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RESEARCH

Harvesting *Asparagopsis*: understanding regrowth and associated community dynamics

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Abstract

The red seaweed *Asparagopsis taxiformis* can reduce methane emissions in livestock by over 90%, but its mariculture remains in its infancy and biomass for research and commercial use relies partly on wild populations. Knowledge on the impacts of harvesting *A. taxiformis* is lacking, emphasising the need for ecological research to guide the development of its sustainable harvesting. This study examined the regrowth potential of *A. taxiformis* meadows following small-scale harvesting. A harvest experiment testing the methods, handpicking and cutting, was conducted in Gladstone, Queensland, Australia, during the austral winter, with plots monitored over six months. Harvesting immediately affected percent cover and shoot length. Handpicked and cut plots exhibited regrowth within four to five months in terms of cover, which notably exceeded or were slightly above that of control plots. The shoot length of harvested plots paralleled that of control plots and was mainly influenced by seasonality. Control plots exhibited reduced growth at three months, suggesting that harvesting mimicked the seasonal reduction in biomass after the winter peak. This study also demonstrated the importance of vegetative propagation in the regrowth of *A. taxiformis*. The sessile benthic community in harvested plots underwent temporal shifts similar to those in the control plots, indicating that harvesting did not substantially alter community dynamics. Approximately 19 taxa of mobile fauna were recorded within *Asparagopsis* meadows, potentially indicating its habitat role. Overall, these findings provide ecological insights into the harvesting impacts on this seaweed, with further studies needed to assess broad-scale and long-term impacts.

Keywords Sustainable utilisation · Rhodophyta · *Asparagopsis* · Harvesting · Great Barrier Reef · Regrowth · Methane mitigation

Introduction

Global algae production is currently estimated at over 35 million tonnes (wet weight) annually, with seaweeds accounting for the vast majority of this volume (FAO 2024). Traditionally, the seaweed market has been driven by seaweed for food consumption and for various applications in the industrial sectors, particularly through the extraction of marine hydrocolloids. However, the seaweed industry is rapidly diversifying, with applications such as bioplastics, animal feed additives, pet food, and biostimulants showing potential market growth in the future (The World Bank 2023; Janke 2024). Among the emerging seaweed markets is for livestock feed ingredients for enteric methane emissions management, which is projected to generate approximately US$ 300 million by 2030 (The World Bank 2023). Among the key seaweed genera in this market is *Asparagopsis* (Rhodophyta, Bonnemaisoniales), which has garnered significant attention for its high concentration of halogenated compounds, most notably bromoform, which can suppress enteric methane production in ruminants (Kinley et al. 2016, 2020; Machado et al. 2016; Ahmed and Nishida 2024) and enhance productivity in feedlot cattle (Kinley et al. 2024). There are currently two recognised species: *Asparagopsis armata*, which thrives in temperate waters, and *Asparagopsis taxiformis*, which thrives in warm-temperate to tropical

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waters (Bonin and Hawkes 1987; Chualáin et al. 2004; Andreakis et al. 2007).

Despite its promise, the lack of a publicly available, well-established protocol for the closed life-cycle cultivation of *Asparagopsis* limits the supply of biomass, which currently relies on select well-established cultivators. Wild-harvested *Asparagopsis* is expected to continue as a biomass resource (Visch et al. 2023), as ocean and land-based cultivation continues to develop rapidly (Jia et al. 2022). Wild harvesting plays a central role not only in contributing to the biomass demand for feed production but also in supporting ongoing research for developing *Asparagopsis* cultivation. Natural populations are an important source material for feeding trials, strain selection, seedstock development, and other early-stage cultivation research efforts.

Despite the growing interest, the ecological studies on *Asparagopsis*, particularly *A. taxiformis*, remain largely unexamined, especially studies tackling the effects of harvesting on the growth and structure of its meadows. Ecological research has predominantly addressed the impacts of invasive populations, mainly in the Mediterranean (Zanolla et al. 2017, 2018a, 2018b). These studies focused on faunal assemblages in *A. taxiformis* in comparison to those of native seaweeds. However, in Australia, particularly in the Great Barrier Reef, *A. taxiformis* is native (Andreakis et al. 2016), and the ecological dynamics of these native populations may be different from those of invasive counterparts. These differences, alongside the current utilisation of wild biomass, underscore the need for studies on the ecological impacts of harvesting native populations of *A. taxiformis*.

Additionally, most harvesting studies focused on brown seaweeds, such as *Ascophyllum nodosum* (Guiry et al. 2013; Lauzon-Guay et al. 2021) and kelps (Ulaski et al. 2020; Vance et al. 2023), which comprise a large portion of global wild seaweed collection because of their high alginate content (Monagail et al. 2017). Only a few studies have focused on red seaweed species in terms of harvesting, which include *Corallina officinalis* (Magill et al. 2019); *Gelidium* spp. (Carter and Simons 1987; Higgins et al. 2022), *Palmaria palmata* (Garbary et al. 2012), *Mazzaella laminarioides* (Vargas 2019), *Chondrus crispus* (Mathieson and Burns 1975; Chopin et al. 1992), and species from Bangiaceae (Griffin et al. 1999; O'Connell-Milne and Hepburn 2015). Furthermore, seaweed, in general, may contribute to coastal ecosystem services such as nutrient cycling and sediment stabilisation (Cotas et al. 2023; Eger et al. 2023). Although the role of *Asparagopsis* in these processes still requires examination, knowledge on its capacity to regenerate after harvesting also provides essential information for understanding and maintaining its functions within reef ecosystems.

The present study aims to contribute to these ecological gaps by investigating the effects of harvesting on the growth and community structure of the warm-water species *A. taxiformis*, native to the Great Barrier Reef (GBR), Australia. Specifically, the objectives were to: (1) assess the effects of harvesting on the growth of *A. taxiformis* and its associated benthic community assemblage based on different methods (cutting and handpicking) and (2) conduct an inventory of the mobile fauna associated with *A. taxiformis* meadows to provide preliminary data on its ecological role and inform future evaluations of harvesting impacts.

Understanding potential ecological impacts of harvesting is a fundamental aspect of the sustainable management of native seaweed resources. Within the GBR and other locations globally, this knowledge contributes to helping ensure ecosystem integrity and resilience, informing broader conservation efforts.

Materials & methods

Study area

Field experiments were conducted at Manning Reef (−23.856853°, 151.359956°), located at the inner side of Facing Island in Gladstone Harbour, Queensland (Fig. 1). The site is characterised by large patches of coral rubble with sandy substrate in between. *Asparagopsis taxiformis* is found growing on this rubble or gravel and sometimes associated with other seaweeds. Manning Reef is exposed to fast-moving currents that reach 0.8 m s^{-1}. Previous studies have noted that 1.1 m s^{-1} velocities are typical in the tidal channels of Gladstone Harbour, which can be even higher near the bottom (Conaghan 1966). Plots were established in the intertidal zone at approximately mean low water and were exposed during extreme spring low tides. Tides during the experimental period ranged from 0.12 to 4.60 m (Queensland Government 2025).

