**Presence of macroalgal (*Sargassum* spp.) propagules reduces feeding on algal turfs by coral reef fishes**

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Running page head: Macroalgal propagules suppress grazing rates

## Highlights

* Presence of macroalgal propagules reduced grazing on algal turfs on coral reefs
* Grazing of algal turfs dominated by small-bodiedblennies, rather than larger herbivorous fishes
* Reduced grazing on propagules may lead to macroalgal expansion on coral reefs

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**Key words:** Grazing lawn, macroalgae, herbivory, coral reef, incidental grazing, blenny, *Ecsenius,* epilithic algal matrix

**Abstract**

Incidental grazing of seedlings of woody plants or macroalgal propagules by herbivores is often assumed to be a key process preventing shifts from assemblages of small, highly productive herbaceous plants, to larger, less productive woody vegetation. The proliferation of macroalgal biomass on coral reefs following reductions in herbivory has led to a widely-held view that grazing fishes control macroalgal assemblages through the removal of macroalgal propagules within turf algal assemblages. However, it has never been explicitly tested whether fishes target, avoid or incidentally graze on these early life stages of macroalgae. Here, we investigate how the presence of propagules of a common coral reef macroalga (*Sargassum swartzii*) within turf algal assemblages influenced feeding by grazing fishes. We established algal turf assemblages on small (11 × 11 cm) terracotta tiles, and seeded half of the tiles with propagules of *S. swartzii* (mean density = 10.12 propagules/cm2). Paired tiles (with and without propagules) were either exposed to local herbivorous fish assemblages or placed within exclusion cages within two habitats (reef crest and reef flat) on Lizard Island, northern Great Barrier Reef, for six days. Although survival of *Sargassum* propagules was 39% lower on tiles exposed to local fish assemblages than on caged tiles, video observations revealed that the presence of *Sargassum* propagules reduced grazing rates on algal turfs by 36%. Indeed, 18 of the 21 fish species recorded took fewer bites on algal turfs containing propagules than those without, with small-bodied fishes (f. Blenniidae: *Ecsenius* spp) accounting for 85% of all bites recorded. These results indicate that while grazing is an important source of mortality for *Sargassum* propagules, grazing fishes reduce feeding in areas with propagules and may lead to a mosaic of grazing intensity across reef habitats, and potential lead to the gradual expansion of macroalgal biomass on coral reefs.

## Introduction

Herbivory is a key process influencing the biomass, productivity, and composition of primary producer communities across a range of terrestrial and aquatic ecosystems (Lubchenco and Gaines, 1981; Hay et al., 1983; McNaughton, 1984; Gill and Beardall, 2001). While the nature of herbivory and its importance relative to other processes varies among ecosystems, areas of high grazing intensity are typically characterised by a low standing biomass of highly productive herbaceous vegetation; a ‘grazing lawn’ (sensu Bell 1971; McNaughton 1984). Marked reductions in grazing intensity can, however, cause shifts to communities characterised by a high standing biomass of larger, less productive and less palatable woody vegetation (e.g., Anderies et al., 2002; Folke et al., 2004; Hughes et al. 2007; Hempson et al., 2015). While the prevention of such shifts is often related to the grazing of woody seedlings or macroalgal propagules (McNaughton, 1984; Olff et al., 1999; Uytvanck et al., 2008), the extent to which seedlings are incidentally consumed or targeted is likely to vary among grazing species and ecosystems (Olff et al., 1999; Smit et al., 2006).

Within coral reef ecosystems, shifts between short turf algal assemblages and stands of tall, fleshy (typically brown) macroalgae have been linked to changes in rates of herbivory (Done, 1992; Hughes 1994). On reefs with functionally intact herbivore assemblages, over 90% of daily algal production is consumed by grazing fishes and invertebrates (Hatcher and Larkum, 1983; Polunin and Klumpp, 1992), with algal assemblages dominated by short, highly productive algal turfs (*sensu* a grazing lawn). However, reductions in grazing intensity due to overfishing or experimental exclusion can release algal communities from top-down control and ultimately lead to a shift to tall, fleshy macroalgae (e.g., Lewis 1986; Hughes 1994; Hughes et al. 2007; Rasher et al. 2013). Such shifts to macroalgal-dominance following reductions in grazing, coupled with the inability of most grazing fishes to consume large fleshy macroalgae (Bellwood et al., 2006; Hoey and Bellwood, 2009), has led to the assumption that incidental grazing of macroalgal propagules is important in preventing the establishment of macroalgae on coral reefs.

