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REPORT

Holdfasts of *Sargassum swartzii* are resistant to herbivory and resilient to damage

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Abstract The importance of herbivory in both preventing and reversing shifts to macroalgae dominance on coral reefs has been extensively investigated. However, most studies examining the capacity for herbivores to consume fleshy macroalgae (e.g., *Sargassum*) have investigated removal of the 'leafy' biomass without considering the susceptibility of other components of the macroalga, in particular the holdfast, to herbivory. Here, we investigate the susceptibility of *Sargassum* components (blades, stipes and holdfasts) to herbivory and investigate the capacity for *Sargassum* to regrow following damage to the holdfast. We placed entire thalli of *Sargassum swartzii* on the reef crest at Lizard Island, northern Great Barrier Reef, for 24 d, and used photographs and video recordings to quantify rates of removal over this period. The blades of the *S. swartzii* were rapidly removed (100% in 2 d), whereas the stipes were less susceptible to herbivores, with 72% of experimental thalli having partial stipes remaining after 24 d. Only one holdfast (out of 54) was removed during the experiment, while all of the remaining holdfasts were largely undamaged. When *S. swartzii* holdfasts were experimentally damaged, we found no detectable effect on thallus height or holdfast size among regrown thalli after 1 y. There was, however, a 50% reduction in survival for *S. swartzii* individuals when 75% of the holdfast was removed. This study shows that holdfasts of *S. swartzii* are extremely resistant to herbivory, and that incidental bites on *S. swartzii* holdfasts are unlikely to affect their growth or survival unless three-quarters of the holdfast is removed. The capacity of *Sargassum* to regenerate from damaged holdfasts, coupled with the low rate of herbivory on holdfasts, suggests that sustained browsing (preventing regrowth of the stipe and blades) may be more important in reversing macroalgae dominance than physical removal of holdfasts by herbivorous fishes.

Keywords Herbivory · *Sargassum* · Holdfasts · Regime shift · Coral reef · Resilience · Nitrogen

Introduction

Coral cover is declining in all major reef regions, largely due to the combined effects of global climate change and local anthropogenic stressors (De'ath et al. 2012; Heron et al. 2016; Hughes et al. 2017). This reduction in coral cover often leads to an expansion of the cover of algae and other organisms (Norstrom et al. 2009) that rapidly colonise the dead coral skeletons (Diaz-Pulido and McCook 2002). Reefs with relatively intact herbivore assemblages appear to be able to compensate for this increased algal production, maintaining algal communities in a cropped state and facilitating the recovery of coral assemblages (e.g., Adam et al. 2011; Gilmour et al. 2013). However, on reefs where herbivore assemblages have been reduced, the

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capacity to absorb the increased algal production is compromised; releasing algal communities from top-down control that may ultimately lead to a new regime dominated by fleshy brown macroalgae, such as *Sargassum* (Bellwood et al. 2004; Mumby and Steneck 2008). Such regime shifts represent a fundamental change in habitat structure and functioning, and once established can be difficult to reverse (Scheffer et al. 2001; van de Leemput et al. 2016; Harborne et al. 2017).

The apparent stability of macroalgal-dominated regimes has been attributed to a range of positive feedbacks that enhance macroalgal growth and/or limit the replenishment and recovery of scleractinian corals (Hughes et al. 2007; Mumby and Steneck 2008; Hoey and Bellwood 2011; Dell et al. 2016; van de Leemput et al. 2016). For example, herbivorous fishes have been shown to avoid dense stands of macroalgae, which, in turn, may lead to further expansion of the macroalgae (Hoey and Bellwood 2011). The settlement of coral larvae, and the growth and survival of corals, are inhibited by the presence of macroalgae (Venera-Ponton et al. 2011; Webster et al. 2015) and can potentially lead to further declines in coral cover and expansion of macroalgae (Hughes and Tanner 2000). The presence of these feedbacks suggests that removal of established macroalgae in reef habitats will require greater levels of herbivory than those initially required to prevent macroalgae from becoming established (Mumby et al. 2007; van de Leemput et al. 2016). However, the capacity of herbivores to initiate a change from a macroalgal-dominated regime towards a coral-dominated regime is likely to depend not only on the overall rate of herbivory, but also on the specific nature of herbivory. Notably, the species of herbivores (and their specific functions) that are necessary to reverse regime shifts are different to those that prevent the initial proliferation of macroalgae (Bellwood et al. 2004).

