tables, see supplementary Tables 2 and 4.

Results

Harvest effects measured at plot scale

The biomass harvest yields from the experimental plots were highly variable both between and within harvest treatments and among the different harvest events, yet with a significantly ($P < 0.001$) higher yield for the full harvest across all locations and harvest events and with no significant difference ($P = 1$) between tips or thinning harvests (Fig. 3. Supplementary Table 2.a).

In Isefjorden, all plots were exposed to a second full harvest 14 months after the first harvest, which resulted in significantly higher yields when compared to the first full harvest (4.7±0.3 kg m^{-2} as compared to 2.7± 0.2 kg m^{-2}, P =0.0028 (Supplementary Table 2.b)). However, separating these second harvest yields by the type of harvest treatment originally applied and testing for differences, indicated no significant difference in second harvest yields between the plots which was exposed to the full harvest twice ($P = 0.46$).

UAV based estimates of *Fucus* areal cover (%)

The *Fucus* areal cover was significantly affected by harvest method at all locations. In Begtrup (P=0.042. Supplementary Table 2.c)), few data for control plots (n = 2) limited the statistical testing to effects between the different harvest methods (n = 7), where pairwise comparisons (pre/post-harvest) only showed a significant difference in areal cover between tips and full harvested plots ($P = 0.039$). In Knebel 2019 (P=0.024. Supplementary Table 2.d), similar comparisons showed significant differences between full harvest, tips and thinning plots on the *Fucus* areal cover. In the Knebel 2020-22 survey

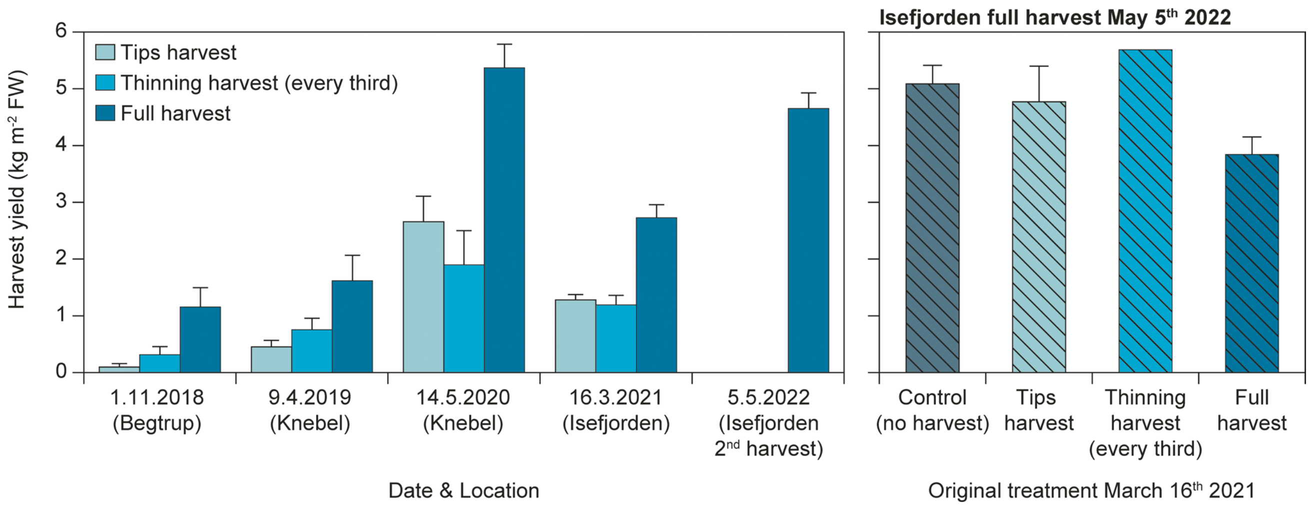


Fig. 3 Harvest yields (kg FW m^{-2}) of *Fucus* in the experimental plots subjected to different harvest treatments during the different harvest events in Begtrup, Knebel and Isefjorden. The second harvest event in Isefjorden is shown in more detail, showing the harvest yields separated according to the original harvest treatment of the plots. Data are given as mean values ± 1 SE (n=4 - 12 depending on site and time). Note that n=1 for the second harvest in the Isefjorden plots that were originally exposed to the thinning harvest. Statistics are given in Supplementary Table 2.a