Despite the potential importance of incidental grazing of macroalgal propagules in shaping algal communities on coral reefs, the vast majority of research on the susceptibility of macroalgaeto herbivory has focused on the consumption of larger and later life stages (i.e., adult) macroalgae (e.g., McCook 1997; Hoey and Bellwood 2009; Vergés et al. 2011; Loffler et al. 2015). Few studies have investigated the susceptibility of propagules to grazers (but see Diaz-Pulido and McCook 2003; Loffler and Hoey 2019). Rather, the mortality of macroalgal propagules has largely been inferred from changes in algal communities following reductions in, or exclusion of, herbivorous fishes. It is currently unknown if grazing fishes can detect the presence of macroalgae propagules within turf algal assemblages, and if so, whether the presence of propagules alters their feeding behaviour.This study, therefore, aimed to investigate if the presence of *Sargassum* propagules (a common macroalga on degraded coral reefs (Hughes, 1994; Rasher et al., 2013; Graham et al., 2015)) within the turf algal matrix affects the feeding behaviour of grazing fishes.

## Materials and Methods

### Study Location

This study was conducted at Lizard Island in the northern Great Barrier Reef (GBR), Australia (1440’S, 14528’E; Fig. S1). Lizard Island is a high continental island approximately 40 km from the Queensland coast, with adjacent islands creating a large lagoonal area, and fringing reefs surrounding each island. The reefs surrounding Lizard Island had low coral cover at the time of the study due to the two cyclones and coral bleaching events that occurred from 2014-2017 (Madin et al., 2018; Hughes et al. 2019).

To determine if the presence of *Sargassum* propagules affected grazing rates on algal turf assemblages, paired experimental tiles with established algal turf assemblages (one containing *Sargassum* propagules, the other without) were exposed to local herbivorous fish assemblages for six days. This research was conducted at each of two reef crest (1.5-3.5m depth) and reef flat sites (0.5-2.5m depth) in early December 2017 (Fig. S1). These two habitats were chosen due to differences in their algal and herbivorous fish assemblages. The reef flat sites were characterised by a higher abundance of macroalgae, predominantly *Sargassum cristaefolium*, *Turbinaria ornata* and *Halimeda* spp., and lower fish biomass than the reef crest sites (Hoey and Bellwood 2009, 2010a; Table S1, Fig. S2). Conversely, the reef crest sites had a higher cover of turf algae and greater fish biomass than the reef flat (Table S1, Fig. S2).

### Cultivation of algal assemblages

Algal turf assemblages were cultivated on 76 small terracotta tiles (110 × 110 × 10 mm), and half the tiles were seeded with *Sargassum* propagules. Thirty-eight tiles were placed on the bottom of each of two 1000 L outdoor aquaria (76 tiles in total) with supplemental aeration and flow through unfiltered seawater to seed tiles with a bacterial film and algal turf assemblage. The two aquaria were positioned side by side and received fresh seawater from the same source. Each tile was marked with a unique number on one edge using a permanent marker. After ~2 days, tiles within one aquarium were seeded with propagules of *Sargassum swartzii*.

To obtain propagules, fifty adult, reproductive *S. swartzii* thalli were collected by hand from the inshore reefs of the Turtle Group (1443’S, 14512’E), approximately 28 km west of Lizard Island and 11 km from the mainland. Although there are several *Sargassum* species present at Lizard Island (including *S. swartzii*:Hoey and Bellwood 2010a, b), the higher density in the Turtle Group ensured that sufficient reproductive thalli of the same species could be obtained. *Sargassum* thalli were transported back to Lizard Island within 3 h of collection in 80 L plastic aquaria filled with seawater. Approximately 5 h after collection the *Sargassum* thalli were placed in an 80 L aquarium filled with cold (9C) seawater for 10 minutes to stimulate propagule release (following Carl et al. 2014). *Sargassum* thalli were then transferred to one of the 1000 L aquaria containing settlement tiles at ambient seawater temperature (26 C). The water flow to both aquaria was turned off and both aquaria were supplied with supplemental aeration. The *Sargassum* thalli were agitated by hand twice per day to further encourage release of the propagules. After three days the adult *Sargassum* was removed and flow-through seawater was resumed for both aquaria.

The tiles were cultured in these aquaria with flow-through seawater and supplemental aeration for a further ten days, to allow the *Sargassum* propagules time to firmly attach to the tiles (Fletcher and Callow, 1992). At settlement, propagules were approximately 0.2 mm in height, and only visible under a dissecting microscope. All 76 tiles were then translocated to a sheltered back reef site (depth 1-3 m) on the leeward side of Lizard Island (Fig. S1) and placed within mesh cages (320 × 150 × 40 mm, 5mm plastic mesh; two tiles per cage) for 21 days to allow turf algal assemblages to establish in the absence of herbivory. After 21 days, the tiles were collected, transported back to the research station in aquaria filled with seawater, and placed into large aquaria with flow-through seawater, and the density of *Sargassum* propagules on each tile quantified.

The density of propagules on the 38 tiles with settled propagules was quantified within 24 h of collection using 14 replicate 1 × 1 cm quadrats placed haphazardly on the upper surface of each tile. Propagules were ~2-3 mm tall, with a mean density of 10.12 ± 0.24 (SE) propagules cm-2. There was no difference in the height of turf algae between tiles with and without propagules (see supplementary materials).