Herbivorous reef fishes may be broadly classified into two groups, macroalgal browsers and grazers. Macroalgal browsing fishes typically consume large, fleshy macroalgae, such as *Sargassum*, and have been suggested to be important in potentially reversing macroalgal-dominated regime shifts (Bellwood et al. 2006). In contrast, grazing fishes typically feed on the Epilithic Algal Matrix (EAM; a conglomerate of short, productive algal turfs, macroalgal propagules, detritus and microbes) and are thought to play an important role in the prevention of shifts to macroalgal dominance by consuming small macroalgal propagules growing within the EAM (Bellwood et al. 2004; Mumby 2006). Previous research has shown that while the removal of macroalgal biomass by browsers can be rapid, it is dependent upon the actions of a limited number of species; grazing fishes appear to be largely incapable of removing large fleshy macroalgae from the reef (Hoey and Bellwood 2009). Although this distinction is important, these studies have not considered the capacity of herbivores to remove different components of the macroalgae (but see Streit et al. 2015) and rarely consider the ecology of the macroalga itself. Importantly, the capacity of herbivores to remove the macroalgal holdfast has never been considered, despite the ability of some macroalgae such as *Sargassum* to regrow from holdfasts when the stipes and blades are removed (Ang 1985; Vuki and Price 1994; Loffler and Hoey 2018). Investigating the capacity of herbivores to damage and/or remove macroalgal holdfasts, and the effect of holdfast damage on the subsequent growth and survival of the macroalgae is critical to further understanding the feedbacks maintaining and expanding macroalgal communities.

The purpose of this study was to investigate rates of herbivory on different components of *Sargassum swartzii* thalli, specifically comparing the rate and extent of removal of blades, stipes and holdfasts for thalli translocated into areas with high levels of herbivory. We also investigated the resilience of *S. swartzii* to physical damage of holdfasts, testing whether increasing levels of experimental damage (up to 75% removal of the area of holdfasts) impacted the survival and size of individuals during the next growing season.

Methods

Study sites

This study was conducted over 1 y (November 2016 to November 2017) at both the mid-shelf reef of Lizard Island (14°40′S, 145°28′E) and the inner-shelf reefs of the Turtle Group (14°43′S, 145°12′E) in the northern Great Barrier Reef (GBR), Australia (Fig. S1). Lizard Island is a granitic island in the northern GBR. The Turtle Group Islands are approximately 28 km west of Lizard Island and 11 km from the mainland coast. The fringing reefs surrounding the islands in the Turtle Group are characterised by low coral cover on the south-east and north-east aspects with large beds of *Sargassum* (up to 1.5 m tall) at depths less than 3 m (Hoey and Bellwood 2010a). *Sargassum* spp. is rare at Lizard Island, but does occur in areas of low herbivory, such as in damselfish territories (Hoey and Bellwood 2010b) and on the reef flat (A.S. Hoey pers. obs.).

Herbivory of *S. swartzii*

To compare rates of herbivory between the major components of *Sargassum* (blade, stipe, and holdfast) and to identify the species responsible, we exposed assays of whole *Sargassum swartzii* thalli to local herbivore assemblages on Lizard Island and recorded any feeding using stationary underwater video cameras. Twenty-four pieces of reef substrate with attached *S. swartzii* thalli were collected from the Turtle Group reefs using a hammer and chisel (carbonate pavement; 15–20 cm diameter) to ensure holdfasts were collected in their entirety. Each piece of reef substrate had between 1 and 4 individual *S. swartzii* thalli attached. The combination of *S. swartzii* thalli attached to pieces of reef pavement is hereafter referred to as 'assays'. These assays were transported back to Lizard Island Research Station within 3 h of collection and placed in a 1000 L aquarium (2 × 1 × 0.5 m) with flow-through seawater and supplemental aeration. The number of *Sargassum* thalli, the height of each thallus and the diameter of its corresponding holdfast were recorded, and each assay labelled with a small numbered plastic tag. For each holdfast, we recorded the maximum diameter and perpendicular diameter to the nearest 0.1 mm using callipers. Assays were deployed within 48 h of collection.

To quantify the rate and extent of herbivory, assays were deployed at two reef crest sites (2–3 m depth) exposed to the prevailing south-easterly winds (Fig. S1). Twelve randomly selected assays were placed at each site, with eight exposed to local herbivore assemblages and four placed inside herbivore exclusion cages to control for the effects of handling, translocation and survival of the *S. swartzii* over the 24-d experimental period. Each assay was secured to a 20 × 20 × 4 cm paving tile using a cable tie, placed on an area of bare substratum (i.e., covered by turf algae yet free of live coral and other macroinvertebrates) and secured to the reef with thin galvanised wire (0.5 mm) threaded through natural holes in the reef (Fig. S1). Exclusion cages (40 × 30 × 30 cm with 1 cm^2 mesh) were secured over control thalli and held in place with lead weights that were cable tied to the bottom corners of each cage. All assays were positioned at a similar depth (2–3 m) with a minimum of 2 m between adjacent assays.

To estimate the reduction in *S. swartzii* biomass during the experimental period, each assay exposed to herbivores was photographed every 1–4 d (weather dependent) for the first 19 d and again after 24 d. A 30-cm ruler was held adjacent to each assay to provide a scale for quantifying leaf area. Photographs of caged assays (i.e., controls) were taken at the beginning and end of the experimental period. The total surface area of the *S. swartzii* was estimated by tracing around it in the photographs using the program ImageJ, and for each replicate, the components remaining (i.e., blades, stipes, and holdfast) were recorded. By quantifying changes using photographs, we minimised handling and disturbance during the experimental period.