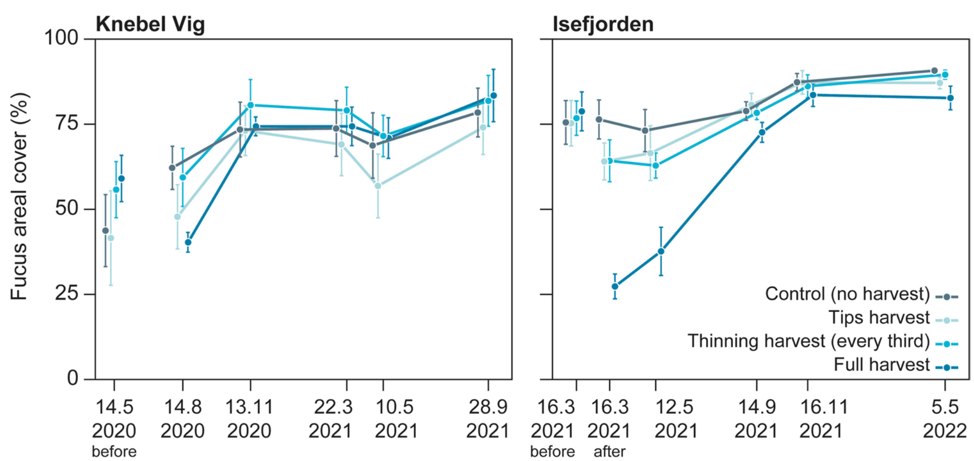


Fig. 4 Areal cover (%) of *Fucus* as a consequence of the different harvest treatments estimated from the UAV imagery classification during the campaigns in Knebel and Isefjorden. Note that before-harvest data for Knebel in May 2020 are visual estimates of areal cover (%) and that after-harvest data is not available. Data are shown as means ± 1 SE (n = 4)

(p=0.0052. Supplementary Table 2.e), which also included repeated measurements of areal cover, there also was a significant effect of time ($P < 0.001$) (Fig. 4). Here, the effect of harvest treatment on areal cover of *Fucus* was significant only on the 14 August 2020. Temporal effects could be seen within all groups throughout the survey, as biomass cover was generally higher during winter and spring than during summer and autumn. In Isefjorden, which also included repeated measures, the significant effect of harvest treatment on *Fucus* areal cover was documented only for the full harvest immediately after harvest, and on 12 May 2021 ($P < 0.001$. Supplementary Table 2.f). A significant effect of time was also evident, as the areal cover increased after the harvest event, here there were no observable seasonal patterns but just a steady increase in areal cover (%) (Fig. 4). Recovery of the *Fucus* areal cover (%) for the fully harvested plots was observed on 13 November 2020 for Knebel and on 14 September for Isefjorden, roughly 6 months after the harvest event in both cases.

Correlations between UAV-based estimates of *Fucus* areal cover (%) and harvest yield

No significant correlation was found for tips harvest biomass yields ($P = 0.31$) (Fig. 5). In contrast, significant positive correlations were found between the pre-harvest *Fucus* areal cover and both the full ($P > 0.001$) and the thinning ($P = 0.012$) harvest biomass yields.

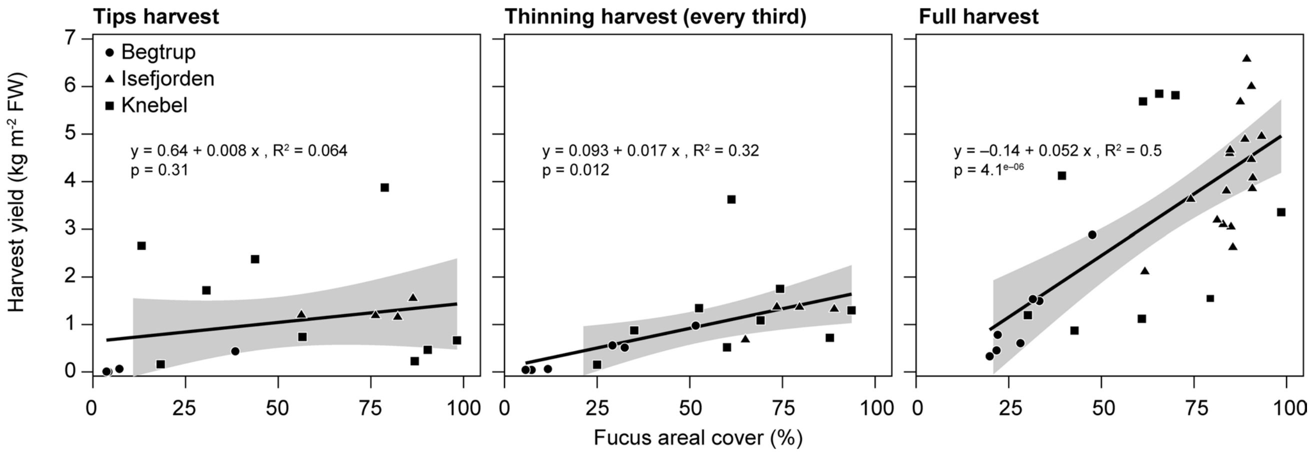


Fig. 5 Correlations between the *Fucus* pre-harvest areal cover (%) and harvest yield (kg FW m^{-2}) for the experimental plots subjected to the three different harvest treatments (tips, thinning or full harvest) for all campaigns in Begtrup, Knebel and Isefjorden. Linear regression equations and model fits are shown (grey areas indicate 95% confidence intervals)

