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Short communication

Herbivory as a limiting factor for seagrass proximity to fringing reefs in Moorea, French Polynesia

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ABSTRACT

Seagrasses are important foundational species that frequently display distinct depth distributions, although the drivers of these patterns can be spatially and temporally variable. While the pantropical seagrass *Halophila decipiens* is known from waters as shallow as 1 m deep, in Moorea, French Polynesia we only found it > 6.4 m deep. To explore factors affecting depth distribution, we transplanted *H. decipiens* into 3 habitats: the existing seagrass bed (control), just outside the seagrass bed, and shallower habitat adjacent to a fringing coral reef. Results showed that growth was not significantly different between the control and just outside of the seagrass bed; however, number of shoots and rhizome length were significantly reduced adjacent to the reef. Transplanting seagrass into the shallow reef site with and without herbivore exclusion cages showed that *H. decipiens* grew in herbivore exclusion treatments, but lost both shoots and rhizomes in the control. These results indicate that *H. decipiens* can grow in shallow habitats adjacent to reefs on Moorea, but that herbivory pressure, presumably from the reef, limits its depth distribution.

1. Introduction

Seagrass beds are some of the most productive ecosystems worldwide, providing important ecological and economic benefits to coastal regions. They are the primary food resource for many organisms, provide shelter and nurseries, sequester carbon (Larkum et al., 2006), attenuate water flow, and reduce vertebrate pathogens (Lamb et al., 2017). While seagrasses play key roles in coastal ecosystems, knowledge of the factors that limit their depth distribution is constrained by high spatial variability in a complex mosaic of abiotic and biotic conditions regulating their distribution.

Some of the factors that can shape local or small-scale distribution of seagrasses include chemical characteristics of sediment (Krause-Jensen et al., 2011) and physical disturbances (El Allaoui et al., 2016). Seagrasses also display distinct patterns of depth zonation as a function of abiotic factors such as light attenuation (Duarte, 1991), desiccation (Kahn and Durako, 2009), and characteristics of the seagrass itself such as the ability to tolerate high irradiance (Björk et al., 1999), among others. Similarly, biotic interactions, including competition for resources (Greve and Binzer, 2004) and grazing (Hay, 1981), can control local patterns of distribution. Herbivory may play an important role in controlling local distributions as seagrasses provide a suite of resources for grazing organisms (Heck et al., 2008). Further, grazing pressure can vary as fish communities are impacted by fishing pressure and can be spatially variable as a result of fear of or release from predation (Madin et al., 2011). For example, in the Caribbean Sea, grazing by surgeonfishes, parrotfishes (Randall, 1965), and the urchin *Diadema* (Ogden et al., 1973) can completely eliminate seagrasses from habitats adjacent to coral reefs. While it is clear that herbivory can control local distribution patterns of seagrass (Nowicki et al., 2018), what remains unknown is whether top down control by grazing can shape depth distributions.

The seagrass *Halophila decipiens* is pantropical and can inhabit a broad depth range (0–85 m deep) (Den Hartog, 1970). However, on the

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island of Moorea, French Polynesia, *Halophila decipiens* is known from only three sites, all reported at > 6 m deep (Moorea Berkeley Biocode-biocode.berkeley.edu). Given that *H. decipiens* can occur in other parts of world as shallow as the intertidal, it is unclear what limits this species from occupying shallower waters of Moorea. Here we examine two factors that may limit the distribution of *H. decipiens* in Moorea. We characterized the shallowest depth limit of *H. decipiens* at two sites and conducted two *in situ* experiments to evaluate the abiotic and biotic processes that shape these distribution patterns. We hypothesize that *H. decipiens* cannot survive and grow outside the limits of the existing seagrass beds. Further, we hypothesize that proximity of *H. decipiens* to the reef is limited by herbivory.