To identify the fishes responsible for removal of *S. swartzii* blades and stipes, and any fishes grazing on the experimental rocks, a small remote underwater video camera (GoPro) attached to a dive weight was placed ∼ 1 m from each uncaged rock. The video cameras were deployed once per day (between 08:00 and 09:00, for 3.5 h) on the first 3 d and every 2–4 d thereafter (weather dependent), until day 19 (9 d of video per rock). No video was taken between day 20 and the conclusion of the experiment (day 24). After 24 d, the rocks were collected and the diameter of remaining holdfasts and the height of any remaining *S. swartzii* thalli were re-measured as previously described.

The entire video footage (∼ 450 h) was analysed and each fish larger than 10 cm that took bites on the *S. swartzii* thallus and/or experimental 'rock' was recorded. Fishes smaller than 10 cm were not included due to difficulties in accurately quantifying individual bites and/or identifying individuals to species. Due to difficulties in determining whether fishes observed taking bites from the surface of the rock were biting the *S. swartzii* holdfast or adjacent to the holdfast, all bites on the rocks were recorded.

Carbon and nitrogen content of *S. swartzii* components

To determine whether any differences in feeding could be related to the elemental composition of the *S. swartzii* components, the carbon and nitrogen content of the *S. swartzii* tissues were analysed. Samples of holdfasts, stipes and blades were taken from five distinct *S. swartzii* thalli collected from the Turtle Group and freeze-dried for 48 h. Samples (min. 0.2 g dry weight) were then sent to OEA Laboratories LTD, UK to quantify carbon and nitrogen content using an elemental analyser, giving the percentage of carbon and nitrogen as grams per 100 g dry weight (% dw).

Survival and regrowth of damaged *S. swartzii* holdfasts

To determine if damage to a holdfast affects the subsequent survival and regrowth of the thallus, four levels of damage were inflicted on holdfasts of *S. swartzii* in November 2016 and their condition monitored after 12 months. Two sites on the leeward aspect of reefs in the Turtle Group were selected. These two sites were characterised by numerous shallow bommies densely covered with *S. swartzii* and interspersed with areas of sand and coral rubble. At each site, three 4 m^2 patches of *S. swartzii* of similar height were haphazardly selected, with at least 4 m between adjacent patches. Within each patch, all *Sargassum* were cut with scissors just above the holdfast. A small numbered tag was attached to the substratum with a galvanised nail next to each holdfast to allow individual holdfasts to be identified. Any other holdfasts within a 10 cm radius of the tag and experimental holdfast were removed using a hammer and chisel. The diameter of the tagged holdfasts was measured (using the same method previously described), photographed and haphazardly allocated to one of four treatments: (a) control (not manipulated/damaged), (b) 25% of holdfast removed, (c) 50% of holdfast removed and (d) 75% of holdfast removed. As a result of removing 75% of the holdfast, the original point of stipe growth was removed in this treatment but was not entirely removed in any of the other treatments. A Stanley knife was used to make a vertical cut through the holdfast, and the 'offcut' (either 25, 50 or 75%) was then scraped off the substratum, being careful not to disturb the remaining portion of the holdfast. A photograph of the holdfast was also taken after the damage was inflicted, to facilitate re-identification.

After 12 months (i.e., November 2017) each experimental patch was systematically searched and the remaining tags and holdfasts identified. If there was no holdfast within 10 cm of a tag, the individual was recorded as dead. For each surviving holdfast, the height of its thallus was measured to the nearest centimetre using a tape measure and the diameter of the holdfast was measured as described above. A photograph was taken of the holdfast and its corresponding tag. All before and after photographs were examined to ensure that the correct holdfast had been identified and measured. The loss of some tags led to an unbalanced design, with the tags corresponding to 14 control, 16.25%-removed, 22.50%-removed and 27.75%-removed treatments remaining.

Statistical analyses

All statistical analyses were conducted using R version 3.4.1. R packages rstan and rstanarm were used to run Bayesian analyses. All models used Gaussian distributions. Weakly informative priors were used, with 5000 iterations, a warmup of 2500, three chains and a thinning factor of five. Diagnostic plots were analysed to ensure there was convergence of chains, no autocorrelation and that priors were sufficiently wider than the posterior values. All Rhat values were < 1.05 and ESS values were > 0.6.

To compare the size of holdfasts before and after deployment between caged and exposed thalli, a Bayesian generalised linear model was used, with date and treatment included as fixed factors. Differences in elemental composition (i.e., carbon and nitrogen content) among components of the *S. swartzii* were analysed with Bayesian generalised linear mixed effects models. Component (holdfast, stipe or blade) was included as a fixed factor with each *S. swartzii* used as a random factor to account for any differences among *S. swartzii* individuals. Any differences in the survival, holdfast diameter or thallus height of damaged holdfasts among treatments 1 y after damage was inflicted was analysed using Bayesian generalised linear mixed effects models. Damage inflicted was included as a fixed factor and patch was included as a random factor.