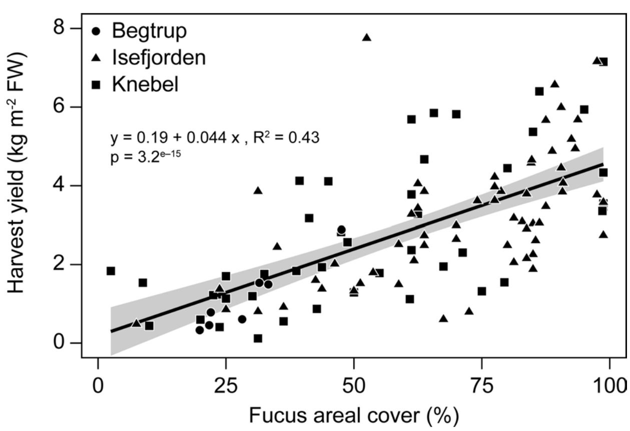


Fig. 6 Correlation between *Fucus* pre-harvest areal cover (%) and harvest yield (kg FW m^{-2}) for the fully harvested experimental plots and calibration plots for all campaigns in Begtrup, Knebel and Isefjorden. Linear regression equations and model fits are shown (grey areas indicate 95% confidence intervals)

Calibration plots and combined *Fucus* cover (%) and harvest yield correlation

The inclusion of the 81 calibration plots - additional points, each representing a specific combination of *Fucus* harvest yield and the pre-harvest areal cover - improved the significance level of the linear regression between the UAV estimated *Fucus* areal cover and biomass yields without drastically altering the model fit (Fig. 6). Highly significant relationships with good model fits could be achieved by making linear regressions between harvest yield (kg m^{-2} FW) and *Fucus* areal cover (%) for specific combinations of locations, treatments, and dates (Supplementary Fig. 1). Still, there was a large variation in how well the UAV-based areal cover explained the biomass harvest yield: When applying full harvest, between 25–93% of the variation in biomass yield was explained by the UAV-based areal cover, when applying thinning harvest, 25–98% of the variation was explained, and when harvesting of the tips, 16–99% of the variation in biomass yield was explained by the UAV- based areal cover (Supplementary Fig.1). There was no significant difference ($P = 0.135$) between the visual and UAV-based estimates of *Fucus* areal cover (%) (Supplementary Table 2.h)

UAV image analysis and accuracy assessment

The overall accuracies of the classifications performed on the images obtained from Knebel ranged between 79% and 88% with an average of 83% (Supplementary Table 1). The overall accuracies obtained from Isefjorden ranged between 84% and 95% with an average of 89%.

The largest source of error resulting from the classification of the images obtained in Knebel was the class "substrate" being wrongly classified as *Fucus*. While the producer accuracy of *Fucus* was >90% in four out of five images obtained in Knebel, it reached only 75% in the classification of the image obtained in May. A similar pattern was observed for the Isefjorden images, where the three images obtained in May had the lowest overall accuracies (<86%) due to low producer accuracies of *Fucus* ranging between 71% and 82%.

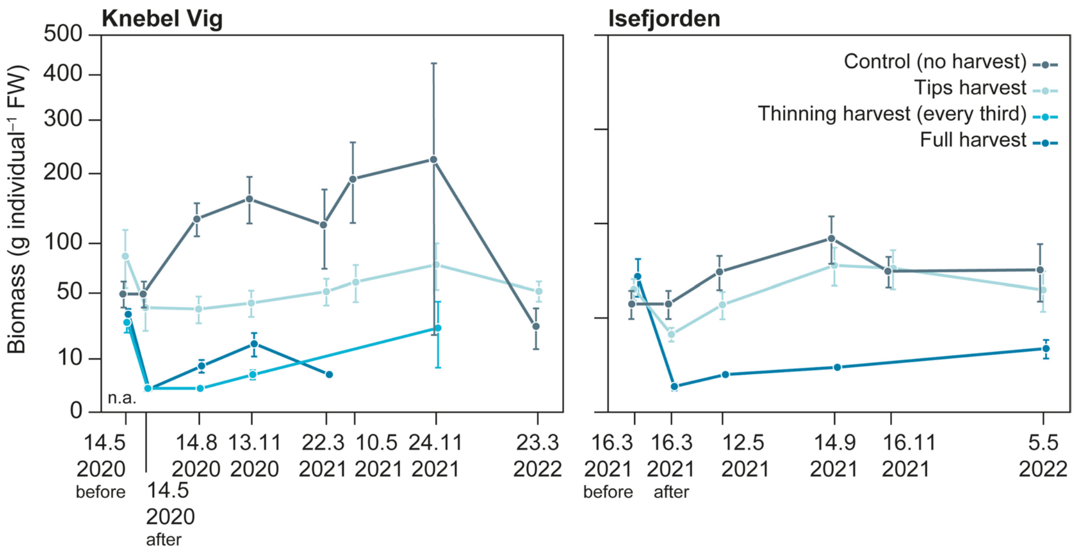


Fig. 7 Changes in individual *F. vesiculosus* biomass (g FW individual^{-1}) as consequence of the different harvest treatments (tips, thinning or full harvest) during the campaigns in Knebel and Isefjorden. Data are mean values ± 1 SE (n = 1–10) on a square root scale