2. Materials and methods

Our study occurred in July 2017 at two sites along the northern shore of Moorea, French Polynesia. Site 1 (17° 29′ 34′' S, 149° 51′ 4′' W) is at the mouth of Opunohu Bay and consists of a sandflat ~100 m wide bordered by a fringing reef. Site 2 (17° 28′ 51′' S, 149° 49′ 27′' W) is on the backreef near the mouth of Cook's Bay and is bordered by a patch reef system and a deep natural channel.

To determine the upper depth limits of *H. decipiens*, we quantified seagrass density along the shallow margin of the seagrass bed at both sites using visual transects and noted the shallowest occurrence (Duarte and Kirkman, 2001). We deployed a 30 m baseline transect parallel to the shore along a contour ~two meters inside the upper edge of the seagrass bed. We then placed perpendicular transects from five randomly-selected points along this baseline, extending each towards the shore until encountering the shallowest seagrass shoot. At every meter along each perpendicular transect we recorded depth, counted shoots per 0.25m^2 quadrat (pairs of leaves were recorded as one shoot), and extrapolated shoot density to m^2. Because tidal amplitude only varied ~ 0.15 m at our sites (Hench et al., 2008), we conducted surveys regardless of tidal height.

To determine if *H. decipiens* can survive and grow outside the limits of the existing seagrass beds, we conducted a single factor experiment at Site 1, where we transplanted seagrass into three habitats. First, to determine whether *H. decipiens* could survive in the shallower habitat near the fringing reef, we transplanted seagrass to the sand flat at 2–4 m depth and 1 m from the fringing reef (~18 m from the seagrass bed). Second, to determine whether *H. decipiens* could survive just outside the seagrass bed, we transplanted seagrass within 1–2 m of the margin at 6–8 m depth. Third, as a control for excavation and replanting effects, we excavated and replanted seagrass inside the donor bed at 8–9 m deep.

To begin the experiment, we carefully excavated 30 individual rhizomes with attached roots, shoots, and growing tip from inside the seagrass bed. We counted the initial number of shoots and trimmed rhizomes to similar lengths, making sure to leave the apical tip. Rhizomes averaged 16.5 cm (± 0.7 SE) in length with an average of 8.3 (± 0.3) SE shoots. We transplanted 10 rhizomes into each of the three habitats by excavating a shallow trench of the approximate depth where the rhizomes were extracted, laying roots and rhizomes into the trench, and covering them with the excavated sediment ensuring the shoots remained above the sediment. We then secured each transplant to the benthos with metal U-shaped stakes and ensured blades and shoots were clear of sediment. In this experiment, we lost two ramets transplanted outside the seagrass bed, and two ramets transplanted to the shallow reef.

After 20 days, we re-excavated each transplant, re-counted the number of shoots, and re-measured rhizome length. We calculated change from initial for each response variable (*i.e.* shoot number and rhizome length). After data met assumptions of normality and homogeneity of variance, we conducted one-way ANOVAs using 'stats' package for each response variable (R Core Team, 2019). Significant ANOVAs were followed by Tukey's honest significant difference test (Tukey HSD) to identify treatments that differed.

To explore whether herbivory limits the distribution of *H. decipiens* adjacent to the reef, we performed a paired transplant experiment manipulating herbivore access. We transplanted 20 rhizomes into the same shallow sand flat as in the first experiment using the same methods. Transplants initially averaged 17.9 cm (± 0.8 SE) in length and included 10.4 (± 0.4 SE) shoots. To test for herbivory effects, we deployed transplants in pairs, one rhizome protected by herbivore exclusion cages, while the other was placed in an open cage that allowed herbivory while controlling for cage effects. Closed and open cages were 10 × 40 × 10 cm (L x W x H) and constructed from hardware cloth with 1 cm openings (Carpenter, 1986). Open cages were identical to the closed cages, but with the top and one long side of the cage removed, allowing access for herbivorous fishes and invertebrates. No transplants were lost in this experiment.