Results

Herbivory of *S. swartzii*

Within 2 d of deployment, all blades had been removed from all thalli exposed to herbivores, corresponding to an 88% decrease in surface area, from 320 ± 31 cm^2 on day one to 40 ± 7 cm^2 on day two (Fig. 1a). Thereafter, the surface area of the thalli decreased slowly, from 22 ± 4 cm^2 on day three to 7 ± 2 cm^2 on day 19. After 24 d the majority of assays (72%) still had partial stipes present and only 28% of assays had stipes completely removed (Fig. 1c). Only one holdfast (out of 53) was removed after 24 d of exposure to local herbivore assemblages. For caged controls, surface area and height of assays decreased by 27.5% and 28.9%, respectively, over the course of the experiment. All control thalli had holdfasts, stipes and blades remaining at the conclusion of the experiment.

Video analysis revealed that the rapid consumption of the blades of the *Sargassum* in the first 2 d of deployment was primarily due to the feeding by two fish species: *Naso unicornis* and *Siganus doliatus* (Figs. 1b, 2). These fishes took 66 and 17% of total bites on the *S. swartzii*, respectively, on the first 2 d of deployment. Bite rates on the *S. swartzii* decreased markedly once the blades had been removed. For example, *Naso unicornis* took 98% of its bites in the first 2 d, when the *S. swartzii* thalli had blades remaining.

The number of bites taken on the surface of the experimental rocks increased from an average of 39 ± 13 bites 3.5 h^{-1} on day one, to 81 ± 25 bites 3.5 h^{-1} on day ten before dropping to 58 ± 9 bites 3.5 h^{-1} on the last day of video (day 19; Fig. 1b). The majority of bites were taken by two surgeonfishes, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (taking 40 and 21% of total bites on the rocks, respectively; Fig. 2). Bites by parrotfishes accounted for 11% of total bites, with *Scarus niger* and *Chlorurus spilurus* being the predominant parrotfish species (4 and 3% of total bites, respectively; Table S1). Evidence of feeding (i.e., parrotfish feeding scars) on the rocks was variable; some rocks were highly grazed (Fig. 3), yet others had few grazing scars. Interestingly, feeding marks were concentrated on the rocks, with little evidence of grazing scars on holdfasts, suggesting that fishes may have avoided feeding on the holdfasts (Fig. 3). Indeed, none of the exposed holdfasts remaining at the end of the

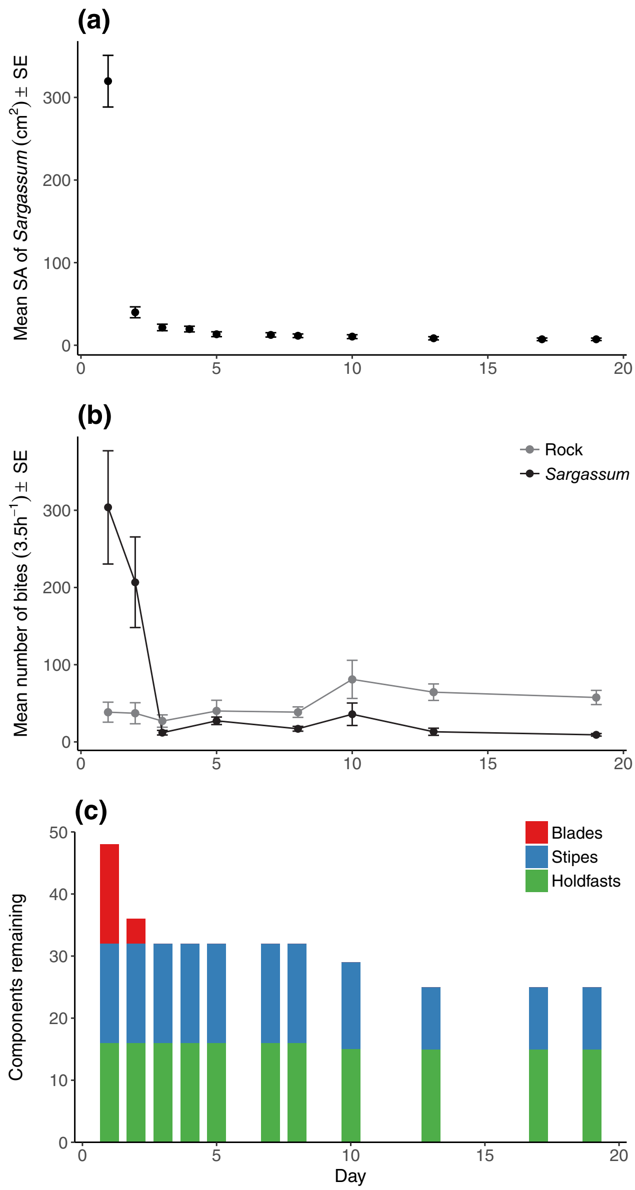

Fig. 1 a Mean surface area (SA) of *Sargassum swartzii* thalli throughout experiment ± SE; **b** Mean number of bites in 3.5 h on deployed rocks and their attached *S. swartzii* thalli, ± SE; **c** Components of exposed *S. swartzii* thalli remaining throughout the study: there were 16 assays exposed to herbivores (i.e., for day one, 16 assays × 3 components = 48). Experiment was concluded after 24 d, however, feeding observations (i.e., video footage) were only taken to day 19. No further removal of components occurred between day 19 and day 24

experiment decreased in diameter compared to controls (Fig. S2, Table S2).