Harvest experiment

Experimental field plots (approximately 3 m apart) were established by marking two diagonal corners with 1-m-long stakes, using a 25 × 25 cm quadrat to delineate the plot area. Plots were selected when > 60% cover of *A. taxiformis* was observed. Two treatments were applied, cutting and handpicking, alongside control plots which were left unharvested. Each treatment, including the control, was replicated across five plots. Harvesting was conducted within the quadrat, which had a mesh bag with its opening facing the current to retain all collected biomass. Cutting was done using garden shears, targeting at least 10 mm above the holdfast to keep it intact. Handpicking involved removing thalli by hand while wearing gloves, which often resulted in the removal of a substantial portion of the holdfast. Only fronds with holdfast

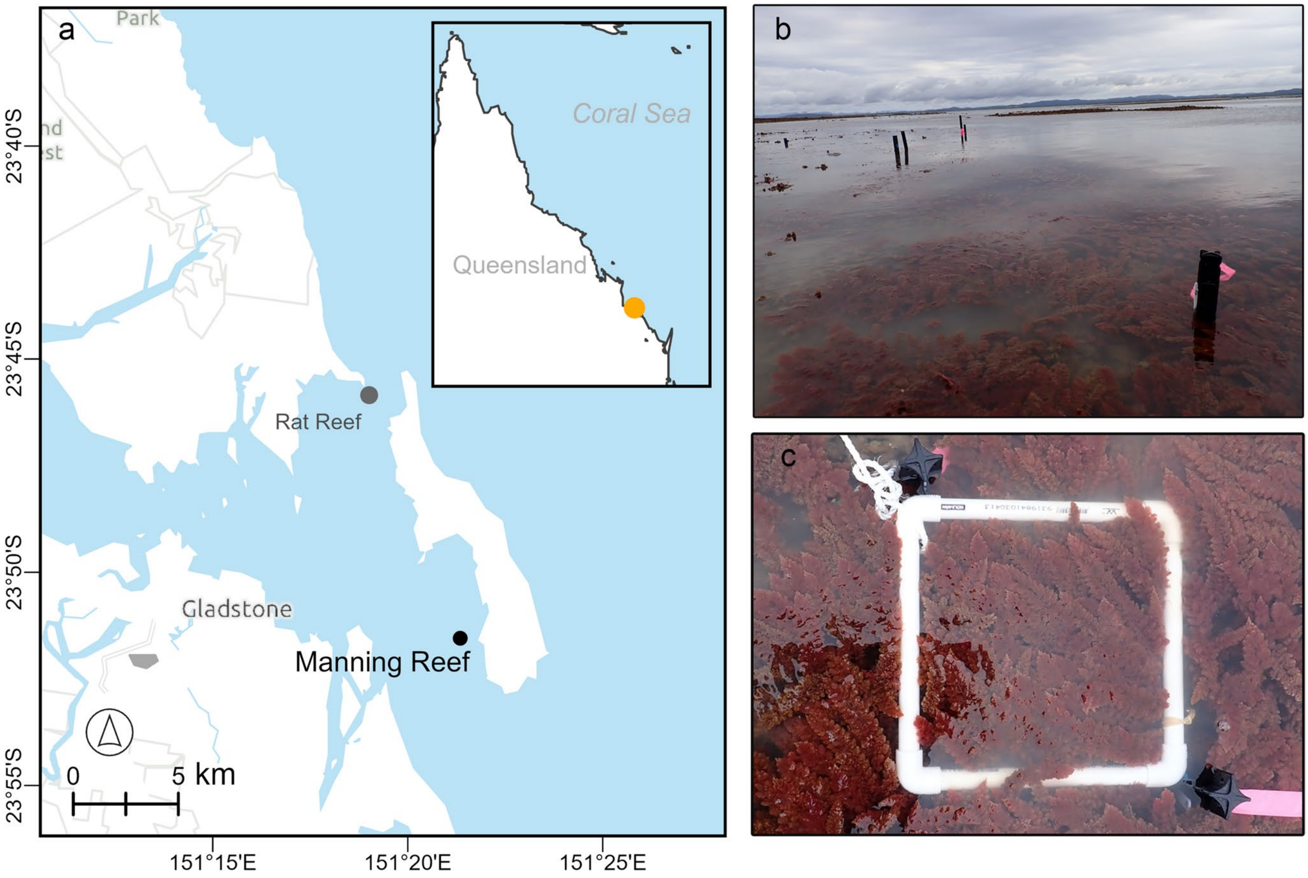

Fig. 1 Study area and experimental design. (**a**) Location of Manning Reef in Gladstone, Queensland. (**b**) View of Manning Reef showing stake markers used for plot demarcation. (**c**) *Asparagopsis taxiformis* within an experimental plot. Quadrat was placed between markers when harvesting and monitoring

inside the quadrat were harvested. Representative photographs of control and harvested plots (cutting and handpicking) are shown in Fig. S1 (Online Resource). Plots were harvested by handpicking or cutting in June 2024 (austral winter), with a final total harvest for both treatments (cutting and handpicking) and control conducted in December 2024. Seaweeds collected in June and December were transported in ambient seawater in cooler boxes to the Coastal Marine Ecosystems Research Centre (CMERC), Central Queensland University, Gladstone, for processing.

Seaweed regrowth

Parameters related to the growth of *A. taxiformis* were recorded from June to December 2024. Specifically, the percent cover of *A. taxiformis* and the lengths of the longest shoots ($n = 3$) were recorded within each quadrat (25 cm x 25 cm) that was placed inside the marked plot. Percent cover was estimated visually from a top-down perspective, considering only thalli with holdfasts that were inside the quadrat. Any shoots extending into the quadrat from outside were carefully moved aside. Shoot length was measured using a measuring tape. All measurements were performed by the same person to reduce observer bias.

Measurements were taken at six time points: pre-harvest (immediately before June harvesting), immediately after harvest, and at 3, 4, 5, and 6 months post-harvest (September, October, November, and December, respectively). The December monitoring was conducted immediately prior to the total harvest. All measurements across the time points were recorded in situ, except for the ‘immediately after harvest’ timepoint. Measurements immediately after harvesting in June were obtained from photographs of the harvested plots, as direct field measurements were not possible because of the short tidal windows and reduced visibility with the rising tide. Percent cover was estimated from these images. The shoot length of *A. taxiformis* immediately after harvest could not be reliably measured from photos; therefore, this time point was not included in the analysis. For shoot length in cutting plots, the aim was to leave approximately 10 mm above the holdfast; however, actual lengths typically varied and ranged from 10 mm to 30 mm.

The harvested seaweeds were rinsed in sterile seawater, spun in a salad spinner to remove excess seawater, and dried in the oven (50–60 °C) until constant weight.