Harvest effect on individual scale

Biomass harvest recovery capacity

Despite large variations between individuals and loss of replicates throughout the experimental period, the development in individual biomasses over time showed that individuals exposed to any of the various harvest treatments generally remained lower in biomass than the controls (Fig. 7).

For both Knebel and Isefjorden, the fully harvested individuals did not recover in biomass during the investigation periods, whereas individuals exposed to the tips harvest treatment showed some increase in individual biomass and ended up comparable to the control. The thinning harvest treatment, carried out in Knebel, resulted in an individual biomass development very similar to the full harvest, although with a slower recovery during the first six months. Control individuals from both locations showed similar seasonal patterns in biomass development as was observed on plot scale (Figs. 4 and 7). Loss of parts of, or whole, marked individuals was observed for both locations.

Shoot - number and length - harvest response

Fucus vesiculosus continuously produced new shoots of varying lengths from both the cut areas, the sides, and the disc. These responses were documented for individuals subjected to harvest treatments as well as for some of the controls subjected to natural weathering (Figs. 8 and 9A+B).

The overall trend was that harvesting of the tips resulted in the highest number of new shoots, while shoot length dynamics seemed more dependent on location and season.

The documentation of shoot responses in Begtrup was affected by a loss of marked individuals and entire treatments. Despite differences in experimental duration, 159 days (2018-19) and 70 days (2019), the shoot number was ca. 10 times higher in the shorter 2019 campaign, whereas shoot lengths were about half the size in the 2019 campaign, when considering the tip harvest treatment. For both of the Begtrup campaigns, the highest shoot numbers originated from the tip harvest and the longest shoots were the side shoots.

In Knebel new shoots originated initially mostly from the cut areas, but this changed toward a higher appearance of shoots from both the cuts and the sides by the end of the survey and generally with lower shoot numbers from the discoid holdfasts. Shoot numbers varied throughout the survey, with indications of a slight decrease in March 2021 and 2022 and the highest overall shoot numbers from the tips harvest throughout the survey. The longest shoots were observed from the cut areas and the tips treatment, but shoot length increased overall throughout the survey, with an intermittent decrease during spring 2021.

In Isefjorden some marked individuals had new shoots – mainly from the disc - already from the beginning of the experiment. Throughout the survey, a more even distribution of numbers of shoots between disc, side and cut shoots was observed and there was a pattern of the tip harvest generating the highest total number of new shoots. The shoot lengths increased steadily over time and were similar between treatments and origin.

New *F. vesiculosus* shoots proliferating on the concrete tiles used in the experimental setup were observed in both Knebel and Isefjorden.