Carbon and nitrogen content of *S. swartzii* components

The nitrogen content of *S. swartzii* differed among components, with the holdfasts (0.81 [0.72, 0.92] % dw, mean and 95% credible intervals), and blades (0.81 [0.74, 0.87] % dw) having greater nitrogen content than the stipes (0.48 [0.38, 0.59] % dw; Fig. 4, Table S3). The carbon content of holdfasts was highest at 33.4 [32.2, 34.4] % dw, with stipes and blades lower at 30.4 [29.3, 31.4] and 28.6 [27.7, 29.4] % dw, respectively (Fig S3, Table S4). This meant that the holdfasts and blades had similar C:N ratios of 42 [35, 49] and 36 [31, 41], respectively, while the stipes had a ratio of 64 [57, 71] (Fig. S4, Table S5).

Survival and regrowth of damaged *S. swartzii* holdfasts

Experimentally imposed damage to holdfasts of *S. swartzii* resulted in dissimilar survival over the subsequent year. Those holdfasts that had 75% of the holdfast removed experienced significantly higher mortality (mean and 95% credible intervals; 60 [44, 81] %) compared to all other levels of damage (half: 26 [6.1, 44] %, quarter: 7 [− 15, 25] %, control: 20 [1, 40] %; Fig. 5c; Table S6) over 12 months. All surviving holdfasts were, on average, 40–60% larger than their initial pre-damage size, with no significant difference in the diameter of surviving *S. swartzii* holdfasts among treatments (Fig. 5a; Table S7). There was very weak evidence of a difference between the height of the control *S. swartzii* (mean and 95% credible intervals; 56 [18, 97] cm) and the *S. swartzii* that had 75% of the holdfast removed (89 [50, 128] cm), but no differences between any other treatments (Fig. 5b; Table S8).

Discussion

Despite widespread recognition that herbivory is essential to the effective functioning of coral reef ecosystems, by limiting the areal extent and biomass of macroalgae (Hay 1981; Bellwood et al. 2004; Graham et al. 2013), the removal of macroalgal holdfasts by herbivores has been largely overlooked. Our results show that while initial removal of *S. swartzii* blades was rapid, the subsequent removal of the stipes and holdfasts was negligible; only one of 53 holdfasts was removed during the 24-d deployment. Removal of the leafy *Sargassum* biomass was largely attributed to feeding by *Naso unicornis* and *Siganus doliatus,* as reported in previous studies (Hoey and Bellwood 2009, 2010a; Bennett and Bellwood 2011; Michael et al. 2013; Chong-Seng et al. 2014). Despite high grazing on many of the exposed rocks, feeding scars were concentrated in the areas free of holdfasts. Interestingly, the experimental removal of 75% of the holdfast reduced survival of *S. swartzii*, but lower levels of damage had no effect on survival. Further, damage inflicted on holdfasts had a limited effect on the height of regenerated thalli after