### Herbivore exposure

To determine if the presence of *Sargassum* propagules affected the feeding rate of grazing fishes, and if any feeding on the tiles affected the density of *Sargassum* propagules, the 76 tiles were paired (one tile with propagules and one without: 38 pairs) and deployed on the reef for six days. To standardise the deployment of tiles to the reef, each pair of tiles was attached to a small concrete bricks (L × W × H: 250 × 80 × 50 mm) using stainless steel base plates (following Trapon et al. 2013). Each base plate was attached to the brick using cable ties threaded through the holes in the base plate to the brick. A bolt attached to each base plate was passed through a hole in the centre of each tile and a wing nut used to secure the tile to the plate. Using this method, the gap between tiles in each pair was no greater than 2 cm.

Paired tiles were randomly allocated among habitats and sites, with ten paired tiles allocated to each site except one reef flat site where only eight pairs were allocated. At each site, half of the tile pairs were left exposed to local fish assemblages, and half were placed within exclusion cages (L × W × H: 300 × 150 × 40 mm; 5mm mesh) to control for any effects of handling and rates of propagule mortality in the absence of herbivory. Each tile pair within a site was separated by at least 3 m. After six days, the tiles were collected and transported back to the research station in plastic aquaria filled with seawater. The density of *Sargassum* propagules on each tile with propagules was quantified within 24 h of collection, as described above.

At each site, feeding on four of the exposed tile pairs was recorded using remote underwater video cameras (Go Pro HERO3 and HERO4). A GoPro camera attached to a small dive weight was placed approximately 50cm from each of four tile pairs at each site (16 cameras per day) between 08:00 and 09:00 and recorded continuously for three hours. This process was repeated for five days with the same tile pairs being recorded throughout the experiment. The entire video footage (~240 h) was viewed and for each individual fish observed taking bites on the tiles, the species, total length (TL) of the fish, and number and location of bites (i.e., on a tile with or without propagules) was recorded. Length of the fish was estimated to the nearest centimetre using the tile length (110 mm) as a scale. For those fishes that were too small to accurately identify to species, they were recorded to the lowest taxonomic level possible (usually genus).

*Fish surveys*

Herbivorous fish assemblages at each reef crest and reef flat site were quantified using three replicate 50 m belt transects. One diver recorded all larger bodied, roving herbivorous fishes from the families Acanthuridae, Kyphosidae, Labridae (tribe Scarini: parrotfishes), Pomacanthidae and Siganidae within 2.5 m of either side of the transect tape (50 × 5 m) whilst simultaneously laying the transect tape. A second diver waited two minutes, then followed the first diver and recorded the site-attached, small-bodied fishes from the families Blenniidae, Gobiidae and Pomacentridae one metre either side of the transect tape (50 × 2 m). Transects were laid parallel to the reef crest with a minimum of 10 m between adjacent transects.

### Statistical analysis

#### Propagule survival

To determine if the survival of *Sargassum* propagules was influenced by exposure to herbivores, a Bayesian generalised linear model with a gamma error distribution and a log-link function was used. The proportion of propagules remaining on each tile after six days on the reef was used as the response variable. The model included the fixed effects of habitat, treatment (caged or uncaged) and site, with an interaction term included for the relationship between habitat and treatment. Including site in the interaction did not improve model fit, determined using leave-one-out cross-validation (Vehtari et al. 2018), therefore site was included as an additive fixed effect. Weakly informative priors were used on slope coefficients (normal(0,5)), intercept coefficients (normal(0,5)) and the error standard deviation (Cauchy(0,5)), with 5000 iterations, a warmup of 2500, a thinning factor of five and three chains. Planned contrasts were used to compare the survival of propagules on caged vs. exposed tiles between habitats and sites using 95 % higher posterior density intervals.

#### Grazing

To determine if grazing differed between tiles with and without propagules, Bayesian interactive generalised linear mixed effects models with a negative binomial error distribution and a log-link function were used. The run for the total bites for all species combined, and for any species that took bites on at least three tile pairs each day (i.e., *Ecsenius stictus,* *Pomacentrus* spp*.* and *Ctenochaetus striatus*). A negative binomial error distribution was used because the models fitted with Poisson error distribution showed evidence of overdispersion. The models included the fixed effects of substratum (with vs without propagules), habitat and site, with an interaction term included for the relationship between habitat and substratum. Including site in the interaction did not improve model fit, determined using leave-one-out cross-validation (Vehtari et al., 2018), therefore, site was included as an additive fixed effect. *Ctenochaetus striatus* only took bites on tiles on the reef crest, therefore habitat was not included in the model for this species. Day nested within tile was included as a random factor, to account for the non-independence of days, and tiles within a pair. For the model of total bites (i.e., all species combined) weakly informative priors were used on intercept (normal(0,5)) and slope coefficients (normal(0,5)) and error standard deviation (Cauchy(0,5)) with 5000 iterations, a warmup of 2500, three chains and a thinning factor of three. For the models of the bites of individual species, weakly informative priors were used on intercept (normal(0,3)) and slope coefficients (normal(0,3)) and error standard deviation (Cauchy(0,4)). 6000 iterations were used, with a warmup of 3000, a thinning factor of four and three chains. Planned contrasts were used to compare the difference in bites between substratum with and without propagules in each habitat and site combination.

