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Algal turf productivity on coral reefs: a meta-analysis

Authors:

Sterling B. Tebbett *, David R. Bellwood

Addresses:

[1] Research Hub for Coral Reef Ecosystem Functions, College of Science and Engineering and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

***Corresponding Author:**

Email: sterling.tebbett@my.jcu.edu.au

Phone: (07) 47815729

Abstract

Algal turfs are an abundant and highly productive component of coral reef ecosystems. However, our understanding of the drivers that shape algal turf productivity across studies and among reefs is limited. Based on published studies we considered how different factors may shape turf productivity and turnover rates. Of the factors considered, depth was the primary driver of turf productivity rates, while turnover was predominantly related to turf biomass. We also highlight shortcomings in the available data collected on turf productivity to-date; most data were collected prior to global coral bleaching events, within a limited geographic range, and were largely from experimental substrata. Despite the fact turfs are a widespread benthic covering on most coral reefs, and one of the major sources of benthic productivity, our understanding of their productivity is constrained by both a paucity of data and methodological limitations. We offer a potential way forward to address these challenges.

Keywords

Algal turfs; Coral reef; Ecosystem function; Herbivory; Productivity; Sediment

1.0 Introduction

Globally, millions of people directly rely on highly productive, shallow-water coral reef ecosystems (Moberg and Folke 1999; Woodhead et al. 2019). This productivity is harnessed by people in the form of fishable biomass (Teh et al. 2013; Samoilys et al. 2017; Lau et al. 2019; Robinson et al. 2019b), with fishes acting as conduits that shunt primary productivity up the food chain (Russ and St. John 1988; Rogers et al. 2018; Morais et al. 2020). It is posited that primary productivity and its utilisation by herbivorous fishes are two of the eight core ecosystem processes that are fundamental to the functioning of coral reefs (Brandl et al. 2019). If the goal of coral reef scientists and managers is to sustain the functioning of coral reef ecosystems into the future, especially in productive states that continue to provide key services to people (Hughes et al. 2017; Bellwood et al. 2019a), then understanding the nature of primary productivity in these ecosystems is clearly important.

The highly productive nature of coral reefs is epitomised by the diminutive algal turfs, small <2 cm tall multispecies assemblages of algae (Fig. 1b), that cover the hard substratum in these ecosystems (Adey 1998; Connell et al. 2014; Tebbett and Bellwood 2019). Indeed, it has been widely suggested that these algal turfs are the major contributors to benthic productivity on coral reefs (e.g. Adey and Steneck 1985; Carpenter 1985; Hatcher 1988; Klumpp and McKinnon 1989). Productivity is considered herein as the biomass (g Carbon) produced by algal turfs in a given area over a given time (m^{-2} day^{-1}). This contribution of algal turfs to productivity is set to increase as global climate change, and a suite of other stressors, reduce coral cover on reefs, leading to an inevitable increase in algal turf cover (Holbrook et al. 2016; Brown et al. 2017; Ellis et al. 2019; Koester et al. 2020; Vercelloni et al. 2020). However, while the highly productive nature of algal turfs piqued the interest of formative reef scientists (e.g. Odum and Odum 1955; Wanders 1976; Hatcher 1981; Adey and Steneck 1985; Carpenter 1985; Russ 1987), we currently lack a full understanding of how algal turf productivity varies across previous studies and different coral reefs.

A broad suite of drivers have been linked to the productivity of algal turfs (Klumpp and McKinnon 1989; Hatcher 1990). These potential regulators of algal turf productivity are likely to include light availability (Carpenter 1985; Klumpp and McKinnon 1989), hydrodynamic activity (Roff et al. 2019), nutrients (Williams and Carpenter 1988; Sura et al. 2019) and sediment loads (Tebbett et al. 2018a). All such drivers vary among reefs. In addition to these drivers, the methods employed for quantifying algal turf productivity (e.g. the substratum algal turfs were grown on) may also shape our understanding of this process. However, to-date, the studies that have quantified algal turf productivity on coral reefs have not been considered together in a comparative framework, limiting our understanding of how and why algal turf productivity varies across studies and among coral reefs. This comes at a time when anthropogenic activity is altering the strength of many biophysical drivers on the world’s reefs (Harborne et al. 2017; Hughes et al. 2017; Williams et al. 2019; França et al. 2020), with algal turfs set to play an ever more central role in the functioning of coral reef ecosystems into the future (Bellwood et al. 2019b; Tebbett and Bellwood 2019).