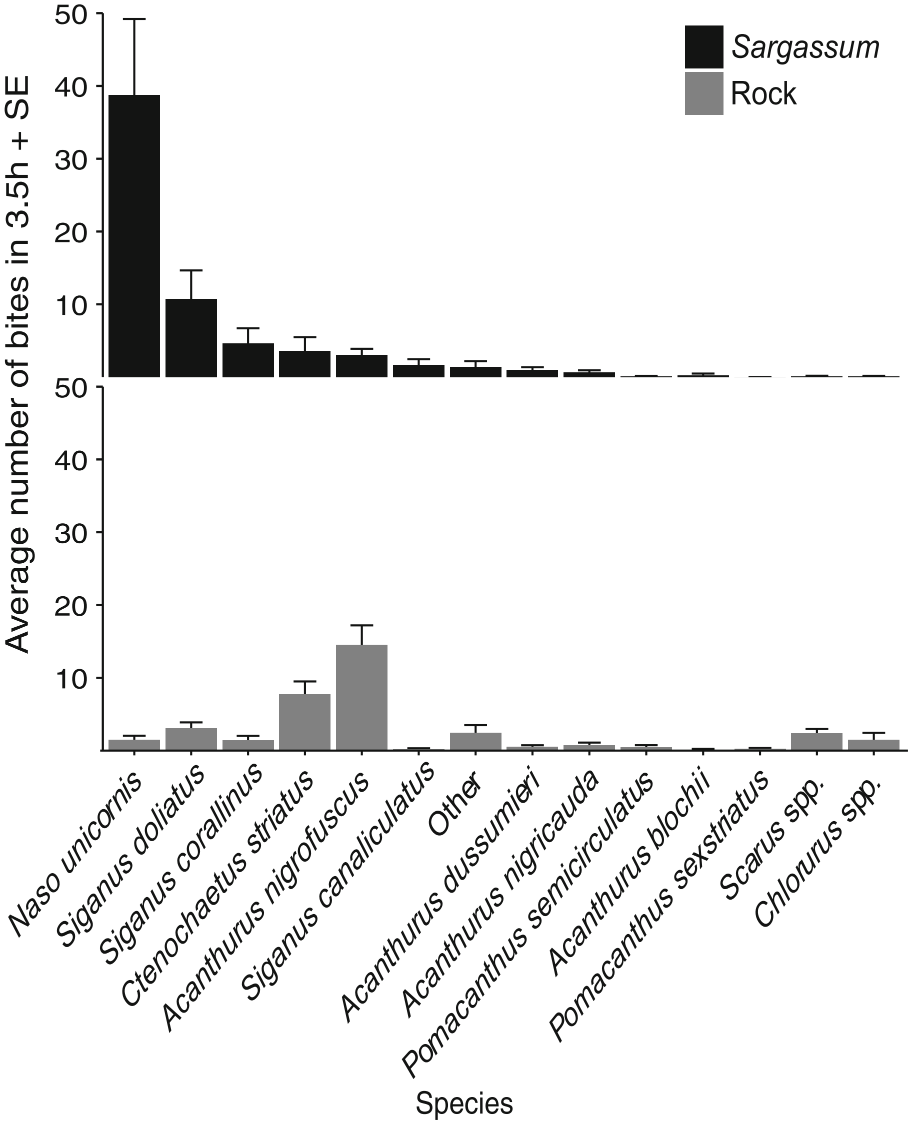

Fig. 2 Average number of bites taken on assays in 3.5 h of video over the course of the experiment. Fish species are ordered by the number of bites on *Sargassum swartzii.* For full list of species and their corresponding bite count, see Table S1

1 y. Collectively, these results suggest that herbivorous fishes appear to avoid holdfasts, at least for *S. swartzii*, and that holdfasts of this species seem extremely resilient to physical damage.

This study demonstrates the remarkable capacity of *S. swartzii* to regenerate from holdfasts that have had up to three-quarters of their area removed from the substratum. Temperate phaeophytes have been reported to have a similar capacity to regenerate from small pieces of holdfast (McCook and Chapman 1992; Westermeier et al. 2013). In the present study, the diameter of *S. swartzii* holdfasts and height of the thallus did not substantially differ across treatments 1 y after damage was inflicted. However, mortality increased when three-quarters of the holdfast was removed from the substratum (60% mortality) when compared to undamaged controls, and half and quarter-removed treatments (7–26% mortality). Gorham and Lewey (1984) suggest that the spring growth of *Sargassum muticum* is not predominantly supported by stored polysaccharide reserves in the holdfast, although stores of nitrogen within the holdfast were observed to deplete during this rapid growth phase suggesting nitrogen may somewhat limit the capacity for regeneration. While the mechanisms supporting the regrowth of *Sargassum* from small pieces of holdfast are unclear, this high mortality could be due to a weakening of the holdfasts' attachment to the benthos after damage (Westermeier et al. 2013), or having too few resources to successfully regenerate, as a holdfast's energetic resources are likely to be finite (Gomez and Westermeier 1991). Notably, in the 75% removed treatment, the original point of stipe growth was removed. It is unknown if having this point of growth removed affected *S. swartzii*'s capacity for regrowth. Nevertheless, this study demonstrates that herbivores must remove over a certain

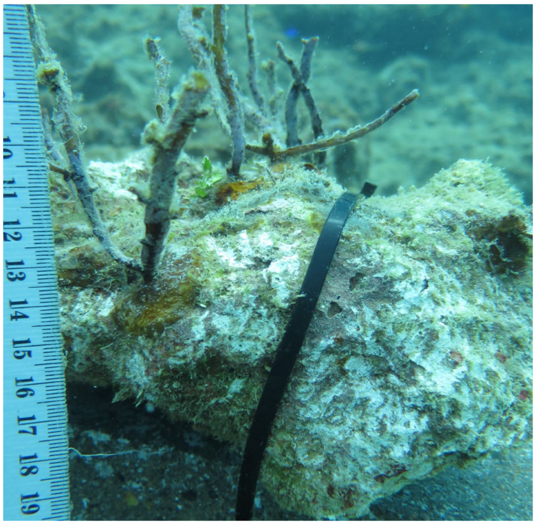

Fig. 3 Example of grazing scars surrounding the holdfast on rocks exposed to herbivory. This photograph was taken 4 d after deployment. At the conclusion of the experiment, stipes had been removed from this rock, however, the holdfasts remained intact and had not decreased in size, despite the high grazing impact on the rock