For all models, diagnostic plots were examined to ensure chains were well mixed and had converged on a stable posterior distribution, that there was no evidence of autocorrelation and that priors were sufficiently wider than posterior values. All values of Rhat were less than 1.05 and sampling chain estimates corresponded to the observed data.

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018) and Bayesian models fitted in STAN with Markov Chain Monte Carlo sampling using the ‘brms’ package (version 2.10.0; Bürkner 2017, 2018). Summaries of model outputs were created using the ‘tidybayes’ (version 1.1.0; Kay 2019)and ‘emmeans’ (version 1.4.2; Lenth, 2019)packages.

## Results

*Propagule survival*There was a marked decline in the density of *Sargassum* propagules on tiles exposed to local herbivore assemblages compared to those placed within exclusion cages (Fig. 1). The survival of *Sargassum* propagules on tiles within cages on the reef crest was (median [95% Credible Intervals]) 0.98 [0.83, 1.17] compared to 0.46 [0.38, 0.54] on tiles exposed to herbivore assemblages. The difference between caged and exposed tiles was smaller on the reef flat, with survival of propagules on caged tiles averaging 0.95 [0.78, 1.13] compared to 0.69 [0.59, 0.84] on tiles exposed to local fish assemblages.

### Grazing on tiles

A total of 36,401 bites across 21 fish species were recorded across all tiles (Table S1). The total number of bites differed between tiles with and without *Sargassum* propagules (with the overall bite rate being 52-86% higher on tiles without propagules), and between sites and habitats (Fig. 2). At Site 1 on the reef crest, the total bite rate was (median [95% HPD Intervals]) 92.0[5.11, 362.7] bites hr-1 on algal turfs without *Sargassum* propagules compared to 62.8 [3.32, 245.9] bites hr-1 on algal turfs with propagules (Fig. 2). Grazing rates on tiles were generally lower at site 2 (Site 1: 32.9 [5.80, 94.6] bites hr-1; Site 2:19.0 [2.45, 51.5] bites hr-1) but displayed similar trends, with the total bite rate being greater on algal turfs without *Sargassum* propagules (61.9[4.24, 257.6] bites hr-1)compared to those on algal turfs with propagules (41.47 [2.31, 170.6] bites hr-1). Grazing rates were generally lower on the reef flat (9.96[1.31, 30.9] bites hr-1) ­­­­­­ compared to the reef crest (62.6 [5.56, 172.1] bites hr-1), but displayed similar differences between tiles with and without propagules and between sites. On the reef flat, total bite rates on algal turfs without *Sargassum* propagules (Site 1: 19.17 [1.05, 83.3] bites hr-1; Site 2:9.48 [0.46,43.5] bites hr-1) were higher than those on algal turfs with *Sargassum* propagules (Site 1: 10.65 [0.42, 44.1] bites hr-1; Site 2: 5.27 [0.27, 24.0] bites hr-1; Fig. 2).

Of the 21 fish species recorded to bite on the tiles, 18 species (86%) took fewer bites on tiles with *Sargassum* propagules than on tiles without propagules (Table S1), with a single species, *Ecsenius stictus* (f. Blenniidae), accounting for 85% of total bites recorded across all tiles. Of the three taxa for which bites rates were analysed, there was strong evidence that *E. stictus* (1.73 [1.37, 2.21] times) and *Pomacentrus* spp. (2.84 [1.32,5.07] times) took more bites on tiles without *Sargassum* propagules than tiles with propagules on both the reef crest (*E. stictus*:34.68 [0.32, 233.8] vs. 22.08 [0.10, 140.9] bites hr-1; *Pomacentrus* spp: 0.10[0.0007, 0.40] vs 0.04 [0.0004, 0.18] bites hr-1) and reef flat (*E. stictus*:1.67 [0.004, 12.11] vs 0.89 [0.002, 6.69] bites hr-1; *Pomacentrus* spp.: 0.32 [0.009, 1.2] vs 0.10 [0.001, 0.39] bites hr-1; Figs. 3a, b). There was no evidence of a difference in bite rate due to the presence of *Sargassum* propagules for *Ctenochaetus striatus* (without propagules: 0.16[0.000006, 1.45, 2.46], with propagules: 0.15 [0.000005, 1.41] bites hr-1, respectively Fig. 3c).

*Fish surveys*

The abundance and diversity of fishes was higher on the reef crest than the reef flat; 434 individuals from 48 species were recorded on the reef crest and only 80 individuals of 22 species were recorded on the reef flat (Table S3). These patterns were largely due to the difference in scarines, siganids and acanthurids between habitats (Table S3). The abundance of *Ecsenius* spp (f. Blenniidae) was almost 9-fold higher on the reef crest compared to the reef flat, with an average (mean ± SE) of 8.8 ± 2.6 individuals per 50m2 on the reef crest compared to 1 ± 0 per 50m2 on the reef flat (Table S3). Abundances of pomacentrids was comparable, with 9.5 ± 2.0 on the reef crest and 10.5 ± 4.29 on the reef flat. There was an average of 6 ± 1.6 *Ctenochaetus striatus* individuals per 50m2 on the reef crest and none seen on the reef flat.