Considering the rapidly changing nature of reefs, it is surprising that we currently lack a clear understanding of how and why the productivity of a core group of benthic primary producers varies among reefs and across past studies. The aim of this study, therefore, is to gather available data on coral reef algal turf productivity and assess how it varies among coral reef locations. In doing so, we will explicitly consider how the available data in this research field, and the methods employed to quantify algal turf productivity to-date, may have shaped our understanding of algal turf productivity. To achieve these aims, this study will utilise a robust analytical framework to bring together data from disparate studies and provide an insight into the cross-study drivers of algal turf productivity on coral reefs.

2.0 Methods

2.1 *Productivity database compilation*

To assess how algal turf productivity varies across coral reefs we first had to compile a database of productivity measurements from previous studies. This was achieved by undertaking an extensive search of the literature. Initially, we undertook a formal search in Google Scholar using the search terms '("algal turf" OR "epilithic algal") AND (production OR productivity OR growth) AND "coral reef"'. This search yielded 4010 results in April 2020 (not including patents or citations). To check how comprehensive Google Scholar was we also ran this search through Scopus and Web of Science. These two search engines only yielded a total of 1945 and 78 results, respectively. We initially filtered the 4010 studies returned by Google Scholar for any potentially relevant studies based on the title and abstract, yielding a pool of 105 potentially relevant studies. To ensure that our search was comprehensive, and that we did not overlook any, more cryptic, studies, we also undertook two general searches of the literature in Google Scholar using the search terms 'algal turf productivity' and 'algal turf productivity coral reefs' and filtered the 1000 most relevant studies in each case. This process yielded an additional 26 potentially relevant studies. Based on our prior knowledge in this research field there were also 5 additional studies that we were aware of and thought may contain relevant information on algal turf productivity. These 5 additional studies were added to the pool of potentially relevant studies for a total of 136 studies. It is important to note that these 5 additional studies were not found in the searches because they were relatively old and published in unusual journals, conference proceedings or in a PhD thesis. These studies would have been overlooked without extensively reading the relevant literature.

Each of the potentially relevant studies was then evaluated against a specific set of criteria to determine if it could be included in our analysis. These criteria were: a) that quantification of productivity was performed in-situ on the reef; b) details of the sampling month/depth/specific location were provided; c) the study quantified ‘productivity’ directly (N.B. data on ‘yield to herbivores’ [i.e. the amount of algal biomass removed by herbivores] was not included; see Russ, [1987] for details of how productivity and yield to herbivores differ) in g Carbon m^{-2} day^{-1} (or in a form that could be converted into this unit of measure); d) the substratum that turfs were grown on had been conditioned to some extent on the reef; and e) the algal community examined fell within the general definition of small <2 cm tall multispecies assemblages of algae on a hard benthic substratum, i.e. algal turfs (Steneck and Dethier 1994; Connell et al. 2014; Tebbett and Bellwood 2019).

We applied the above criteria to ensure that: a) algal turf productivity was reflective of natural conditions on the reef and the relevant drivers at the study location (i.e. productivity was not measured under laboratory conditions where these drivers were altered); b) suitable information was available to assess potential drivers underpinning the productivity values recorded (especially depth and sampling month); c) we did not confuse ‘yield to herbivore’ measurements as ‘productivity’ measurements; d) we focused on the units most widely used for primary productivity on coral reefs (Hatcher 1988; Klumpp and McKinnon 1992; Russ and McCook 1999); e) values were not biased by initial algal turf settlement dynamics (Diaz-Pulido and McCook 2002; Fricke et al. 2011); and f) we only examined ‘algal turfs’ rather than macroalgae or productivity of entire reef communities. It should be noted that our definition of ‘algal turfs’ includes non-algal cyanobacteria (see Borowitzka et al. 1978; Diaz-Pulido and McCook 2002) and the methods commonly used to quantify algal turf productivity (e.g. scraping algal biomass from coral blocks) is likely to include contributions from endolithic algae and cyanobacteria in the surficial layers of the substratum matrix (e.g. Odum and Odum 1955; Tribollet et al. 2002). After this filtering process we were left with a pool of just 17 studies (14 were derived from the initial formal search, 2 from the general search and 1 study that we were aware of). Our search and filtering procedures were based on PRISMA protocols (Moher et al. 2009) with a flow-diagram provided in the supplementary material (Fig. S1).