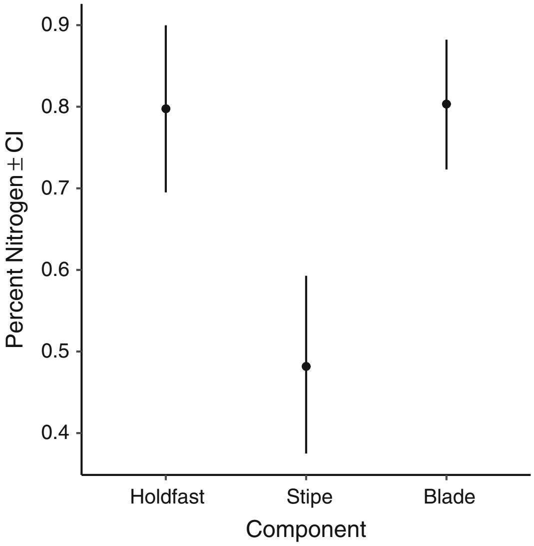

Fig. 4 Per cent nitrogen in *Sargassum swartzii* components, presented as mean ± 95% credible intervals. The stipe component had a significantly lower nitrogen content than the holdfast and blade components

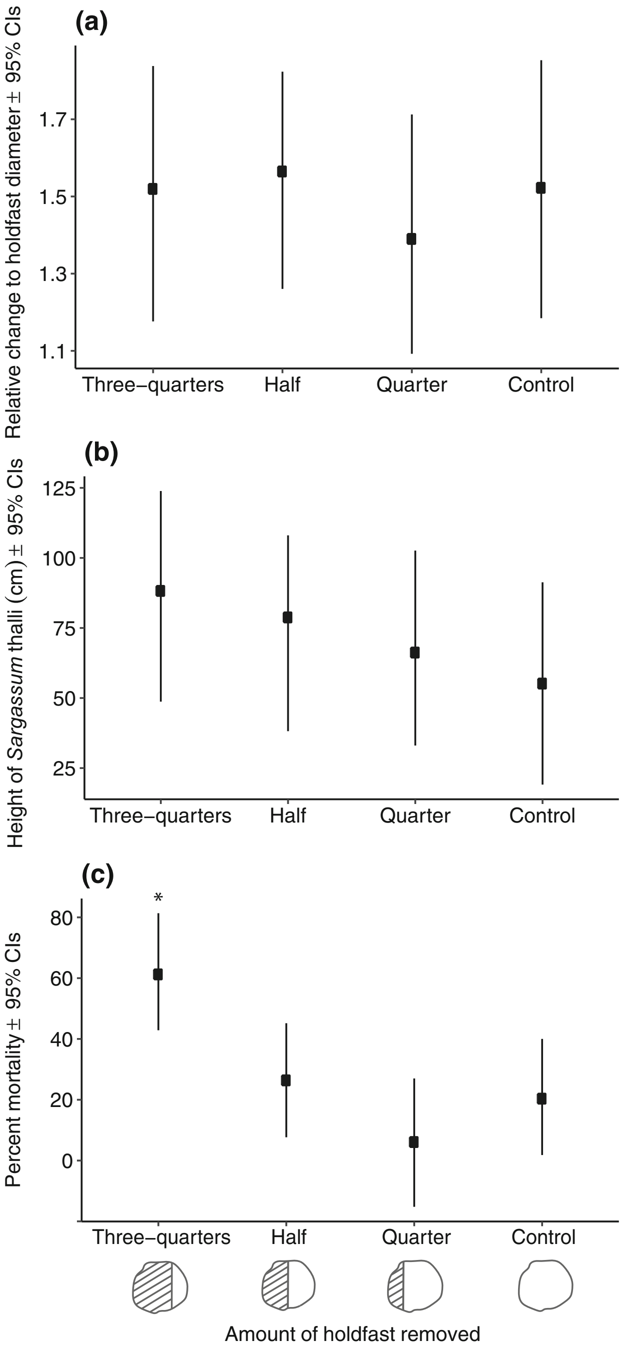

Fig. 5 **a** Relative change to holdfast diameter of surviving holdfasts 1 y after damage was inflicted ± 95% credible intervals. The initial size of the holdfasts (before any damage was inflicted) is compared to the final size of holdfasts (1 y post-damage). A relative change of 1.5 would indicate that the holdfast has increased in size by 50%; **b** Height of *Sargassum swartzii* thalli (cm) ± 95% CIs 1 y after damage was inflicted on holdfasts; **c** Per cent mortality of *S. swartzii* holdfasts 1 y after damage was inflicted ± 95% CIs. Asterisk indicates significant difference

threshold amount (here, 75%) of the holdfast before the regenerative capacity of *S. swartzii* is reduced. Holdfasts are, therefore, likely to be highly resilient to grazing.