## Discussion

Incidental grazing is often assumed, either implicitly or explicitly, to be a major source of mortality for the seedlings of woody plants and propagules of fleshy macroalgae (e.g., McNaughton, 1984; Olff *et al.* 1999; Mumby, 2006), but has rarely been tested. Our results show a ca. 40 % reduction in the survival of *Sargassum* propagules within turf algal assemblages exposed to herbivores compared to those maintained within exclusion cages (pooled across habitats and sites), supporting the role of grazing as a source of mortality of *Sargassum* propagules. However, analysis of video footage revealed that the presence of *Sargassum* propagules within algal turf assemblages reduced feeding rates of grazing fishes by 36 %, suggesting that these fishes could not only detect the presence of *Sargassum* propagules but also reduced their feeding rates in areas where the propagules were abundant. Further, previous studies have emphasised the importance of large-bodied grazing fishes, primarily parrotfishes, surgeonfishes and rabbitfishes, in preventing macroalgal establishment (e.g., Bellwood et al. 2006; Mumby 2006), yet our results point to the potential importance of small-bodied grazers (i.e., blennies) as a significant source of mortality for propagules of *Sargassum*, and potentially other macroalgal taxa.

In areas where rates of herbivory are high, grazing species are assumed to incidentally consume seedlings or propagules contained within cropped ‘lawns’ (Choat, 1982; McNaughton, 1984; Mumby, 2006). However, our results provide evidence that grazing coral reefs fishes are able to detect small macroalgal propagules (2-3mm in height) within turf algal assemblages and correspondingly reduce their grazing rates in these areas. Previous studies have suggested that herbivore feeding preferences are largely determined by the physical, chemical and nutritional properties of the primary producers they target (e.g., Hay and Fenical, 1988; Hanley et al., 2007; Clements et al., 2009; Rasher et al., 2013), which may explain the apparent avoidance of *Sargassum* propagules by grazing fishes in the current study. However, unlike mature thalli, *Sargassum* propagules do not have a tough morphology, and propagules (<1 cm in height) of the tropical congener *Sargassum mangarevense* produce 75 % fewer phenolic compounds than adults (Stiger et al., 2004). Irrespective of the mechanism, the difference in grazing rates on areas with and without propagules could lead to a mosaic of short, productive turfs and larger, less productive macroalgal stands on coral reefs, as has been reported in terrestrial savannahs (McNaughton, 1984; McNaughton et al., 1997; Augustine and McNaughton, 1998), and may provide a mechanism that allows for the expansion of macroalgal beds. *Sargassum* propagules predominantly settle within one metre of the parent alga (Kendrick and Walker, 1991, 1995) and any reduction in grazing due to the high density of propagules may promote the maintenance and expansion of *Sargassum* on coral reefs. This adds to a growing number of studies that have identified positive feedbacks reinforcing *Sargassum*-dominance on coral reefs (Nugues et al., 2004; Hughes et al., 2007; Hoey and Bellwood, 2011; Webster et al., 2015; Dell et al. 2016; Clements et al., 2018).

While previous research has emphasised the importance of large-bodied grazing fishes in preventing macroalgal establishment on coral reefs (Done, 1992; Diaz-Pulido and McCook, 2003; Bellwood et al., 2006), our findings suggest that the contribution of small cryptic fishes, such as blennies, to the consumption of algal materials on coral reefs may be greater than previously assumed. Cryptobenthic fishes likely have a high capacity for consumption of algal turfs and associated components due to their high abundance, high metabolism and fast growth rates (Depczynski and Bellwood, 2003; Brandl et al., 2018; Brandl et al., 2019). Recent research has highlighted the important contributions of these often-overlooked fishes to the functioning of coral reef ecosystems, and suggests cryptobenthic fishes are a cornerstone of coral reef trophodynamics (Brandl et al., 2019). Our results suggest they may also play an important role in the grazing and removal of macroalgal propagules.

We found a significant decrease in the density of *Sargassum* propagules on tiles exposed to herbivores, yet how this grazing-related mortality of small propagules translates to populations of adult *Sargassum* is largely unknown. Combining growth estimates of *Sargassum* propagules from a pilot study at the sites used in the present study (height increased from 0.2 to 3.8 mm over 16 days: 0.23 mm day-1; Loffler, unpub. data) with the mortality rates from this study (reef crest: 55%.6 days-1; reef flat 31%.6 days-1) suggest that only 0.37 % of propagules on the reef crest and 7.5 % on the reef flat would survive to reach 10 mm in height. Although these estimates are speculative and assume growth and mortality rates are relatively constant over this time period, the difference in estimated survival between habitats is consistent with the among-habitat distribution of *Sargassum* on many GBR reefs (e.g., McCook, 1997; Fox and Bellwood 2007; Wismer et al. 2009), and broadly . similar to mortality rates for propagules of temperate *Sargassum* species (>99%.yr-1; Kendrick and Walker, 1994).