From our pool of relevant studies, we then extracted data on algal turf net primary production (g Carbon m^{-2} day^{-1}). Where possible we also extracted data on turnover or calculated this based on standing biomass estimates provided in the studies. Here turnover was considered as the ratio of production (g C m^{-2} day^{-1}) to standing biomass (g C m^{-2}) measured in % day^{-1} (Odum and Odum 1955). From each study, data were sourced from tables or, where necessary, extracted from graphs using webplot digitizer (Rohatgi 2019) (full details of data extraction procedures for each study are reported in supplemental Table S1). In addition, all mean ± SE values used in the dataset are provided in Table S3 and the raw data extracted from each study is presented in Figure S2.

2.2 *Explanatory variable compilation*

In addition to extracting productivity and turnover data from each study, we also extracted information on available, relevant, variables to assess why and how productivity data vary. Firstly, we extracted information on the water depth in which each observation was quantified. Water depth was considered because it is a key environmental gradient that is strongly correlated with light availability (Roberts et al. 2019), hydrodynamic exposure (Fulton and Bellwood 2005), sediment loads (Purcell 2000) and herbivory (Cooper et al. 2019), all of which have been linked to algal turf productivity levels (Carpenter 1985, 1986; Tebbett et al. 2018a; Roff et al. 2019).

Secondly, seasonal influences were considered by quantifying the sampling month for each observation reported in the study. Seasonal influences were standardised between northern and southern hemispheres as the month since first winter month (i.e. December = 1 in northern hemisphere locations, June = 1 in southern hemisphere locations). The yearly seasonal cycle has previously been related to algal turf productivity as both temperature and day length (light availability), vary during this cycle which influences productivity (Carpenter 1985) as well as herbivory (Van Rooij et al. 1998; Longo et al. 2019).

Thirdly, hydrodynamic exposure of the study location (windward, leeward or protected [lagoonal]) was noted based on information reported in each study. Again, hydrodynamic exposure has previously been linked to algal turf productivity (Roff et al. 2019), and it influences other factors such as algal turf sediment loads (Tebbett et al. 2017a), herbivory (Bejarano et al. 2017), turbidity/light availability (Whinney et al. 2017) and mass transfer to algal turfs (Carpenter and Williams 2007).

Fourthly, the reef identity was recorded. This reef identity factor accounted for the lack of spatial independence present in the dataset due to multiple measurements coming from the same reefs. This reef identity factor also concatenated the range of broader-scale drivers (e.g. sea surface temperature, water clarity, proximity to land, sediment loads, herbivore abundance, hydrodynamic exposure and light availability) that vary among reefs (e.g. Cheal et al. 2012; Fabricius et al. 2014; Assis et al. 2018; Tebbett et al. 2018b; Heenan et al. 2020) and could influence algal turf productivity levels over broader spatial scales. While concatenating these variables into a single categorical factor loses information on what specific variables may be important, it can effectively account for the lack of spatial independence in the database. In addition, limitations with the data, and the high degree of co-linearity among explanatory variables, precluded the consideration of these broader scale factors in more detail.

Fifthly, the study identity was recorded. As above, this study identity factor accounted for the lack of independence present in the dataset due to multiple observations from the same studies. In addition, the study identity factor concatenated the potential effects of a range of ‘study-level’ factors (e.g. the quantification method, study substratum, and the conditioning time of substrata) that could influence productivity values. Notably, different methods have been used to quantify algal turf productivity including respirometry techniques and caging techniques, therefore, differences between these techniques, may have shaped productivity estimates. The surfaces algal turfs are grown on, as well as how long experimental surfaces are conditioned for, can also substantially influence their community composition (Harlin and Lindbergh 1977; Borowitzka et al. 1978; Hixon and Brostoff 1985) with potential impacts on the community’s productivity. While noting this factor, we also specifically recorded the year each observation was taken, as well we the substratum (natural coral reef benthos, block/tile cut from a dead coral skeleton, or artificial tile) from which algal turf productivity was quantified, to facilitate more nuanced insights into the algal turf productivity research conducted to-date.