After 16 days, we re-measured rhizome length and shoot number. The data conformed to assumptions of parametric statistics, and we performed a paired *t*-test to determine significant differences in growth due to herbivory (R Core Team, 2019).

3. Results

The shallowest recorded depth of *Halophila decipiens* in our survey occurred at 6.4 m at Site 1 ($n = 82$) and 8.6 m at Site 2 ($n = 24$). The density of seagrass shoots varied greatly, ranging from 0 to 706.3 shoots/m^2 at Site 1 and 0–433.3 shoots/m^2 at Site 2. However, average densities were similar with Site 1 at 165.8 shoots/m^2 (± 18.2 SE) and Site 2 at 158.9 shoots/m^2 (± 26.2 SE) (t = test, $p = 0.829$). Distribution was patchy, with no seagrass recorded in numerous quadrats.

Changes in both number of seagrass shoots and length of rhizomes differed across transplant habitats (Fig. 1; shoots: ANOVA, $p = 0.0002$, $df = 27$, $F_{2,27} = 11.6$; rhizomes: ANOVA, $p = 0.0003$, $df = 27$, $F_{2,27} = 10.84$). After 20 days, transplants inside and just outside the existing seagrass bed nearly tripled in shoot number while rhizome length doubled. However, there was no difference in growth between these two habitats for either variable (Tukey HSD; $p > 0.05$ for both comparisons). Increases in the number of seagrass shoots averaged 16.2 shoots 20 d^{-1} (± 3.5 SE) and 11.6 shoots 20 d^{-1} (± 4.9 SE) for inside and outside, respectively. Rhizome length increased by 23.6 cm (± 6.5 SE) and 13.9 cm (± 6.9 SE), for inside and outside respectively.

In contrast, transplants in the shallow habitat lost both shoots and rhizomes, making changes in these metrics significantly different than in the other two experimental treatments (Tukey HSD, $p < 0.05$ for both comparisons). Shallow transplants decreased in number of shoots by 77 % over the course of the experiment (decreased by 6.4 shoots 20 d^{-1} ± 1.1 SE), while rhizome length decreased by 72 % from initial values (decreased by 11.9 cm ± 1.6 SE in length). Rhizome growth was 1.2 cm d^{-1} (± 0.33 SE) within the seagrass bed, 0.7 cm d^{-1} (± 0.4 SE) just outside the seagrass bed, and -0.6 cm d^{-1} (±0.08 SE) at the shallow site. Similarly, shoots increased by 0.8 cm d^{-1} (± 0.2 SE) within the seagrass bed, 0.6 cm d^{-1} (± 0.2 SE) just outside the seagrass bed, and lost -0.3 cm d^{-1} (± 0.05 SE) at the shallow site.

After 16 days, shoots of seagrass transplanted to shallow depths and within herbivore exclusion cages increased by an average of 4.9 (± 2.4 SE), which was a 51.1 % (± 20.8 SE) increase (Fig. 2). Rhizome length also increased over initial values by 7.1 cm (± 2.5 SE) or 39.9 % (± 15.4 SE). However, in open cages accessible to grazers, seagrass transplants lost both shoots and rhizomes; shoots decreased 76.6 % (± 8.4 SE) (on average -8.2 shoots) and rhizomes decreased 7.6 % (± 7.1 SE) in length (on average -1.2 cm). These differences resulted in a significant difference between final number of shoots (paired *t*-test, $p = 0.0001$) and final rhizome length (paired *t*-test, $p = 0.005$).

Caged seagrass near the reef experienced average rhizome growth of 0.44 cm 16 d^{-1} (± 0.16 SE), compared to uncaged treatments, which were -0.07 cm 16 d^{-1} (± 0.08 SE). Similarly, growth of shoots increased by 0.31 cm 16 d^{-1} (± 0.12 SE) in caged treatments and decreased by -0.51 cm 16 d^{-1} (± 0.07 SE) in uncaged treatments.