Our mortality estimates for *Sargassum* propagules were based on propagules settled to artificial substrata (i.e., tiles) and protected from herbivorous fishes for the first 3 weeks. As such our morality estimates may differ from those experienced on natural reef substrata as propagules were allowed to firmly attach to the substrata before being exposed to grazing fishes. Conversely, the experimental tiles lacked crevices that have been shown to enhance the survival of early life stages of macroalgae and corals (Nozawa 2008; Brandl et al. 2014; Gallagher and Doropoulos 2017; Loffler and Hoey 2019). Also, our mortality estimates do not consider the potential influence of processes operating within or adjacent to existing *Sargassum* beds on the survival of early life stages of macroalgae (e.g., reduced herbivory: Hoey and Bellwood 2011; Dell et al., 2016), which should be the focus of future studies.

In sum, our findings demonstrate that the presence of *Sargassum* propagules within algal turf assemblages alters the feeding behaviour of grazing fishes. Despite the decreased grazing rate on algal turfs containing propagules, the mortality of *Sargassum* propagules was still relatively high in areas exposed to grazing fishes, especially on the reef crest (ca. 55 % in 6 days) compared to the reef flat (ca. 30 % in 6 days). Just as varying rates of grazing across a landscape can create a mosaic of closely cropped lawns interspersed with taller woody vegetation (McNaughton, 1984), the reduced grazing rates on turf algal assemblages containing high densities of *Sargassum* propagules (ca. 10 propagules.cm-2) may release these propagules from top-down control, representing a mechanism for the maintenance and expansion of macroalgal beds on coral reefs, and ultimately resulting to a mosaic of closely cropped algal turfs interspersed with dense macroalgal beds.

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Figure 1: Differences in the survival of *Sargassum* propagules within algal turf assemblages exposed to local herbivore assemblages (triangles) versus protected from herbivores (circles), between habitats (reef crest and reef flat) and sites at Lizard Island. The proportion of *Sargassum* propagules remaining on each tile was quantified using 14 replicate 1cm2 quadrats before and after tiles were deployed on the reef. Solid symbols are mean model estimates of Bayesian generalised linear model with gamma distributed errors,  95% Credible Intervals, and open symbols are the model residuals.

Figure 2: Differences in the effect of the presence of *Sargassum* propagules on the bite rates of fishes feeding on algal turf assemblages between habitats (reef crest and reef flat) and sites at Lizard Island. Solid symbols are mean model estimates of Bayesian generalised linear mixed effects model with negative binomial distributed errors, ± 95% Credible Intervals, and open symbols are the model residuals.

Figure 3: Differences in the effect of the presence of *Sargassum* propagules on the bite rates of (a) *Ecsenius stictus*, (b) *Pomacentrus* spp. and (c) *Ctenochaetus* *striatus* feeding on algal turf assemblages between sites and habitats (reef crest and reef flat) at Lizard Island. Triangles are mean model estimates of Bayesian generalised linear mixed effects model with negative binomial distributed errors, ± 95% Credible Intervals. Open symbols are partial residuals of the model. Note: *Ctenochaetus* *striatus* only took bites on tiles on the reef crest.