Finally, standing biomass of the algal turfs in g C m^{-2} was extracted for each observation (details of how are provided in Table S1). Unfortunately, this factor could only be quantified for turnover data because it was not available for all productivity observations. While standing biomass is inextricably linked to turnover estimates it represents an important explanatory variable because it provides information on the efficiency of algal turf productivity as biomass increases. Essentially, if turnover is related in some way to algal turf biomass this suggests that the factors associated with changes in algal turf biomass impact the productivity efficiency of turfs.

2.3 *Boosted regression trees*

To examine the relative importance of each explanatory factor in predicting algal turf productivity or turnover, as well as to examine the nature of the relationship between key explanatory variables and productivity/turnover, we used XGBoost (Chen and Guestrin 2016), an Extreme Gradient Boosted Regression Tree. We used this method because Gradient Boosted Regression Trees are a machine learning technique that can yield fast, accurate, predictions while efficiently modelling nonlinearity and multilevel interactions in data that may not be suitable for more traditional analysis (Elith et al. 2008). XGBoost in particular, utilises an algorithm that has been specifically designed to be efficient, flexible and robust, outperforming algorithms used by other Gradient Boosted Regression Trees (Chen and Guestrin 2016). For the XGBoost models we used Gamma distributions and treated algal turf productivity estimates (g C m^{-2} day^{-1}) or turnover (% day^{-1}) as the dependent variable and examined these against the potential explanatory variables.

Prior to running the XGBoost models to make predictions, two tuning steps were performed following Morais and Bellwood (2018). Firstly, the models were fitted repeatedly with combinations of model parameters (learning rate, maximum tree depth, gamma and subsampling rate) that were varied systematically. The combination of parameters that yielded the minimum root mean square error (rmse) was subsequently recorded (productivity model: learning rate = 0.4, maximum tree depth = 7, gamma = 0.1, and subsampling = 0.5; turnover model: learning rate = 0.2, maximum tree depth = 7, gamma = 0, and subsampling = 0.5), while all other parameters were kept at their default values. During the second round of tuning, we fitted the models repeatedly with combinations of parameters drawn randomly from a uniform distribution bounded by the recorded parameters from the first tuning round ± 10 %. Again, we recorded the parameters that resulted in the lowest rmse (productivity model: learning rate = 0.413, maximum tree depth = 8, gamma = 0.093, and subsampling =

0.543; turnover model: learning rate = 0.188, maximum tree depth = 6, gamma = 0.003, and subsampling = 0.493), however, the second tuning step did not improve rmse substantially in either case as it only changed from 0.329 to 0.333 and from 2.288 to 2.172 for the productivity and turnover models, respectively.

The accuracy and precision of our tuned XGBoost models were subsequently evaluated using a cross-validation procedure. To do this, the productivity and turnover datasets were randomly split into training and testing datasets. The training datasets were used to refit the models to generate coefficients for prediction and were based on 80 % of the data. The testing datasets were used to contrast with predictions from the training dataset and were based on the remaining 20 % of the data. We calculated a bias metric by subtracting each algal turf productivity/turnover value predicted by the respective XGBoost model from its actual value (an accurate model has a bias value at or close to zero). Precision of the models was assessed using prediction R^2 values which were calculated by fitting a linear regression model between the raw data values and the predicted values and recording the R^2 from this regression. These cross-validation steps were repeated 1000 times in each case.

Finally, predictions of algal turf productivity as well as turnover were calculated using our tuned and cross-validated XGBoost models across all explanatory variables. To generate a distribution of algal turf productivity and turnover predictions we bootstrapped the models for 1000 iterations and subsequently sampled the median predicted value ± 95 % highest density intervals. The relative importance of different predictor variables, in accounting for variation of algal turf productivity and turnover estimates, were assessed against the expected importance of variables given chance alone (i.e. if all variables were equally involved in explaining variation within the dataset then each variable would account for 20 % or 16.7 % of the variability explained by the productivity or turnover XGBoost models, respectively).