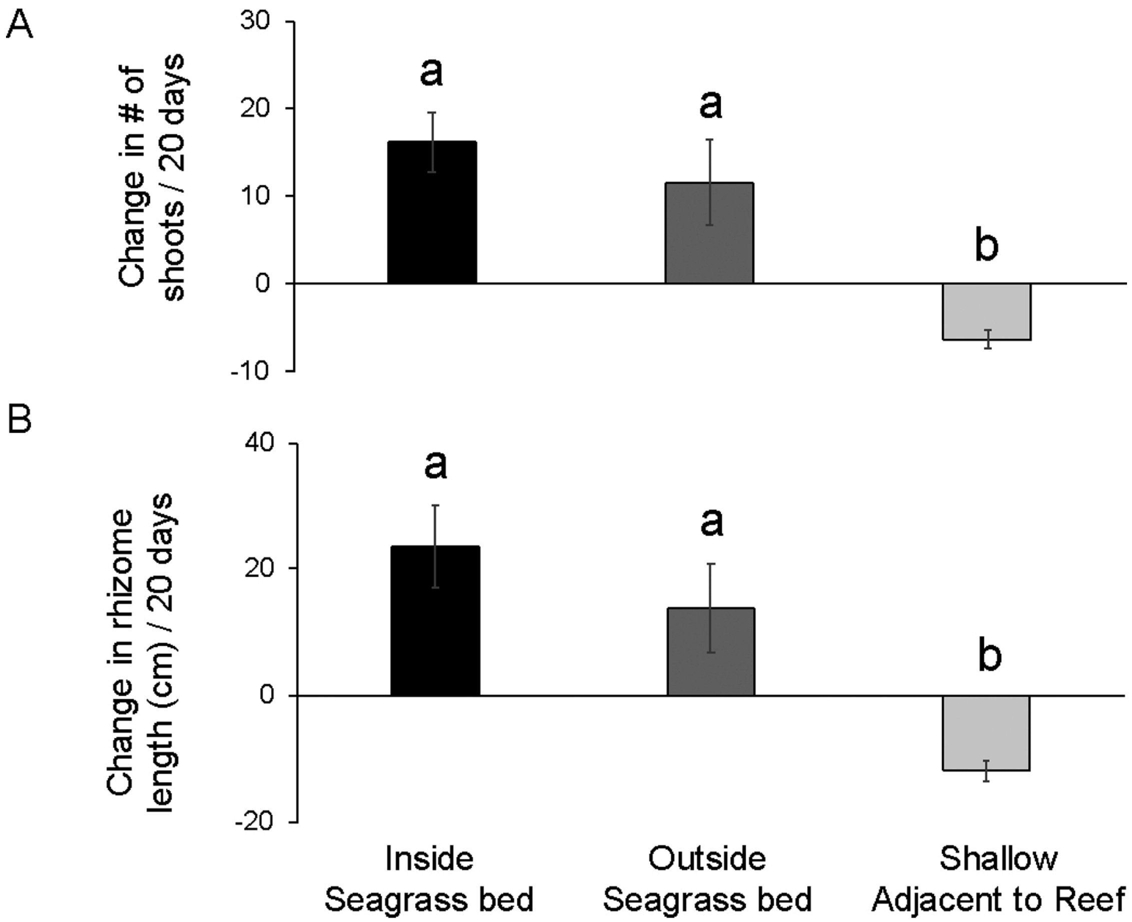

Fig. 1. Changes in (a) shoot number and (b) rhizome length of seagrass transplanted into three habitats: inside seagrass bed, 8 – 9 m deep, outside seagrass bed, 6 – 8 m deep, and shallow habitats, 2 – 4 m deep, 1 m adjacent to fringing reef. Bars are means (± SE). Bars that have different lowercase letters are significantly different.