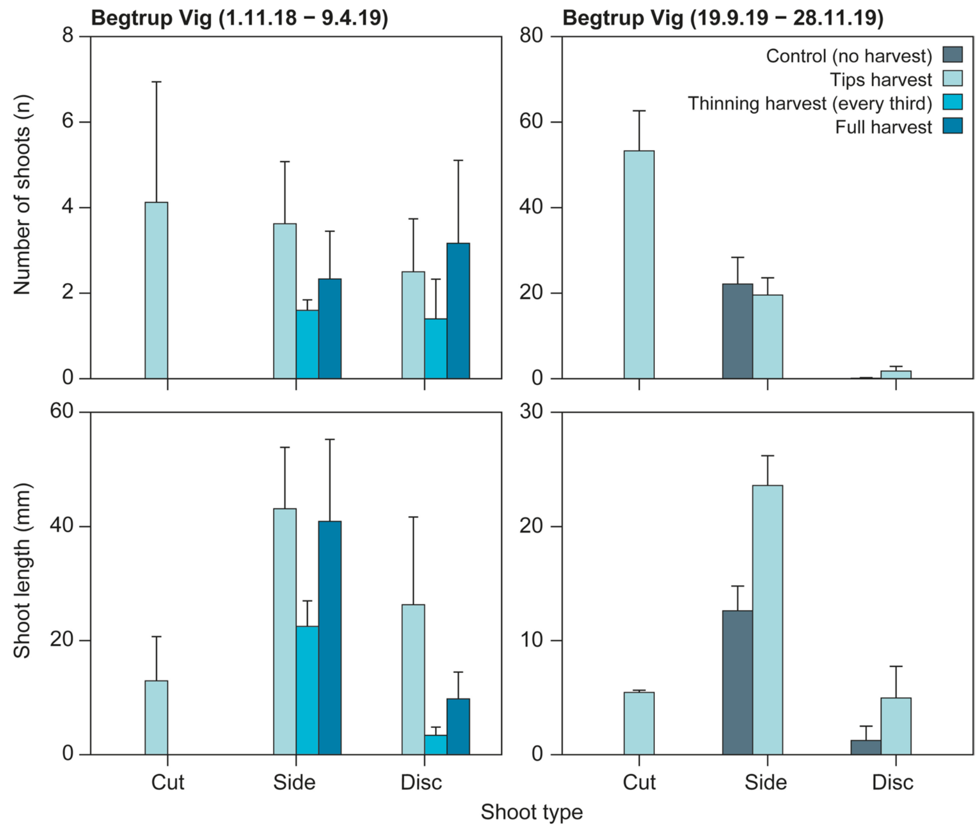


Fig. 8 The shoot number (n) and shoot length (mm) for proliferation shoots originating from either the harvest- or naturally induced cut, the side or the discoid holdfasts of *F. vesiculosus* individuals subjected to the different harvest treatments (tips, thinning or full harvest) for the two harvests conducted in Begtrup. Data are mean values ± SE (n = 1–10)

Biomass composition

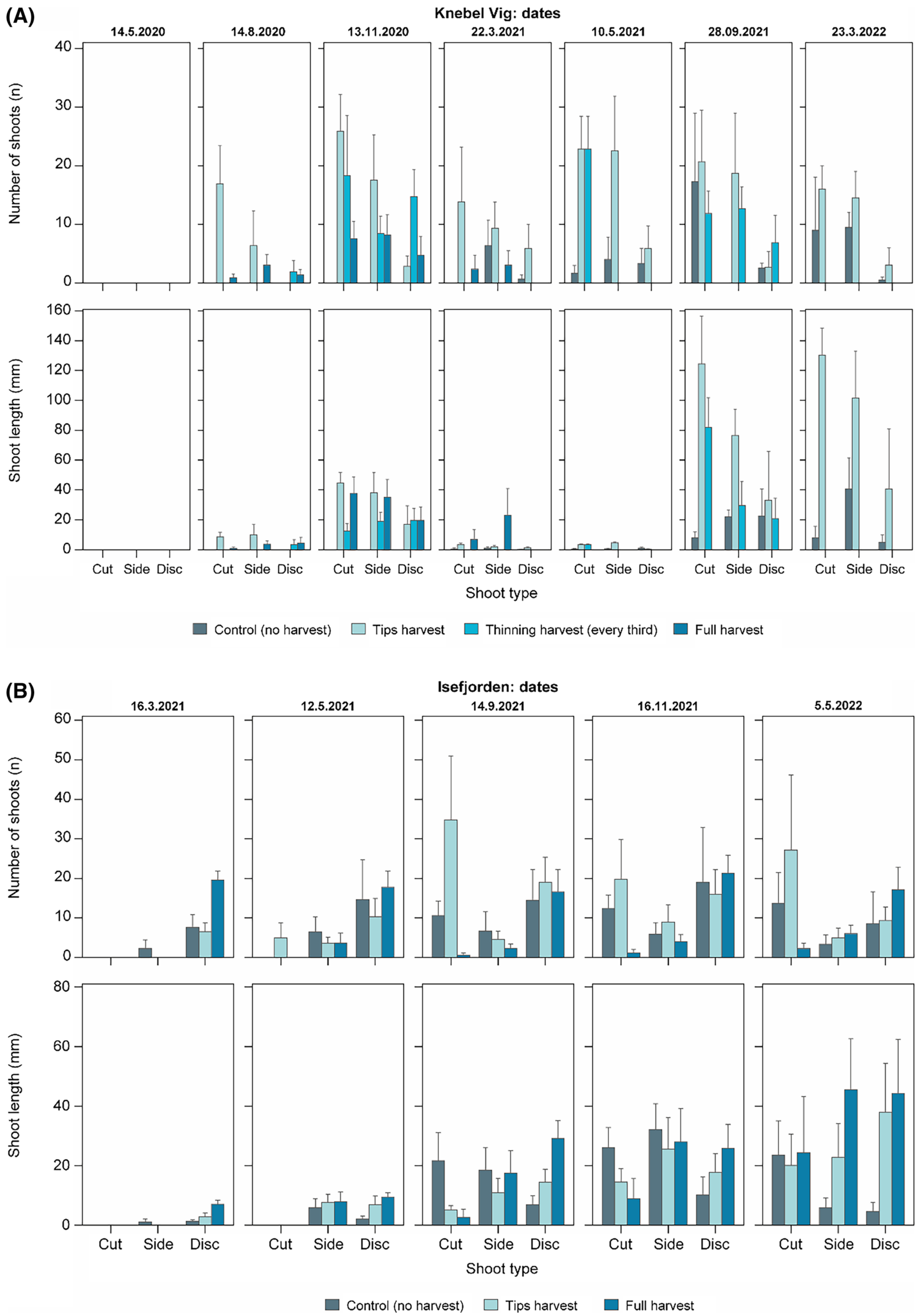
The tissue concentrations of DM, ash, C, N, P as well as critical elements (As, Cd, Hg and Pb) and iodine (I) are given in Supplementary Table 3. No significant differences in tissue composition were observed between harvest methods, season and sites, except for overall higher concentrations of Hg observed in tips (new) tissue ranging from 0.25 – 0.41 mg kg^{-1} DM compared to full harvest (total) tissue ranging from 0.11 – 0.28 mg kg^{-1} DM (p=0.005) (Supplementary Table 4). There was also one record of a higher Pb concentration in the tips (new) tissue at 5.01 ± 0.85 mg kg^{-1} DM as compared to the full harvest (total) tissue at 0.54 ± 0.18 mg kg^{-1} DM for a single location (Knebel) on one sampling occasion (14 May 2020).