All XGBoost modelling was performed in the software R (R Core Team 2019) using the *XGBoost* (Chen et al. 2019) package.

2.4 *Methodological considerations*

In addition to assessing how and why algal turf productivity observations vary among coral reefs, we wanted to further consider how the methods used to quantify algal turf productivity could have shaped our understanding. Specifically, we wanted to consider the implications of quantifying algal turf productivity on experimental tiles/coral blocks, rather than natural reef substrata. Especially, considering recent research that has linked the accumulation of sediment in algal turfs to the growth of turfs (Clausing et al. 2014; Tebbett et al. 2018a; Tebbett and Bellwood 2020). We initially sourced data on sediment accumulation in natural algal turfs (n = 20) and in algal turfs on conditioned coral blocks (n = 43) from Tebbett et al. (2018a). Note the data contained within this previous study represented a direct comparison between natural reef substrata and coral blocks as all sediments were collected from the same location (Lizard Island), in the same habitats (the reef flat between Palfrey and South Island), at the same sites (two sites), during the same sampling period.

Initially, we specifically tested for differences in sediment loads in algal turfs on natural substrata versus coral blocks using a Bayesian generalised linear model (GLM) with a Gamma distribution and log link. Substratum identity (natural or block) and site identity were fitted as interacting fixed effects. The GLM was based on weakly informative priors, 3 chains, a warmup of 500 iterations, a thinning value of 3 and 3000 iterations. Model convergence, fit and assumptions were assessed using trace plots, autocorrelation plots, rhat plots, posterior predictive checks, effective sample sizes and residual plots. These tests suggested the chains were well mixed and had converged on a stable posterior, and that no patterns were present in the residuals. We then predicted potential algal turf productivity (mm growth day^{-1}), as a function of sediment load, on coral blocks and natural reef substrata. To do this we utilised a Bayesian model, relating potential algal turf productivity to sediment loads, formulated in Tebbett and Bellwood (2020), and fed each sampled sediment load to this model to estimate productivity (mm growth day^{-1}) for that specific sediment load. It should be noted that the term ‘productivity’ applies to increases in mass, however, in the case of this model the term ‘productivity’ is applied to increases in turf length. All statistical analyses were performed in the software R (R Core Team, 2019) using the *rstan* (Stan Development Team 2018) and *rstanarm* (Goodrich et al. 2018) packages.

3.0 Results

3.1 *Dataset*

After examining the relevant literature on coral reef algal turf productivity our final dataset consisted of 214 productivity estimates and 155 turnover estimates from 17 and 11 studies, respectively. While we placed no spatial or temporal limitations on the inclusion of studies in this dataset there were some noticeable patterns. Firstly, despite observations being distributed around several of the world’s coral reef regions, the vast majority (54 % and 63 % of productivity and turnover observations, respectively) were from the Great Barrier Reef (Fig. 1a). Secondly, the restricted temporal distribution of these observations was marked, with 80 % and 94 % of productivity and turnover data, respectively, collected prior to 1990 (Fig. 1c). Finally, most of the productivity and turnover observations (92% and 98 %, respectively) were based on experimental substrata (coral blocks or artificial tiles), rather than studying natural reef substrata (Fig. 1d).