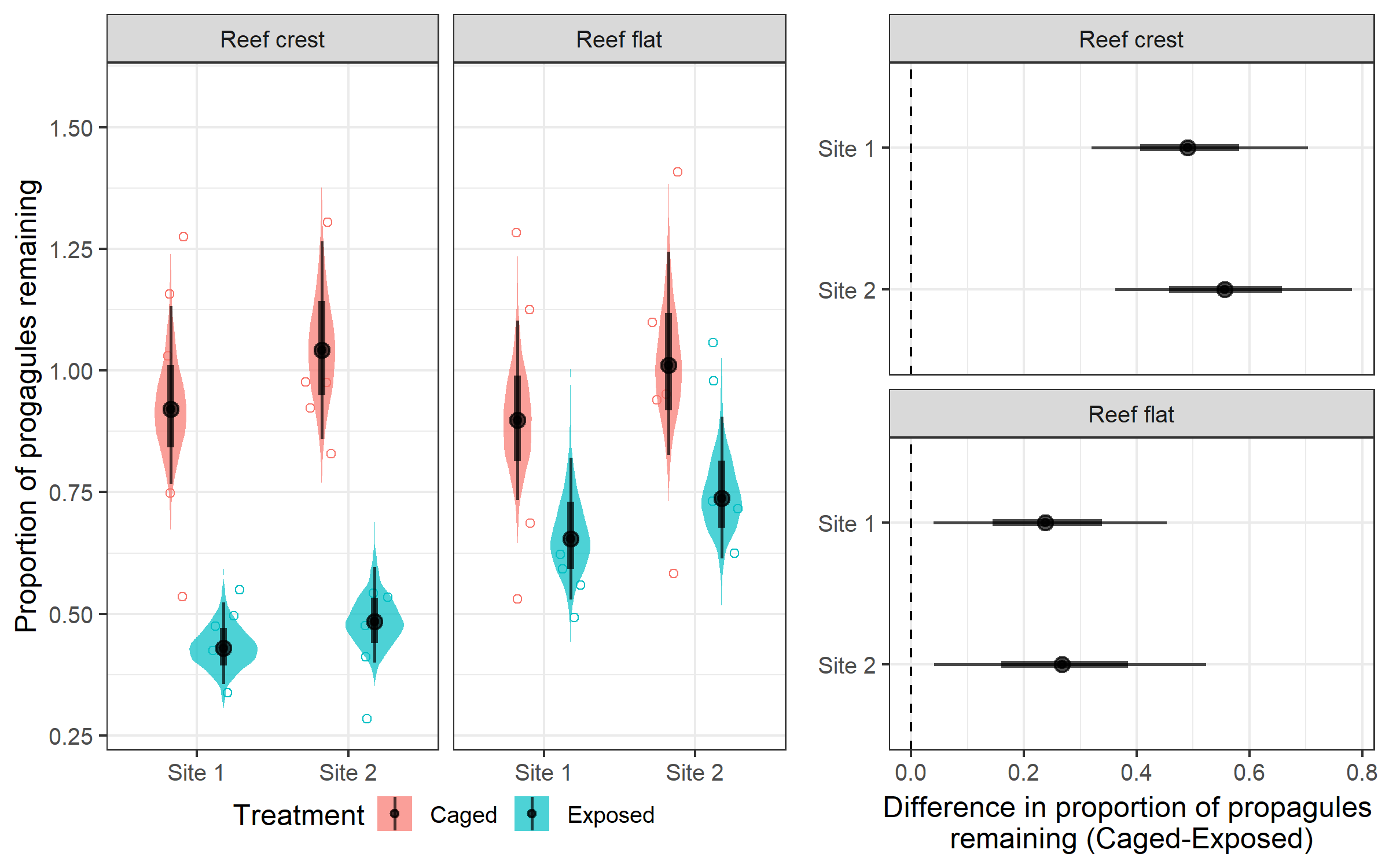


Figure 1

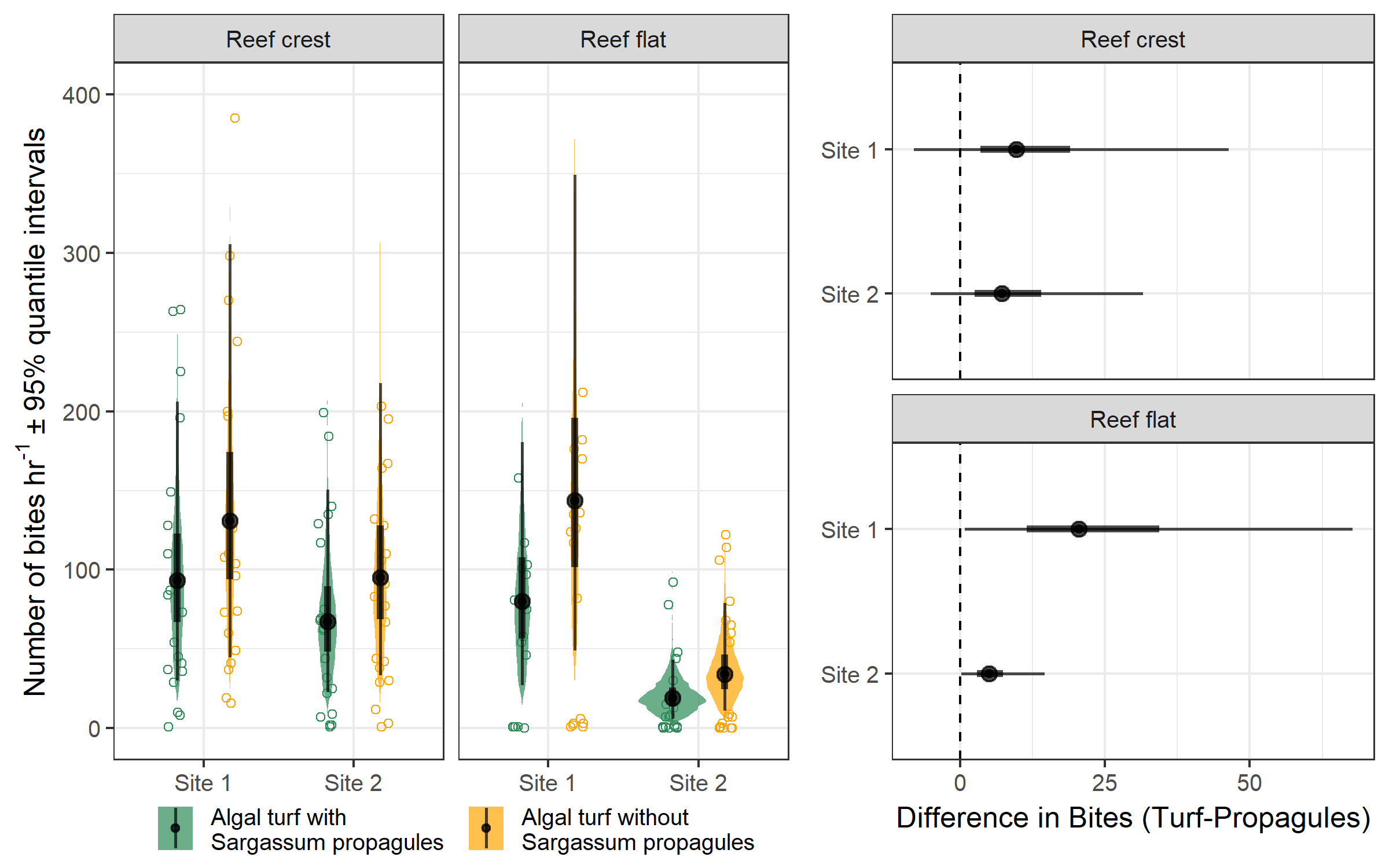