4. Discussion

The distribution of the pantropical seagrass *Halophila decipiens* in Moorea, French Polynesia was quite limited, occurring no shallower than 6.4 m deep. In contrast, other studies found this seagrass is capable of inhabiting depths as shallow as 0.3 m deep (the lowest intertidal) in Bocas del Toro, Panama (Schubert and Demes, 2017) and 1–2 m deep in Hawaii (McDermid et al., 2002). Although the seagrass we transplanted into shallow (~ 2 m deep) habitat lost shoots and rhizomes, this was not a function of unsuitable habitat. Instead, loss was only observed in shallow water habitats when herbivores had access to the transplants. When transplants in shallow water were protected from herbivory by caging, *H. decipiens* survived and exhibited vigorous growth in both length and number of shoots. Combined, these results demonstrate that *H. decipiens* is likely excluded from shallow reefs habitats of Moorea by herbivory pressure, possibly arising from proximity to shallow fringing reefs inhabited by herbivorous fishes.

Our findings also suggest that shallow water habitats of Moorea may not be optimal for *H. decipiens* growth, even in the absence of herbivores, because the seagrass transplanted to the shallow habitat and caged had a slower daily growth rate compared to transplants to deeper water. Shallow transplants possibly experienced photoinhibition, a process noted in the same species (Durako et al., 2003) and other seagrasses (Björk et al., 1999), which would support the growth rate differences we observed. However, an important caveat to this result is that our two experiments from which we compare growth rates (transplants in deep and shallow water without caging, and caged/uncaged shallow water transplants) were conducted sequentially, not simultaneously. As such, differences in growth may be confounded by time.

Seagrasses can be limited by unstable sediment caused by dredging and sediment infilling (Erftemeijer and Lewis, 2006). All three of the habitats into which we transplanted seagrass were once dredged, and therefore differences in sediment instability due to dredging are not likely contributing to among-habitat differences in growth. The lower growth rates of shallow water *H. decipiens* protected from herbivory indicate that abiotic controls, in addition to herbivory, likely contribute to preventing *H. decipiens* in Moorea from successfully establishing in shallow water habitats. Our findings support the current paradigm that *H. decipiens* has a patchy and discontinuous distribution (Den Hartog, 1989; Fonseca et al., 2008). One possibility could be foraging by animals; for example, bioturbators, such as fishes in the family *Haemulidae, Mullidae* and *Lethrinida*e, feed on endofauna in the sediment and disturb vegetation patterns while foraging up to 25 m from reefs (Madin et al., 2019, Steiner and Willette, 2014). Patchiness of seagrass could be a function of changes in herbivory pressure due to proximity of apex predators, as fear of predators can alter foraging behavior, reducing herbivore movement and consumption (Catano et al., 2016, Rizzari et al., 2014).

Although our results demonstrate that *H. decipiens* is limited by herbivory pressure, we did not observe the taxa responsible for grazing. However, other studies that surveyed herbivorous fishes on the reef adjacent to Site 1 found members of the families *Acanthuridae* (surgeon fishes) and Labridae, subfamily *Scarinae* (parrotfishes) (Gaynus, 2019; Keeley et al., 2015) as well as Siganidae (rabbit fishes) in Site 2 (Poray and Carpenter, 2014). Common species of herbivorous fishes in Moorea include *Zebrasoma scopas, Acanthurus nigrofuscus, Chlorurus sordidus,*