Discussion

Using UAVs for mapping of *Fucus* biomass cover and harvest potential

The study confirmed that UAV-derived imagery can be a valuable tool for estimation of *Fucus* areal cover, as also concluded by Svane et al. (2021) and Borges et al. (2023). The analysis of the images using a well-established and easy to apply pixel-based supervised maximum-likelihood classification showed good results on all obtained images and can therefore be suggested as a tool for estimating the biomass cover. Regarding the biomass cover, the largest source of error resulting from the classifications of the images obtained in Knebel was the class substrate being wrongly classified as *Fucus*. This was not the case, or at least not with the same consistency, for the Isefjorden site. A possible reason for that could be the higher number of stones present at the Knebel study site, while sand dominated the substrate in Isefjorden. Stones can resemble *Fucus* in their spectral values while sand is brighter and therefore stands in a greater contrast to *Fucus*. Another interesting observation was made concerning the producer accuracies of *Fucus* resulting from images obtained in May at both study sites in the Tang.nu project. Here, the accuracy assessment showed larger amounts of misclassified *Fucus* compared to images obtained during other months. An explanation for this could be the brighter color of fresh *Fucus* tissue in the plant tips. The spectral values of brighter tissue are closer to those of the substrate, especially of sand.

Not represented in the confusion error matrix, but observed by the authors, were misclassifications of 30–40% within fully harvested plots. Because the accuracy assessment was conducted on the classifications of the entire study sites, this observed misclassification occurring only in fully harvested plots was not represented in the confusion error


(A)
Knebel Vig: dates
14.5.2020
14.8.2020
13.11.2020
22.3.2021
10.5.2021
28.09.2021
23.3.2022
Number of shoots (n)
Shoot length (mm)
Cut Side Disc
Shoot type
Control (no harvest)
Tips harvest
Thinning harvest (every third)
Full harvest
(B)
Isefjorden: dates
16.3.2021
12.5.2021
14.9.2021
16.11.2021
5.5.2022
Number of shoots (n)
Shoot length (mm)
Cut Side Disc
Shoot type
Control (no harvest)
Tips harvest
Full harvest

◂**Fig. 9** The shoot number (n) and shoot length (mm) for proliferation shoots originating from either the harvest- or naturally induced cut areas, the side areas or the discoid holdfasts of *F. vesiculosus* individuals subjected to the different harvest treatments (tips, thinning or full harvest) for the two surveys conducted at Knebel (**A**) and Isefjorden (**B**). Each subplot represents a specific date. Data are mean values ± SE (n = 1–10)

matrix due to the relatively small area of fully harvested plots compared to the whole site. The misclassification in the fully harvested plots was most likely caused by the leftovers of the *Fucus* individuals, such as the holdfast and stem, sharing similar spectral values as the full individuals. As this was a persistent observation throughout the full harvest plots, it could be treated as a known error when applying the method to reduce uncertainty of estimates.

Another way of countering this issue of misclassification could be the application of other image analysis methods than the pixel-based method used in this study. Object-based image analysis (OBIA) has for example on many occasions produced better results in the classification of high spatial resolution data than the traditional pixel-based methods (Blaschke 2010; Weih and Riggan 2010; Myint et al. 2011; Whiteside et al. 2011). This approach is especially useful when working with images of a very high spatial resolution where an object, in this case a *Fucus* individual, is depicted by multiple pixels and therefore making it impossible for a single pixel alone to reflect the characteristics of the individual (Blaschke et al. 2014).