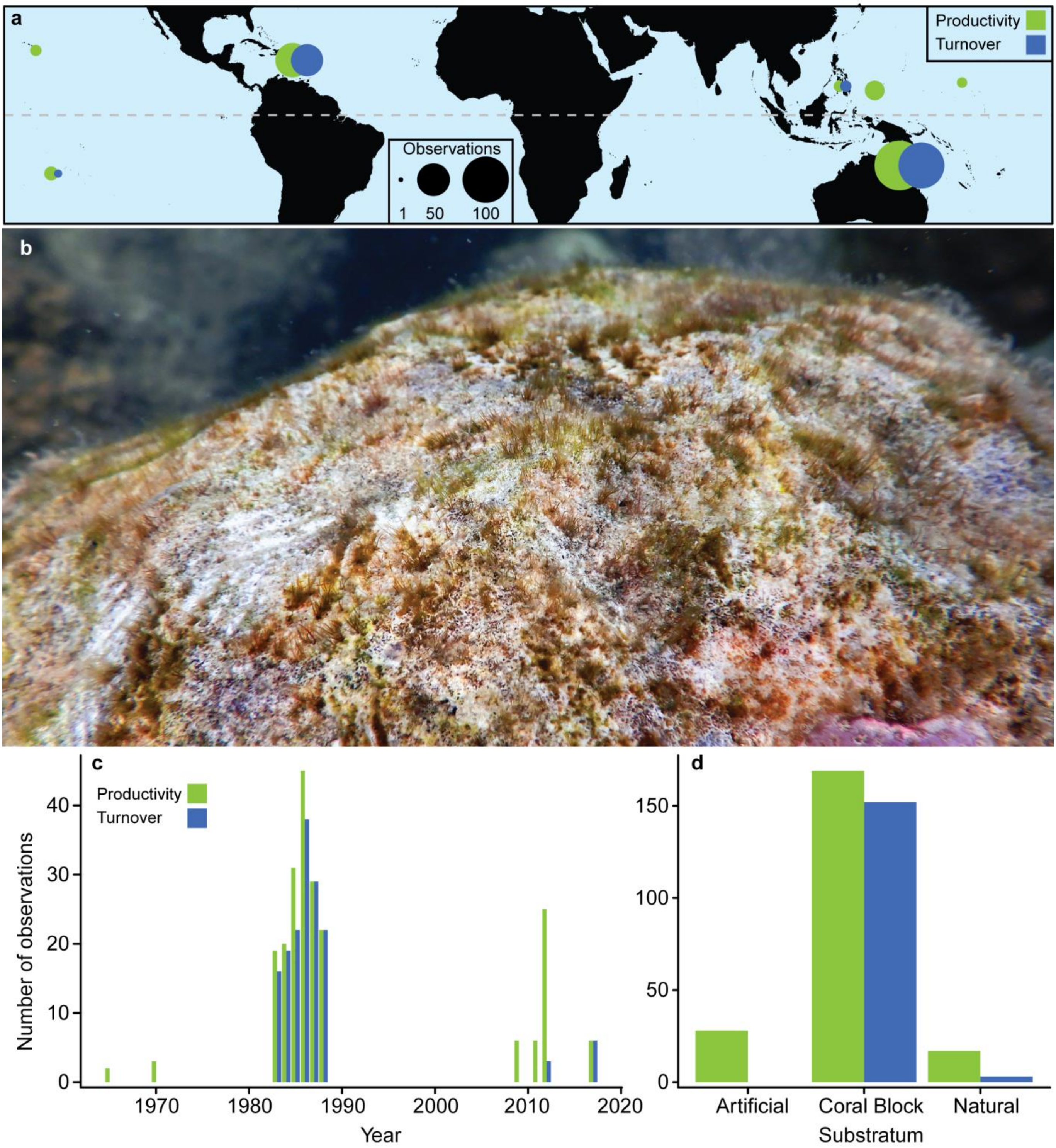

Figure 1 a) The distribution of algal turf productivity and turnover observations from coral reefs around the world in our dataset. b) A short productive algal turf community on a shallow-water coral reef at Orpheus Island on the Great Barrier Reef (photograph: CHR Goatley). c) The temporal distribution of algal turf productivity and turnover observations in

our dataset. d) The frequency by which algal turf productivity and turnover were examined on different substrata in our dataset.

3.2 *Drivers of algal turf productivity and turnover*

The formulated XGBoost models resulted in a median bias that was close to zero (0.26 and 0.349 for the productivity and turnover models, respectively) suggesting that the models were relatively accurate. Furthermore, the median R^2 of the final models were 0.69 and 0.87 (for the productivity and turnover models, respectively), suggesting that the models were relatively precise. These XGBoost models revealed that some of the explanatory variables were far more important than others in accounting for patterns in algal turf productivity and turnover. In terms of productivity, depth was the single most important variable and explained 47.0 % (median) (39.2 % - 55.0 %; upper and lower 95 % highest density intervals) of the variation in productivity accounted for in the XGBoost model (Fig. 2a). In addition, study site (reef) explained more variation in algal turf productivity than expected by chance, accounting for 24.1 % (19.3 % - 30.3 %) of the variation explained. Standing algal turf biomass was the single most important variable for explaining turnover patterns, with this variable accounting for 51.5 % (46.3 % - 58.1 %) of the variation in turnover explained by the XGBoost model (Fig. 2b). The remaining explanatory variables all remained below the relative importance level expected by chance in both productivity and turnover models.