Communities associated with *Asparagopsis taxiformis*

The composition of sessile, benthic organisms associated with *A. taxiformis* in Gladstone was assessed as part of the harvesting experiment. Species were identified, and their corresponding percent cover was estimated. All assessments were conducted by the same observer to minimise bias. Given that the dense and overlapping fronds of *Asparagopsis* sometimes obscured other species, particularly *Lobophora* spp. and *Neomeris annulata*, cover estimates were refined while harvesting, when these species became more visible. In control plots, additional time was allotted to inspect beneath *Asparagopsis*. Care was also taken to avoid disturbing the associated species. However, the incidental removal of some fragments of *Lobophora* was unavoidable because of the attached holdfasts of *Asparagopsis,* but this did not affect the cover estimates upon consideration. Monitoring was thus undertaken at the following time points: 'during harvesting' and subsequently at 3, 4, 5, and 6 months post-harvest. Given that the associated benthic community is sessile, cover estimates for the time point 'during harvesting' practically represent both pre-harvest and immediate post-harvest conditions.

To characterise the mobile fauna associated with *A. taxiformis* meadows, records were drawn from an ongoing project spanning November 2022 to December 2024, of which the harvesting experiment (June–December 2024) was a component. This included observations from snorkelling excursions and microscopic examination of thalli collected for monthly seasonality studies at Rat Reef and Manning Reef in Gladstone (Rula et al., unpublished). During the harvesting experiment, mobile fauna that were observed within and around the *Asparagopsis* meadows were documented in situ. All specimens were identified to the lowest possible taxonomic level.

Data analysis

Statistical analyses were mainly conducted in R version 4.4.1 (R Core Team 2024). Plots were generated using the package 'ggplot2'. Additional multivariate analyses and visualisation were conducted in PRIMER 8 (Quest Research Limited, N Z; Anderson 2024).

Percent cover was converted to proportions and then analysed through generalised linear mixed modelling using the function glmmTMB with a beta distribution (logit link) from the 'glmmTMB' package. Shoot lengths of subsampled shoots within each plot were averaged so that each plot was considered an independent replicate. A linear mixed model was used for shoot length. Both models were fitted by maximum likelihood. Treatment, time, and their interaction were included as fixed effects. The plot ID was also included as a random intercept to account for repeated measures. Residual diagnostics was conducted using the package 'DHARMa'. For percent cover, the likelihood ratio test was implemented to evaluate the significance of the treatment and time interaction using the 'anova' function, wherein the full (interaction) model was compared against the reduced (additive) model. For shoot length, analysis of variance (Satterthwaite's method) was used to evaluate the significance of fixed effects.

As a supplementary analysis, percent cover and shoot length were standardised following the approach of Boada et al. (2024) to isolate the effects of harvesting. Standardisation was performed by dividing each plot's value at a given time point by its corresponding pre-harvest values and the mean of the control at the same time point. The mean control at each time point was also normalised to its pre-harvest value. A generalised linear mixed model with a gamma distribution (log link) was used to analyse standardised cover, and a linear mixed model was used for the standardised shoot length. Residual diagnostics were checked using the package 'DHARMa'. The significance of the interaction was assessed similarly to the actual values of percent cover and shoot length, as described above.

Pairwise comparisons were performed using the package 'emmeans', with Tukey adjustments to account for multiple testing and ensure control of the overall error rate. For significant interactions, the pairwise comparisons across time points were limited to pre-harvest values versus post-harvest values and 'immediately after harvest' values versus post-harvest values. The packages 'multcomp' and 'multcompView' were used to extract the significance letters for each group when applicable.

The dry weight of samples harvested in June was subjected to a two-tailed t-test to compare the cutting and handpicking treatments and evaluate yield and harvesting efficiency. The control plots were excluded from this analysis as they were not harvested at this time point. After six months, the dry weight of all three groups (cutting, handpicking, and control) was assessed through analysis of variance to determine the effects of harvesting treatments by comparing them to the control. Additionally, the dry weight of handpicking upon harvest in June was compared to that after six months with a two-tailed t-test. Direct comparisons of dry weight between June and December were not undertaken for cutting because different harvesting approaches were used: in June, fronds were cut above the holdfast, whereas in December, a total harvest was conducted (i.e., removal of entire thalli, including holdfast).

To examine the effects of harvesting on the sessile benthic community composition, biomass data based on percent cover data were analysed using permutational multivariate analysis of variance (PERMANOVA) with treatment and time as fixed factors and plot ID (nested in treatment) as a random effect to account for repeated measures. Data were fourth-root transformed to reduce skewness, and a Bray-Curtis similarity matrix was constructed with a dummy variable included. PERMANOVA was run with 9999 permutations of residuals under a reduced model with Type III (partial) sum of squares. Post hoc tests were conducted using pairwise PERMANOVA. Standardisation (as applied to seaweed growth) was not used here, given the temporal variability in species presence.

Changes in community assemblage were visualised with threshold metric-multi-dimensional scaling (tmMDS) ordination of the treatment and time centroids, with 100 restarts and minimum stress of 0.001. Similarity percentage (SIMPER) analysis was conducted as a follow up, using time as a factor and a cut-off of 70%, to examine further the patterns in community composition and identify the species contributing most to these patterns.

Statistical significance for all tests was assessed at $\alpha = 0.05$. The p-values presented here are adjusted p-values. Unadjusted p-values are included in the supporting information.

Results

Seaweed regrowth

Harvesting influenced the percent cover of *A. taxiformis* differently across time points (Fig. 2), which was supported by the significantly better fit of the interaction model compared to the additive model ($\chi^2(10) = 48.06$, $p < 0.001$, Table S1, Online Resource). Handpicking caused a sharp decline in percent cover immediately after harvest ($p < 0.001$, Table S2, Online Resource), but regrowth was observed at 3 months post-harvest. A marked increase at 4 months post-harvest was recorded for the handpicked plots, which exceeded that of the control plots ($p = 0.02$). A slight decrease in cover was then recorded at 5 months, which was still comparable to that of the control plots ($p = 0.22$). By 6 months after harvest, the cover of handpicked and control plots increased and converged ($p = 0.80$). The percent cover of handpicked plots at 6 months post-harvest