While confirming that UAV imaging can be used for mapping of the areal cover of *Fucus* beds, the relationship between the *Fucus* cover (%) and harvest yield was highly variable, with the UAV-based areal cover explaining between 16–99% of the variation in biomass yield. This finding was in contrast to the conclusions of Svane et al. (2021) and Borges et al. (2023), that both found UAV-based estimates of *Fucus* standing stocks reliable, albeit underestimating the biomass by 36% (Borges et al. 2023). Hence, the value of UAV-based *Fucus* mapping as a tool for standing stock and biomass harvest yield predictions appears to vary between locations.

Harvest effects on plot scale

In the experimental plots, a substantial variability in *Fucus* harvest yields was observed, which was most notably influenced by the harvest treatment and the standing stock biomass within the plots. Not surprisingly, the biomass yields were significantly lower when employing either the tip or the thinning harvest methods than when performing a full harvest.

The yields observed in the present study (ranging from 0.003 to 5.85 kg FW m^{-2}) were comparable to previous findings ranging from 0.23 – 3.75 kg FW m^{-2} in a study by Keser et al. (1981) and ranging from 3 – 12 kg FW m^{-2} in a study by Knight and Parke (1950). Minor differences in harvest methods and regrowth time limit a direct comparison. The depth distribution of the *Fucus* belt is usually quite narrow in the Danish Kattegat region (Nielsen et al. 2022) and the varying orientation of the experimental plots in the current study (perpendicular or parallel to the coast) likely influenced the results. The yields were typically lower and more variable in plots oriented perpendicular to the coast as these varied in water depth and therefore likely covered areas with both maximum and minimum *Fucus* coverage. The dependency between transects and harvest method in these plots due to the experimental design however, limit conclusions based on these results.

The full recovery observed as *Fucus* cover (not biomass recovery) estimated by UAV within one year may have been due to the removal of intraspecific competition by harvesting the canopy as previously described by Creed et al. (1996). This effect has also been documented when harvesting other fucoids such as *A. nodosum* (Ugarte et al. 2006; Gendron et al. 2018; Lauzon-Guay et al. 2021). The continuous settling of new individuals, as described by Knight and Parke (1950), is likely another contributing factor to the high second harvest yield, as indicated by the observed seedling growth on concrete tiles in the present study. Present findings of biomass recovery are in line with previous studies on *F. vesiculosus* harvest and regrowth, which describe an identical or just slightly lower biomass at the second harvest (Knight and Parke 1950; Keser et al. 1981). The rapid recovery of areal cover on plot scale seen in the present study does – in contrast to the regrowth on individual scale - not support that the most intense harvest method leads to reduced regrowth. This may be explained by growth of either new germlings or suppressed sub-canopy individuals, rather than a regrowth from the cut individuals themselves as suggested by early descriptions (Sauvageau 1920).

This is also in line with the harvest response at the individual scale, showing that the recovery and increase in individual biomass is slower than the response in areal cover. Thus, our study supports previous findings (Knight and Parke 1950; Keser et al. 1981; Creed et al. 1996) that the primary source of regrowth after intense harvest events, originates from growth of new germlings, either by suppressed understory or continuous new seeding – or a combination of both, and not from regrowth from the cut individuals themselves. This observation has also been made for intensely harvested *A. nodosum* (Ugarte et al. 2006). That the apically growing *Fucus* species apparently fail to recover by regrowth of the harvested individuals, leaving recovery after harvest to rely on the growth of new seedlings, emphasizes the vulnerability of *Fucus* species to continuous regular harvest. Available substrate interacting with failure of new recruitment can open for competition from opportunistic or invasive species, potentially not sustaining the same ecosystem services as the perennial *Fucus* (Duarte et al. 2015). This calls for more research on the long-term effects of regular, large-scale harvests interacting with multiple environmental stressors, to ensure knowledge-based sustainable harvest practices and management of coastal macroalgae communities.

Harvest effects on individual scale

This study documented that *F. vesiculosus* has a remarkable ability to produce new shoots, but also that the new shoots did not support full re-growth after harvest of the specific *Fucus* individuals. This shoot regrowth response was evident, regardless of whether specimens were exposed to different harvest treatments or maintained as controls. No clear patterns in shoot response between harvest treatments and campaigns were observed. However, fully harvested individuals were unable to produce new biomass to the same levels as recorded among unharvested or tips harvested individuals in both Knebel or Isefjorden. This confirmed that the lowest regrowth capacity – at the individual scale - was achieved following the most intense harvest, full harvest. This is in line with a previous study of *F. vesiculosus* showing stronger shoot proliferation response when cut 30 cm above the holdfast as compared to individuals cut 15 cm above the holdfast (Knight & Parke 1950). Like Knight & Parke (1950), no individual scale biomass recovery was observed in this study, whereas Sauvageau (1920) found that regularly harvested *F. vesiculosus* individuals possessed a strong capacity for regrowth, which would allow two annual harvest events. This study found that individuals exposed to the full harvest were lost more often than when exposed to other harvest treatments, which might indicate that they perish, as described by Knight & Parke (1950).