Observed differences in rates of feeding among the components of *Sargassum* may be related to the nutritional composition of those components. Browsing fishes, predominantly *Naso unicornis* and *Siganus doliatus,* quickly consumed the blades and fleshy upper portions of the thallus, as has been reported in several previous studies (Hoey and Bellwood 2009, 2010a; Bennett and Bellwood 2011; Michael et al. 2013; Chong-Seng et al. 2014). However, the stipes and holdfasts were not readily consumed and many remained after 24-d of exposure to herbivores. Differences in secondary metabolites (phenolics) among tissues are unlikely to explain observed differences in herbivory; Steinberg et al. (1991) demonstrated that rates of herbivory by tropical fishes were not influenced by the amount of phenolics in different species of *Sargassum*. However, the stipes of *S. swartzii* contain approximately 40% less nitrogen than the blades and holdfasts, which has also been reported in other phaeophytes (Gevaert et al. 2001). This nutritional difference may explain why the stipes were not consumed at the same rate as blades, which were removed within the first 2 d of deployment (Diaz-Pulido and McCook 2003). Although measurements of physical toughness were not performed in the present study, the physical toughness of *Sargassum* is known to differ among components, with holdfasts being the toughest component followed by stipes (Taylor et al. 2002). This may help explain why all holdfasts except one were left intact despite containing a similar amount of nitrogen as blades.

Only a single holdfast (out of 53 holdfasts) was removed and none of the surviving holdfasts showed any significant signs of damage or change in size by the conclusion of the experiment. The fish species that predominantly grazed on the rocks (i.e., the detritivore *Ctenochaetus striatus,* the algal cropping *Acanthurus nigrofuscus* and *Siganus doliatus* and the browsing *Naso unicornis)* are unlikely to have the jaw morphology or feeding mode required to remove holdfasts from the substratum (Purcell and Bellwood 1993; Konow et al. 2008; Fishelson and Delarea 2014; Tebbett et al. 2017). Although *N. unicornis* consumes leathery brown macroalgae, its jaw and tooth morphology facilitates biting tough algae rather than scraping it off the benthos (as in the case of holdfast removal) (Fishelson and Delarea 2014). Indeed, unlike browsing fishes such as *N. unicornis,* most fishes with the ability to remove holdfasts from the substratum (i.e., parrotfishes) generally do not target or consume leathery brown macroalgae, instead gaining the majority of their nutrition from endolithic or epilithic phototrophs, mainly cyanobacteria, found on or within ingested materials (Clements and Choat 1995; Choat et al. 2004; Clements et al. 2016). Their contribution to holdfast removal is, therefore, likely to be limited.

Despite the apparent lack of herbivory of *Sargassum* holdfasts in the present study, the reversal of a macroalgal regime shift has occurred in a number of locations. Bellwood et al. (2006) monitored the reversal of an experimentally-induced ‘regime shift’ dominated by *Sargassum* on an inshore reef of the GBR. Within 2 months of cage removal, experimental and control (adjacent, non-caged) plots were indistinguishable. In Fiji, the implementation of marine protected areas on reefs dominated by *Sargassum* and other brown macroalgae led to increased coral cover and herbivorous fish biomass inside reserves (Rasher et al. 2013). Furthermore, introducing native sea urchins to reefs manually cleared of invasive macroalgae helped prevent the return of the macroalgae in Kane’ohe Bay, Hawai’i (Conklin and Smith 2005; Goreau et al. 2008; Battista et al. 2016). These studies demonstrate that high rates of herbivory can return an area dominated by macroalgae back to coral dominance (Bellwood et al. 2006; Rasher et al. 2013). Nonetheless, high browsing pressure that inhibits successful regrowth of macroalgae from the holdfast may be sufficient to cause mortality of the *Sargassum* without direct removal; Gomez and Westermeier (1991) demonstrate that sustained frond removal in the red alga *Iridaea laminarioides* reduced the ability of the holdfast to produce fronds after 5 months, attributed to the depletion of energetic reserves in the holdfast. If *Sargassum* responds to sustained frond removal in a similar way, perpetual browsing of emergent regrowth may be the most likely mechanism by which regime shifts to *Sargassum* dominance can be reversed in areas without high numbers of sea urchins.

The capacity of *Sargassum* to regenerate from damaged holdfasts, coupled with the low rate of herbivory on holdfasts, may contribute to the stability of macroalgal-dominated states on coral reefs. The findings of this study suggest that recovery of regime-shifted reefs may only reliably occur with sustained high rates of herbivory by certain browsing fishes that can prevent thalli from successfully regenerating from holdfasts, eventually causing mortality of the whole individual. The preferential consumption of the blades and stipes of the *Sargassum*, along with any associated reproductive structures, may decrease the reproductive capacity of *Sargassum*, as has been shown for temperate macroalgae (Poore et al. 2014; O’Brien and Scheibling 2016), further reinforcing the importance of browsing by fishes such as *Naso unicornis* to the reversal of macroalgal-dominated states. Clearly, further research is required to determine if sustained browsing can cause mortality of *Sargassum* without direct removal of the holdfast, or if there is a threshold of herbivory where holdfasts are damaged by incidental herbivory, preventing the *Sargassum* from regenerating. Nonetheless, this research advances our understanding of macroalgae-dominated reefs and provides further insight into why such states are often so resistant to a return to coral dominance.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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