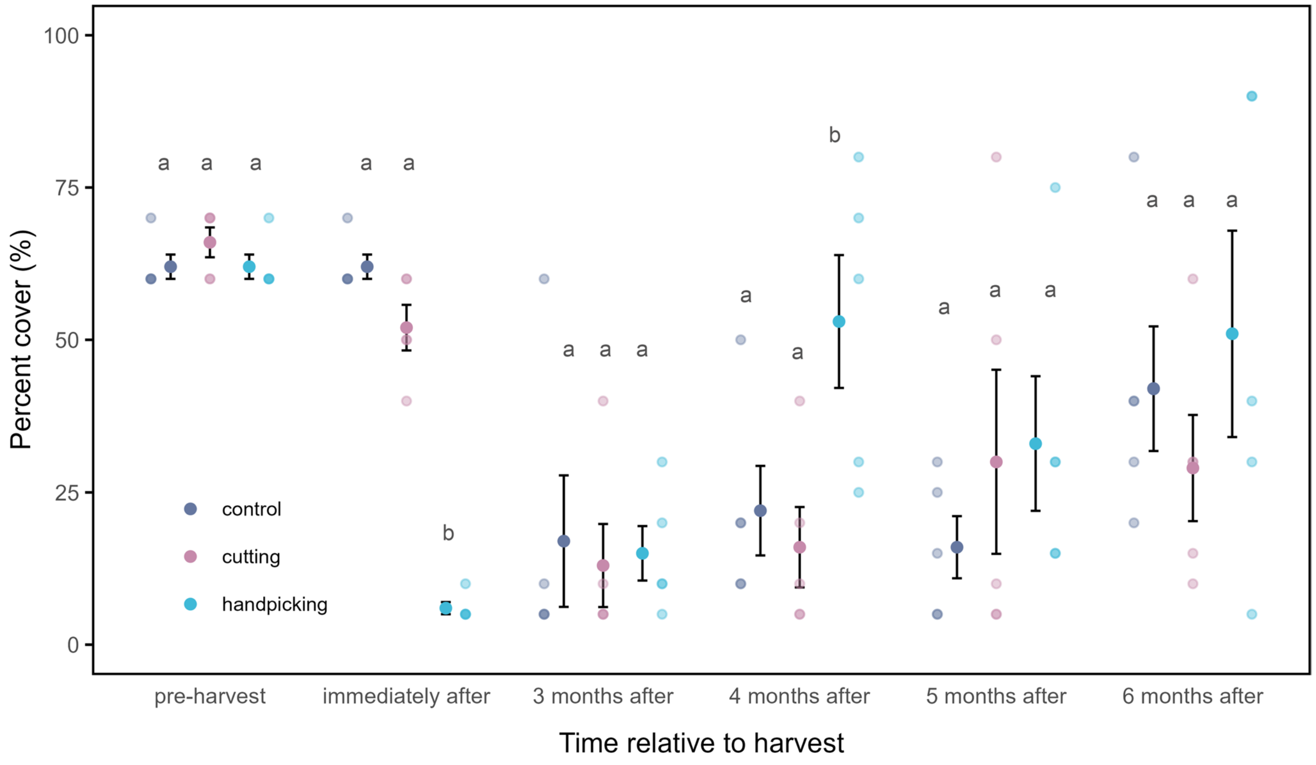

Fig. 2 Percent cover of *Asparagopsis taxiformis* for control, cutting, and handpicking treatments from pre-harvest to 6 months post-harvest. Values presented are arithmetic means and standard errors ($n = 5$). Different letters indicate statistically significant differences across treatments and control at each time point. Significance is based on pairwise comparisons of estimated marginal means of modelled data ($p < 0.05$, Table S2, Online Resource).

was comparable to pre-harvest levels ($p = 0.94$; Table S3, Online Resource).

Cutting slightly decreased the cover of *A. taxiformis* relative to the control plots immediately after harvesting but was generally comparable to the control plot ($p = 0.75$, Fig. 2), which was largely due to the remaining stolons and the short, young shoots that were left attached (Fig. S1, Online Resource). Cut plots remained similar to that of the control plots for most of the experimental period ($p > 0.05$, Table S2, Online Resource). Interestingly, the cover of the cutting and control plots decreased 3 months post-harvest relative to 'pre-harvest' and 'immediately after harvest' time points (Fig. 2; $p < 0.001$, Table S3, Online Resource), suggesting the occurrence of natural dieback in wild populations of *A. taxiformis*.

Results based on standardised values, which excluded the effects of seasonality, showed similar results as above, with standardised cover of harvested and control plots varying over time (Table S4, Online Resource). In particular, these results highlighted that handpicking and cutting plots exhibited regrowth in cover exceeding that of control plots at 4 and 5 months post-harvest, respectively ($p > 0.05$, Table S5, Fig. S3, Online Resource).

Statistical analysis of shoot length showed a significant difference among time points (Fig. 3; $F_{(4,60)} = 46.27$, $p < 0.001$, Table S6, Online Resource) but not among treatments and control ($F_{(2,15)} = 0.74$, $p = 0.49$). Its interaction was also not significant ($F_{(8,60)} = 0.69$, $p < 0.70$). Shortest shoots were recorded at three months post-harvest, and longest shoots were recorded at pre-harvest ($p < 0.001$, Table S7, Online Resource). It is important to note that measurements immediately after harvest was not conducted. Nonetheless, the shoot length of control plots decreased at three months post-harvest time point and aligned with that of the treatment plots, supporting the hypothesis that seasonal decline occurred. The pattern of changes in shoot length over time was similar for both treatments and controls, peaking at five months post-harvest. In general, shoot length after harvesting was lower than pre-harvest levels ($p < 0.001$, Table S7, Online Resource). Results based on standardised shoot length, which removed seasonality effects, did not show any changes in time and across treatments and controls ($p > 0.05$, Table S8, Fig. S4, Online Resource).

As expected, the average dry weight of samples harvested by handpicking (12.46 g) was significantly higher than that harvested by cutting (4.15 g; $t_{(8)} = -4.70$, $p = 0.002$); Fig. 4). After six months, dry weight *A. taxiformis*