Figure 2

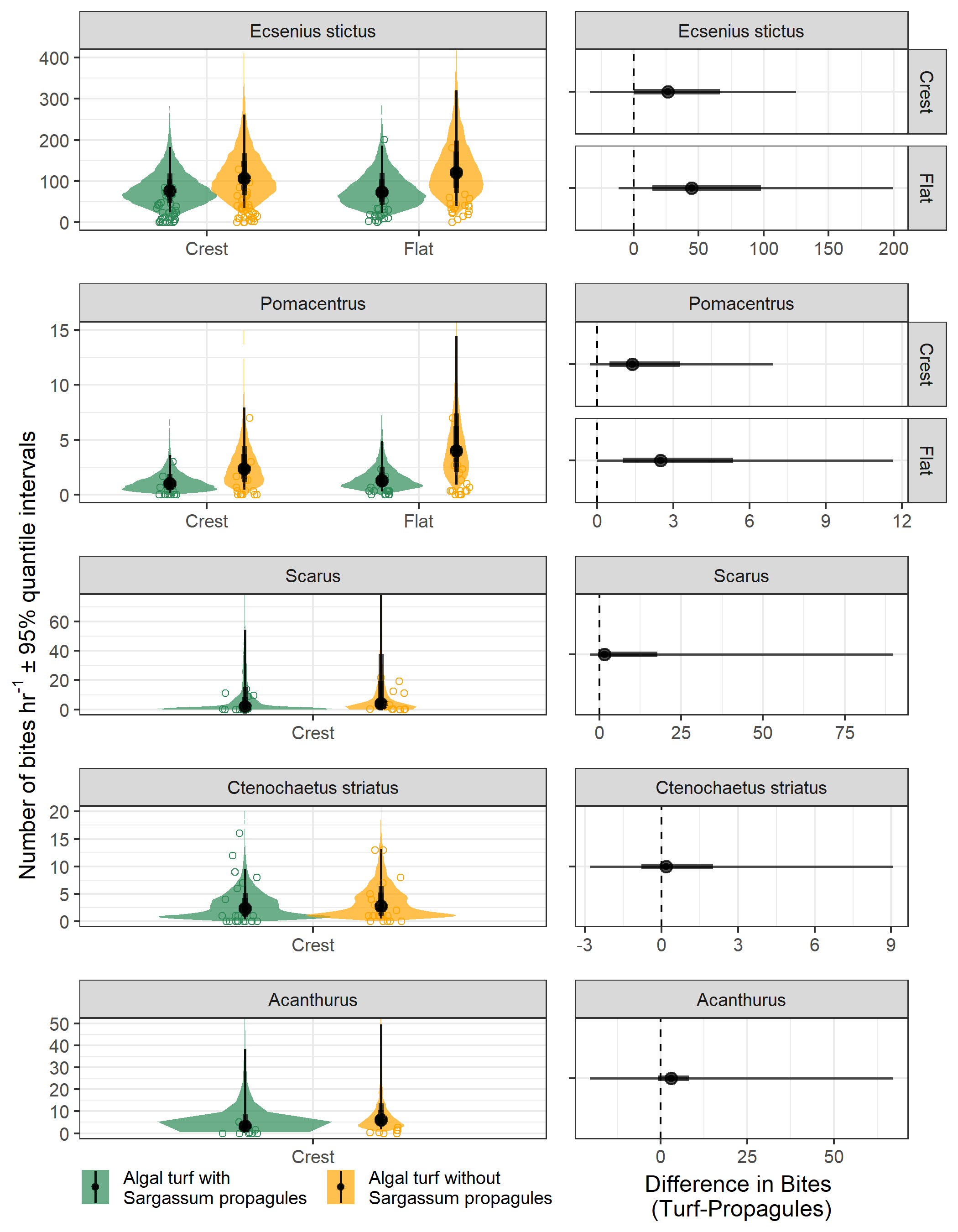


Figure 3