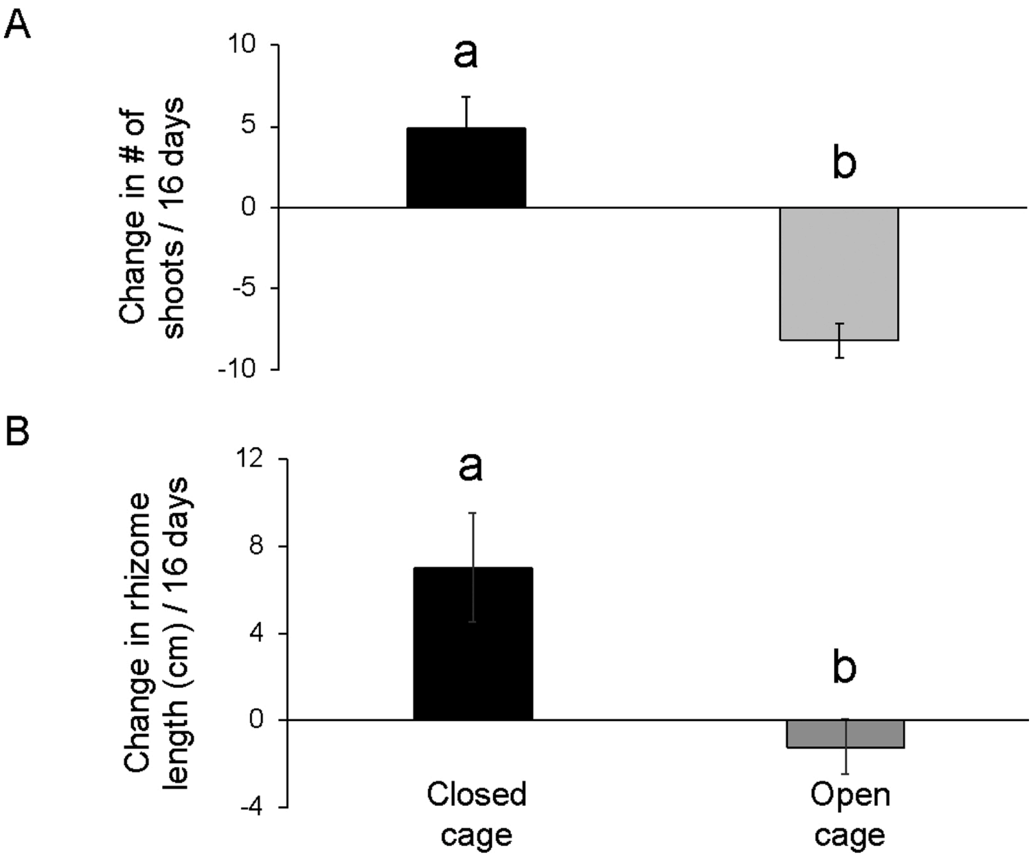

Fig. 2. Changes in (a) number of shoots and (b) rhizome length of seagrass transplanted into closed cages and open cages deployed in the shallow site 2 – 4 m deep, and 1 m adjacent to a fringing reef. Bars are means (± SE). Bars that have different lowercase letters are significantly different.

Ctenochateus striatus, Naso unicornis, Naso lituratus (Fong et al., 2018). Globally, a wide variety of species graze on seagrass (Scott et al., 2018), and stomach content analyses of butterflyfishes (Chaetodontidae) in Moorea detected the presence of seagrass fragments, although the overall frequency was low (Harmelin-Vivien and Bouchon-Navaro, 1983). In the Caribbean, herbivory on seagrasses by fishes and urchins (Randall, 1965, Ogden et al., 1973) resulted in conspicuous zones of bare sand proximal to reefs. These studies show that herbivores in the western Caribbean can be important regulators of seagrasses near areas of refuge (Armitage and Fourqurean, 2006). The high herbivory next to the reef we found in our experiment suggests the same regulatory role for herbivory may occur near Pacific reefs.

Overall, the depth distributions of *H. decipiens* in Moorea appears to be a function of the interaction of herbivory pressure and bathymetry and that if there were shallow soft bottomed areas not in close proximity to reef habitat, *H. decipiens* could grow there. While further study is required to conclusively determine the source of seagrass herbivory proximal to reef habitat, our results provide clear evidence that *H. decipiens* in Moorea is subject to top-down control by herbivores, influencing its depth distribution.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquabot.2020.103294.

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