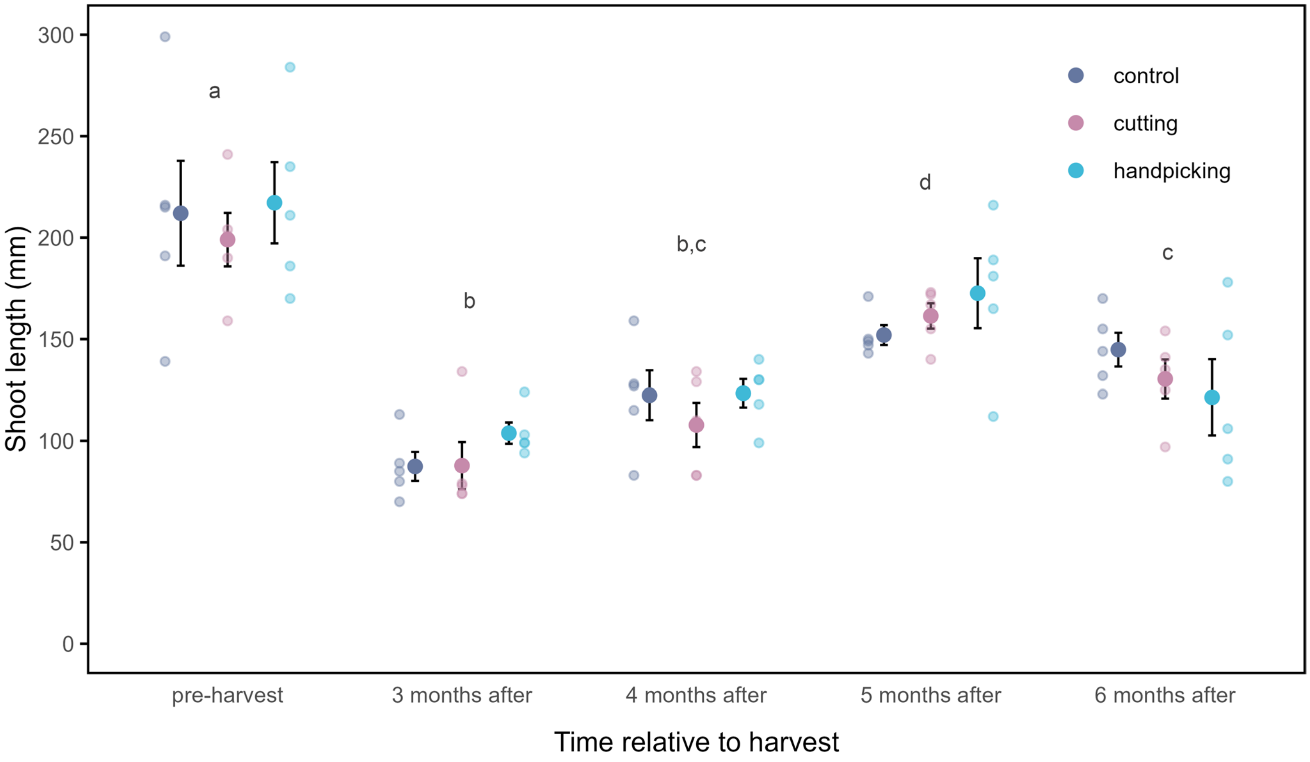

Fig. 3 Shoot length of *Asparagopsis taxiformis* for control, cutting, and handpicking treatments from pre-harvest to 6 months post-harvest. Values presented are arithmetic means and standard errors ($n = 5$). Different letters indicate statistically significant differences between time points. No significant difference was found across treatments and control. Significance is based on pairwise comparisons of estimated marginal means of modelled data ($p < 0.05$, Table S7, Online Resource).

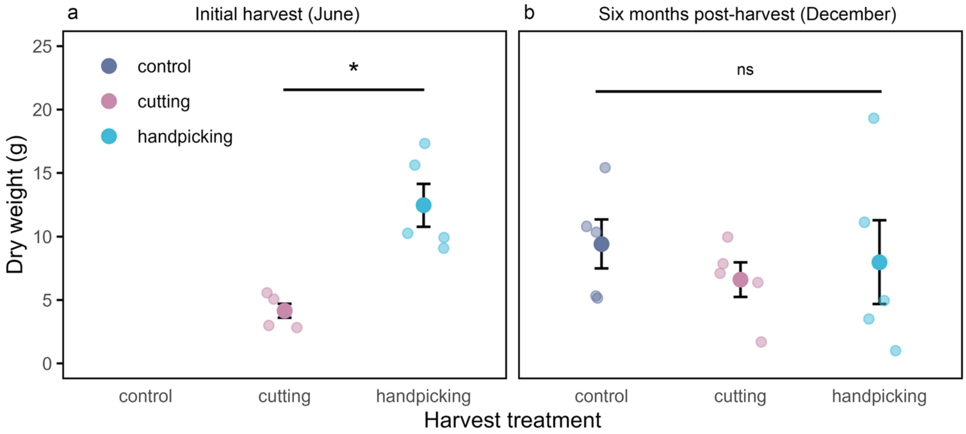

Fig. 4 Dry weight of *Asparagopsis taxiformis* from (**a**) initial harvest in June and (**b**) total harvest 6 months later in December. Values presented are arithmetic means and standard errors ($n = 5$). No dry weight data for control plots in June, as these plots were left undisturbed during the initial harvest. Asterisk denotes statistically significant differences between treatments; and 'ns' indicates no significant differences ($\alpha = 0.05$)

from plots that were harvested by handpicking and cutting were not significantly different from each other and from the control ($F_{(2,12)} = 0.36$, $p = 0.70$). Dry weight of handpicking was lower six months after harvest (7.98 g) than at initial harvest (12.46 g; $t_{(8)} = -1.21$, $p = 0.26$).

Communities associated with *Asparagopsis taxiformis*

Sessile benthic community

Asparagopsis taxiformis was found associated with other brown and green seaweeds such as *Lobophora* sp., *Dictyota* spp., *Dictyopteris* sp., *Halimeda opuntia*, and *Neomeris annulata* (Fig. S5a, Online Resource). Benthic fauna comprised sponges and tunicates, with only 5% cover (Fig. S5b, Online Resource). Altogether, these species constituted the sessile benthic community that was found associated with *A. taxiformis* in this experiment.

Harvesting did not affect species composition of the sessile benthic community (Pseudo-$F_{(2,48)} = 0.27$, $p = 0.98$, Table S9, Online Resource). However, species composition varied with time (Pseudo-$F_{(4,48)} = 9.18$, $p < 0.001$). The interaction of treatment and time was not significant (Pseudo-$F_{(8,48)} = 1.11$, $p = 0.37$), suggesting that the control (undisturbed) and harvested plots (handpicking and cutting) followed similar seasonal trajectories.

Community composition was significantly different from the initial time point but only from four months after harvest and beyond ($p < 0.05$; Table S10, Online Resource). Based on the results of the SIMPER analysis, the brown seaweeds *Dictyopteris* sp. and *Lobophora* sp. were major contributors to these differences, each accounting for more than 30% of the dissimilarity at various time points (Fig. S6). *Dictyopteris* sp. exhibited a marked increase in abundance in the middle of the study period, peaking at five months (November). At six months post-harvest, *Lobophora* sp. was the main driver of dissimilarity between the initial time point and six months post-harvest.

The overall tmMDS plot showed changes in the sessile community within *A. taxiformis* meadows across treatments over the six-month period (Fig. 5a). The resulting ordination had a stress value of 0.113, which is within the 0.20 threshold for an acceptable fit (Clarke 1993). The tmMDS plot illustrated clear temporal variations in the structure of the sessile benthic community within *A. taxiformis* meadows over a six-month period following harvest. The treatments and control had fairly similar compositions during harvest and then clearly shifted together over time in a similar direction. The tmMDS plot for community structure during harvest revealed moderate within-group variation within the control and handpicking treatment, but no distinct clustering among groups was observed (Fig. 5b). Likewise, the tmMDS plot at six months post-harvest showed no clear separation among groups, with samples from all groups broadly overlapping (Fig. 5c). Stress values for these additional plots were 0.117 (during harvest) and 0.126 (6 months post-harvest).