The slightly lower re-growth capacity observed for individuals exposed to the thinning harvest compared to the full harvest during the first six months in Knebel may be due to additional shading in the thinning treatment from the remaining uncut two thirds of *Fucus* individuals, since self-shading has been shown to affect growth negatively in *F. vesiculosu* (Creed et al. 1996). The highly variable shoot number and shoot length dynamics observed in the present study is not linked with recovery in individual biomass and as such they do not support the description by Sauvageau (1920) that individual regrowth can support several annual harvests. The reasoning by Knight and Parke (1950) that younger frondage or tissue has a stronger regrowth capacity than older tissue is supported by the findings presented in the present study as individual regrowth response, indicated by number and length of new shoots, was generally higher when only harvesting the tips, and thus the plants kept some of the younger tissue compared to full harvested plants, where only the older stems and discoid holdfast remained. Exclusively in Isefjorden, the presence of shoots was noted prior to harvesting. These shoots were originating, with few exceptions, from the discoid holdfasts.

We find this almost exclusive origin indicative that these shoots could be settlement and growth of new individuals, rather than growth of new shoots from the marked individuals.

This would fit into the apical growth pattern of *F. vesiculosus* and be in line with the findings by Knight and Parke (1950) of continuous settling of new individuals. The continuous settling of new individuals was also supported by the observed settlement of new *F. vesiculosus* individuals on the concrete tiles used in the present study.

Future Management of *Fucus* beds

The results of the present investigation of *Fucus* regrowth on plot scale after harvest by different harvest methods, point toward that sustainable harvest schemes may be achievable from a population perspective, even from full harvest, where recovery of *Fucus* cover was achieved after roughly six months. From a biomass utilization perspective, there was no difference in the quality of the biomass, based on the different harvest methods, and biomass quality thus, would not be an argument for preferring one harvest method to another. The analyses of biomass quality related to different parts of the *Fucus* frond documented, that the content of heavy metals and iodine did not differ significantly between harvest methods, except for levels of Hg which were higher in the tips, but still below limit values. Thus, in contrast to what was hypothesized based on findings by Stengel et al. (2005) where older, proximal tissue has higher concentrations of metals (Fe and Cu), any harvest method can be applied from the perspective of biomass utilization, as the harvest method did not impact the value of the biomass for food or feed, as even the overall significantly higher levels of Hg were below the recommended levels. Finally, it should be noted that as for many other seaweeds, the concentrations of iodine and arsenic should be taken into consideration regarding uses for food and feed, although the levels of especially iodine are much lower than for reported for commercially cultivated species such as *Saccharina latissima* (Sá Monteiro et al. 2019).

When evaluating harvest methods, it is important to emphasize that this study did not take into consideration the ecosystem effects of the harvest of *Fucus* populations. *Fucus* species are important ecosystem foundation species in temperate coastal areas, and more focus on the health of these populations is expected in future, also in connection to the EU law on Nature Restoration (Valckenaere et al. 2023; EU 2024). In order to protect coastal seaweed forests, more work is needed to investigate especially large-scale and long-term ecosystem effects to ensure sustainable harvest practices, with more focus on harvest time in relation to reproduction and recruitment (Mac Monagail et al. 2017). The UAV-based methods for determination of *Fucus* areal cover will have a potential in future monitoring of *Fucus* beds as it can provide fast knowledge on areal cover on a larger scale. To also reliably predict *Fucus* biomass standing stock, harvest potential and recovery after harvest however, the UAV-based methods require refinement and further development, in order to reduce the frequency of misclassification and adapt to spatial and temporal variations of *Fucus* habitats.

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Authors' contributions Authorship of this study adheres to the general guidelines applicable within the field of study. JUGL: Analysis and interpretation of results. Drafting of manuscript. MMN: Study conception. Data collection. Analysis and interpretation of results.

Drafting of manuscript. PSS: Study conception. Data collection. Analysis and interpretation of results. Drafting of manuscript. AT: Data collection. Analysis and interpretation of results. Drafting of manuscript. MBR: Study conception. Data collection. Analysis and interpretation of results. Drafting of manuscript. SEM: Data collection. Analysis and interpretation of results. Drafting of manuscript. MFP: Study conception. Analysis and interpretation of results. Drafting of manuscript. JJS: Data collection. Analysis and interpretation of results.

Drafting of manuscript. JS: Data collection. Analysis and interpretation of results. Drafting of manuscript. ASS: Data collection. Analysis and interpretation of results. Drafting of manuscript. TB: Study conception. Data collection. Analysis and interpretation of results.

Drafting of manuscript. AB: Study conception. Data collection. Analysis and interpretation of results. Drafting of manuscript.

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Availability of data and material All data that support the findings of this study are included within this paper and its Supplementary information files.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to this article.

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