Mobile fauna in *Asparagopsis* meadows

A total of 19 taxa of marine mobile fauna were observed in association with *A. taxiformis* within Gladstone Harbour, Queensland (Table 1). These included representatives from five phyla: Annelida, Arthropoda, Mollusca, Echinodermata, and Chordata.

Discussion

Seaweed regrowth

In this study, harvesting affected the growth of *A. taxiformis* as shown by the reduction in cover and shoot length post-harvest. Although measurements were not taken

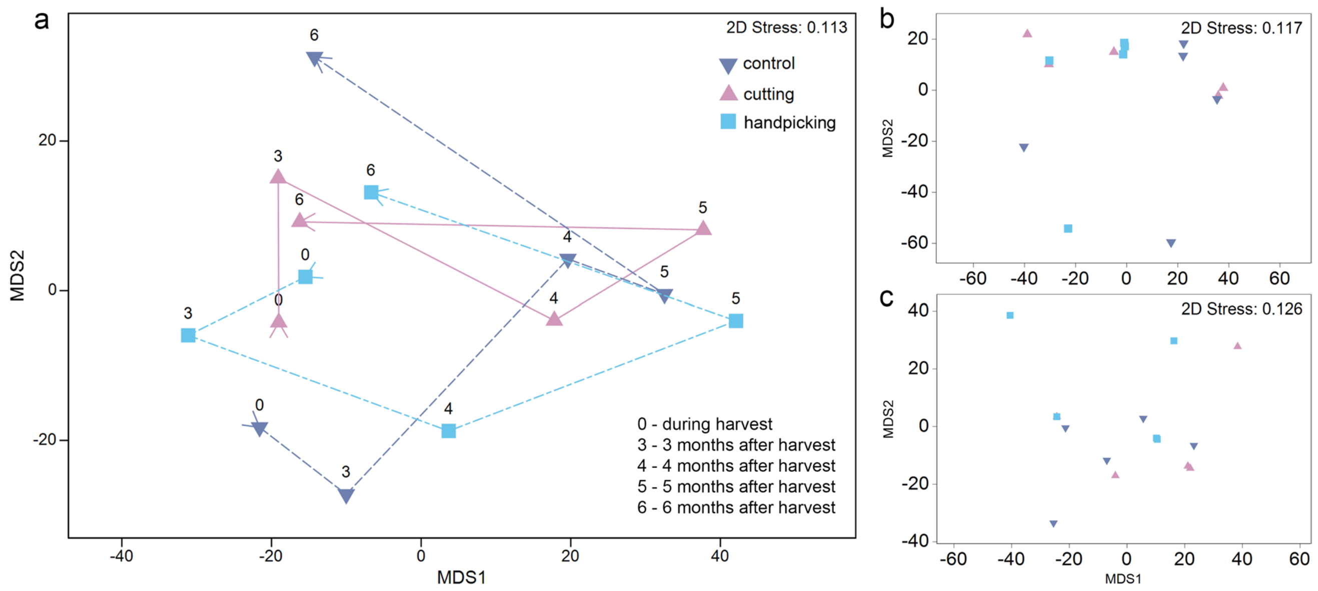

Fig. 5 Threshold metric multi-dimensional scaling (tmMDS) plots showing sessile benthic community structure within *Asparagopsis taxiformis* meadows under control, cutting, and handpicking treatments during a harvest experiment in Gladstone, Queensland. Panel (**a**) shows temporal trajectories over six months, with each point representing the centroid of five replicate samples per treatment at each time point. Panels (**b**) and (**c**) show individual samples per treatment at pre-harvest and six months post-harvest, respectively

immediately after harvesting for shoot length, cutting and handpicking reduced the biomass as photo-documented in Fig. S1 (Online Resource). One of the key findings in this study is the decrease in cover and shoot length of control plots, which was recorded at three months post-harvest. The cover and shoot length of harvested plots therefore became comparable to those of control plots at this time point, suggesting that harvesting mimicked the seasonal decline in wild populations of *A. taxiformis*. These findings are consistent with our previous observations of biomass decline after the austral winter peak (Rula et al. unpublished). Harvesting by handpicking and cutting then exhibited marked rebound in growth at 4 and 5 months post-harvest, respectively, with cover exceeding those of control plots. In terms of shoot length, the temporal patterns in shoot length of the harvested plots paralleled those of control plots. Although these results are promising, the patterns observed warrant validation through long-term monitoring. The regrowth trajectory was different for handpicking and cutting, and seasonal variation may have further shaped these patterns. Future studies should explicitly examine immediate impacts on shoot length following harvesting to assess directly the growth and recovery of *A. taxiformis*.

In handpicking plots, cover rebounded more rapidly than shoot length, reflecting the proliferation of new, young shoots. Vegetative growth is the primary mode of propagation for this species (Zanolla et al. 2018a); therefore, the regrowth observed in the present study was most likely driven by shoots arising from creeping stolons of thalli adjacent to the plots. Spore recruitment via carpospore release is unlikely, since tetrasporophytes were not detected in any of our field surveys before and during the present study.

Despite the high cover of harvested plots at four to five months post-harvest, seasonal effects reduced growth to that of the control plots towards the end of the monitoring period, reflecting the natural summer decline in biomass as documented from our previous observations (Rula et al. unpublished). Although Zanolla et al. (2019) suggested that self-thinning is not characteristic of *A. taxiformis* due to the continual production of new shoots from persistent holdfast structures, this cannot be ruled out in the present study, particularly for the handpicked plots, wherein most of the stolons were removed. Crowding may have contributed to competition in handpicked plots, possibly affecting cover and shoot length. However, the extent to which this process explains the observed patterns requires further studies.

In cutting plots, cover remained aligned with the control plots when cover for handpicked plots substantially increased at four months post-harvest, with variations through time. These findings indicate that the regeneration in plots harvested by cutting possibly prioritised vertical growth rather than horizontal spread, which was observed in handpicking plots. Cutting or trimming has been studied for other seaweed species and is generally regarded as a sustainable harvesting method. In *M. cornucopiae*, cutting 10 cm above the holdfast or at the base of the stipe resulted in cover and frond length returning to control levels one year later (Scrosati 1998); the amount or size of the harvested area was not specified. Similarly, in *Gelidium pristoides*, cutting above the holdfast, based on observations of 30 tufts, enabled regrowth within three to four months and was recommended to ensure vegetative regeneration (Carter and Anderson 1985).

Previous monthly observations showed that shoot length is relatively lower during the December peak than in the June peak of growth, where cover and density tend to be higher (Rula et al. unpublished). This may explain the lack of full recovery of shoot length in both the treatment and control plots to the pre-harvest levels. Long-term monitoring is needed to validate this trend. The experiment was concluded after six months, totally harvesting the plots (including the controls), to avoid the risk of biomass loss from intense die-off during potential heatwaves. This timeframe, although short, allowed us to assess whether regrowth occurred during the second growth cycle (onset of austral summer, December).

The dry weight of harvesting treatments and the control plots were similar by the end of the experiment, which suggests that regrowth could occur in short-term. This finding also suggests that, despite the distinct regrowth patterns between the harvesting treatments, both methods ultimately resulted in comparable biomass levels within six months. Although dry weight could not be directly compared before and after harvesting, since the entire biomass was removed at six months and treatments were only imposed during the initial harvest in June, the similarity between treatments and controls at the end of the experiment still provides a valuable indication that *A. taxiformis* can re-establish biomass based on dry weight similar to that of the control plots within this timeframe. Similar patterns were observed in harvesting studies conducted for other seaweed species. In *G. pristoides*, no significant differences were found between cutting and handpicking (based on 30 tufts) in terms of biomass, as both parameters returned to control levels within three to four months post-harvest (Carter and Anderson 1985). In the multi-species harvest of ‘karengo’ (Bangiaceae) within 0.25 m^2 quadrats, both cutting and handpicking plots regenerated to the same levels as the control plots (O’Connell-Milne and Hepburn 2015). The yield of ‘karengo’ by cutting was lower because holdfasts were left intact, which is similar to the findings from the harvest in June in the present study.

In the current study, the difference in dry weight between the cutting and handpicking treatments does not directly equate to direct differences between the shoots and holdfast (stolon). Cutting retained a considerable amount of stolons and lower parts of shoots (approximately 10–30 mm above the stolon or the holdfast) and also left small, young shoots intact, which were too short to cut. In contrast, handpicking removed nearly all biomass, including most of the holdfast together with the interconnected fronds and small, young shoots. However, a preferential biomass allocation for the stolon is also possible. For clonal species, such as *Asparagopsis* spp., biomass partitioning typically occurs, wherein the bulk of the biomass can be directed either towards the stolon or shoot production, depending on the environmental conditions (e.g., Malta et al. 2005). Further analysis is needed to confirm this strategy for this species, particularly by cutting all shoots (including the small, young recruits) close to the stolon and comparing biomass of stolons (including spacers and rhizoids) and entire shoots. Both explanations coincide with findings on *A. taxiformis* populations in Spain showing that the biomass of the smallest shoots correlates with holdfast production (Zanolla et al. 2017) and that production of stolons fluctuate with season (Zanolla et al. 2019). Together, these findings suggest the ability of this species to adopt growth strategies such as prioritisation of lateral spread and biomass partitioning.

Both harvesting methods demonstrated the importance of vegetative propagation in maintaining the population. Given the absence of tetrasporophytes in the area, which are evidence of carpospore release and recruitment when present, the stolons and adjacent thalli both potentially served as the major source material for regrowth in this experiment. In addition, *A. taxiformis* also produces propagules that extend from the terminal ends of its lateral branches (Mairh 1977; Zanolla et al. 2017), which were also found in many of our samples from Gladstone (Rula et al., unpublished). These propagules from individuals in adjacent areas may have further contributed to its regeneration.

In terms of efficiency, handpicking provided higher yields based on dry weight in June and allows for quick removal of biomass with minimal effort, whereas cutting is more time-consuming, as fronds must be held and carefully trimmed to leave holdfasts intact. Similar recommendations have been made for ‘karengo’ (Bangiaceae), where handpicking was recommended for its ease of use compared to cutting and leaving 10 mm of thallus and holdfast intact (O’Connell-Milne and Hepburn 2015). Further studies could also investigate the impacts of scraping; however, this practice is not recommended by previous studies, given the importance of retaining regenerative structures for regrowth. For example, work on other red seaweeds, including ‘karengo’ (O’Connell-Milne and Hepburn 2015) and *Gymnogongrus furcellatus* (now *Asterfilopsis furcellata*, Santelices et al. 1989), has shown that scraping (0.25 m^2 and 900 cm^2, respectively) can prohibit or substantially slow down regrowth. In light of these findings from the present and previous studies, the availability of adjacent patches as sources of regrowth is essential to support regeneration.

Understanding the regrowth dynamics in *A. taxiformis* also requires consideration of environmental drivers. In this study, seawater temperature and solar radiation exhibited increasing trends toward the summer period (December), reaching 26 MJ m^{-2} and 28 °C (Fig. S7, Online Resource; BOM 2025; AIMS 2017). Elevated light levels have previously been associated with peak growth in the onset of summer (Rula et al., unpublished), which may have triggered the regrowth observed in the current study. With only four time points available from post-harvest monitoring, the dataset is insufficient for a meaningful statistical analysis of environmental influences on growth (low correlation). Additionally, environmental data from eReefs is unavailable because of the damage to the monitoring system due to flooding events (CSIRO 2025), limiting the use of multivariate techniques for analysing growth in relation to combinations of multiple environmental variables. Future studies should integrate environmental monitoring in assessing regrowth dynamics.

A small plot size was used in the present study, given that *A. taxiformis* is typically harvested by hand as observed during large-scale scientific harvesting activities (Smith et al. 2024). For consistency, the same size was applied to the cutting treatment. However, plot or clearing size can influence seaweed regrowth. For example, the recruitment density of germlings of *Ascophyllum nodosum* declined as clearing size (scraped area) increased from 1 to 8 m in diameter (Dudgeon and Petraitis 2001). With small-scale harvesting, the surrounding thalli can provide shading to the harvested plot. In the present study, some shading was present, but the plots were not completely covered by adjacent fronds and were intermittently exposed to light. The presence of adjacent thalli confers advantages such as protection of the holdfast, young shoots, or recruits against thermal stress and desiccation, particularly during low tides (Carter and Anderson 1985; Gendron et al. 2018). In contrast, large-scale disturbances result in higher exposure of these regenerative tissues or recruits to this stress, which may adversely impact recruitment and survival. Overall, patterns of recovery depend on the size, shape, and position of harvested areas, with species-specific responses to these spatial factors (Airoldi 2003), which highlights the importance of examining population dynamics of *Asparagopsis* across different harvesting scales.

The timing of harvest is a critical factor in determining regrowth and recovery. For example, in 'karengo' harvesting by hand late in the season in August produced higher yields than early harvesting in July (0.25 m^2 quadrats), while still allowing regrowth (O'Connell-Milne and Hepburn 2015). In contrast, higher regrowth in terms of length and density was found for autumn harvest than summer harvest of *Lessonia trabeculata* based on 30 m^2 plots (Westermeier et al. 2017). In the present study, the selected harvest timing (June, austral winter), which aligned with the first annual peak in biomass, allowed for regrowth that was likely supported by the second natural biomass peak in December (onset of austral summer, Rula et al. unpublished). The decline in cover in control plots in the middle of the experiment suggests that harvesting around the austral winter peak is advantageous, given that seaweeds would otherwise undergo natural decline. Similar recommendations have been proposed for *Sargassum*, which also exhibits seasonal decay (Ang 1985, 1987). Although harvesting during the major peak (onset of summer, December) was not assessed in the present study, this timing may be feasible if harvesting is conducted just before its natural dieback in mid-summer. However, elevated temperatures from heatwaves can result in intensified declines as observed from our previous surveys (Rula et al., unpublished). The ability of the meadows and its associated communities to withstand harvesting under such environmental stress should be investigated.

Furthermore, although tetrasporophytes were not observed in our surveys, ensuring that sexual reproduction is not hindered is important, as it is still a possible source of recruitment. Harvesting before the peak could potentially reduce both growth and reproductive output, but this warrants further investigation. Harvesting within a week after the austral winter peak is recommended, as this timing coincides with peak reproduction (Rula et al. unpublished) and possible carpospore release. Previous studies noted that carpospore release occurs within 30 h after field collection (Mickelson 2013). Although the timing may vary under natural conditions, the seasonal decline observed in control plots indicates that carpospore release in the wild occurs within a short period. Harvesting a few days to a few weeks after the peak just before the decline, therefore, allows reproduction to occur, which may additionally support population maintenance. Based on moderate- to large-scale scientific harvesting of *A. taxiformis* (Smith et al. 2024), harvesting within this timeframe is feasible given sufficient human resources. However, the logistics also depend on the objectives of the harvest, environmental conditions, and tidal windows, which influence the duration and efficiency of collection. Post-harvest processes such as drying, extraction, or storage can influence the logistics of harvesting and should be incorporated into the overall planning. The feasibility of the suggested timeframe for commercial scale will require further evaluation and optimisation.

Communities associated with *Asparagopsis taxiformis*

Sessile benthic community and harvesting

The sessile benthic community was dominated by brown seaweeds, whose biomass also fluctuated with environmental conditions. *Lobophora* sp. increased three months post-harvest and again at six months, when *Asparagopsis* cover had declined, in both control and treatment plots (Fig. S5a,b, Online Resource). As this species spreads across the substrate, it may have taken advantage of the space made available both by harvesting in the treatment plots and by the natural decline observed in the controls. *Asparagopsis taxiformis* was often observed growing on *Lobophora* sp. (Fig. S8, Online Resource), suggesting limited competitive interaction between the two species.

The peak in abundance of *Dictyopteris* sp. coincided with the onset of decline of *A. taxiformis*. As both species commonly occupied similar substrates, this pattern potentially suggests competition. However, the interaction may also reflect temporal niche partitioning rather than direct competition, given that *A. taxiformis* exhibits senescence in summer and sensitivity to thermal stress based on previous observations (Rula et al., unpublished). *Dictyota* spp. was found interspersed within *A. taxiformis* fronds on the substrate and also contributed to the community shifts.

Similarly, studies on hand-harvesting of *Fucus serratus* within a 25 m^2 area reported no significant impacts on the associated algal community or on suspension feeders, which were mostly sessile, when compared with control plots after 12 months (Stagnol et al. 2013). However, these outcomes may differ if harvesting is carried out in other seasons, when community composition and responses could vary. In particular, harvesting at the onset of summer may alter the influence of algal cover on the associated sessile community under elevated temperatures. Algal cover provides important benefits to benthic organisms by retaining moisture and reducing thermal stress, especially in the intertidal zone (Bertness et al. 1999). Additionally, the scale of harvesting can alter these dynamics. Larger scales can reduce canopy shading and increase light penetration, which can potentially promote colonisation of fast-growing species. Future research should examine the influence of timing of harvest of *A. taxiformis* on community structure, especially during summer.

Mobile fauna in *Asparagopsis* meadows

The range of mobile fauna observed suggests the potential habitat role *of A. taxiformis* meadows. The small invertebrates, including crustaceans, echinoderms, and polychaetes, likely find shelter and feed on detritus, biofilm, and epiphytes such as diatoms found within the meadows. Invasive populations of *A. taxiformis* typically host less diverse epifauna than native seaweeds such as *Halopteris scoparia* (Navarro-Barranco et al. 2018) and *Ericaria brachycarpa* (Mancuso et al. 2021; Mancuso et al. 2022). This reduced diversity may be linked to the halometabolites produced by *Asparagopsis*, which have herbivore deterrent properties (Paul et al. 2006). Some lineages of *A. taxiformis* are native to Australia. Therefore, it is important to determine whether these compounds similarly influence the diversity of associated fauna, highlighting the need for comparative studies with other seaweed species.

In addition, these macrofauna potentially use the meadows for foraging or transit. Seabirds were also found actively fishing in these areas. Squid egg masses at Rat Reef suggest potential spawning habitat, possibly aided by chemical defences deterring predators. Previous studies have cited the role of seaweeds as spawning substrates for the oval squid in Japan, providing squids an alternative site to their typical spawning substrate (seagrass) at high spawning periods or in response to changes in seasonal shifts of seagrass (Kimoto et al. 2023). Surveys conducted in *A. taxiformis* meadows in Middle Reef, Townsville, as well as Great Keppel Island, also showed a variety of organisms within areas where *A. taxiformis* was present, including hard corals, molluscs, and other invertebrates, reef fish, sea turtles, and other seaweeds (Smith et al. 2024; iNaturalist Community 2025).

These findings from the present study and survey reports provide a preliminary overview of the fauna associated with *Asparagopsis* meadows, offering important ecological information to guide future research on harvesting impacts and the development of sustainable harvesting practices. Given that *A. taxiformis* meadows appear to support a variety of associated fauna, precautionary strategies should aim to minimise disturbance to the associated community. Quantitative studies are recommended to better understand the ecological role of native *A. taxiformis* in the marine environment and determine potential impacts of harvesting.

Conclusions

The sustainable harvesting of wild seaweed populations depends critically on understanding their capacity for regrowth and maintaining ecological integrity. This study provides the first assessment of regrowth and associated sessile benthic community dynamics in *Asparagopsis taxiformis* meadows following harvesting. Results indicate that harvesting during the austral winter peak may be a viable approach, given the observed regrowth, natural decline of biomass, and limited effects on the associated sessile community. Handpicking and cutting demonstrated a notable rebound within four to five months. Long-term monitoring is needed to examine and validate these responses. Handpicking and cutting showed distinct regeneration patterns, prioritising horizontal spread and shoot elongation, respectively. This study also highlights the potential habitat function of *A. taxiformis*, underscoring the need to account for its ecological role in the development of sustainable harvesting practices.

Despite the limitations acknowledged above, this study provides valuable insights into the ecology of *A. taxiformis* and the effects of harvesting. These findings highlight the importance of aligning harvesting with seasonal cycles and using environmental monitoring to support adaptive and sustainable management. Further research with longer monitoring and larger scales is imperative for determining full recovery and the broader applicability of these results.

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Declarations

Competing interests NAMR is supported by FutureFeed Pty Ltd through the Elevate Scholarship program. This support does not influence the analysis or interpretation of the research findings. RDK was Chief Science Officer with FutureFeed during this study. All other authors declare no competing interests.

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