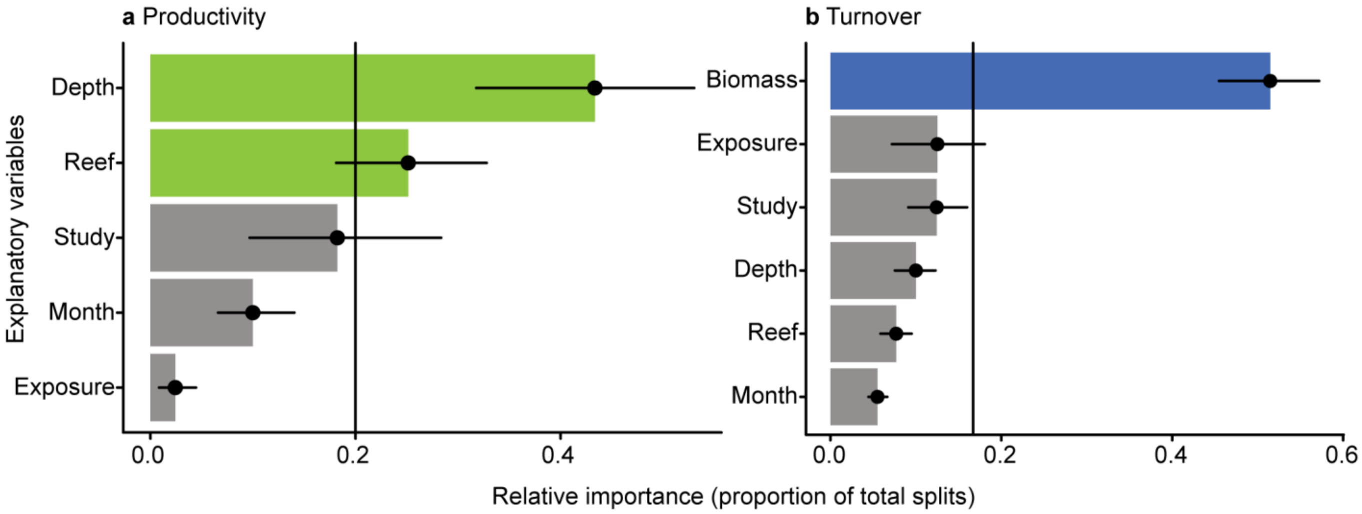

Figure 2 The relative importance of potential explanatory variables in accounting for a) algal turf productivity and b) turnover estimates from coral reefs. Black dots indicate the median relative importance value, while the range presented represents the 95% highest density intervals based on bootstrapping predictions 1000 times. The vertical black line indicates the relative importance expected for each variable by chance.

With the key explanatory variables identified, partial dependency plots provided an insight into how these variables related to algal turf productivity and turnover (Figs. 3, 4). In terms of the relationship between productivity and the key explanatory variables there was a clear decrease in algal turf productivity as depth increased. Notably, productivity remained relatively high down to 5 m, a depth which aligns well with the end of the reef crest habitat and the beginning of the reef slope habitat, before decreasing sharply and remaining relatively low down to 15 m (Fig. 3a). While the general nature of this relationship between depth and productivity appeared to be similar across sites (e.g. Fig. 3a), there was a distinct difference in the magnitude of productivity levels among sites (Fig. 3). Specifically, predicted productivity values from the reef in Tague Bay, St Croix (the only Caribbean site in this dataset) were approximately twice the productivity values from all other reef sites, which were generally very similar (Fig. 3b). Therefore, while decreases in algal turf productivity with depth appear to be a universal pattern, the magnitude of the productivity values may be dependent on the site in question.

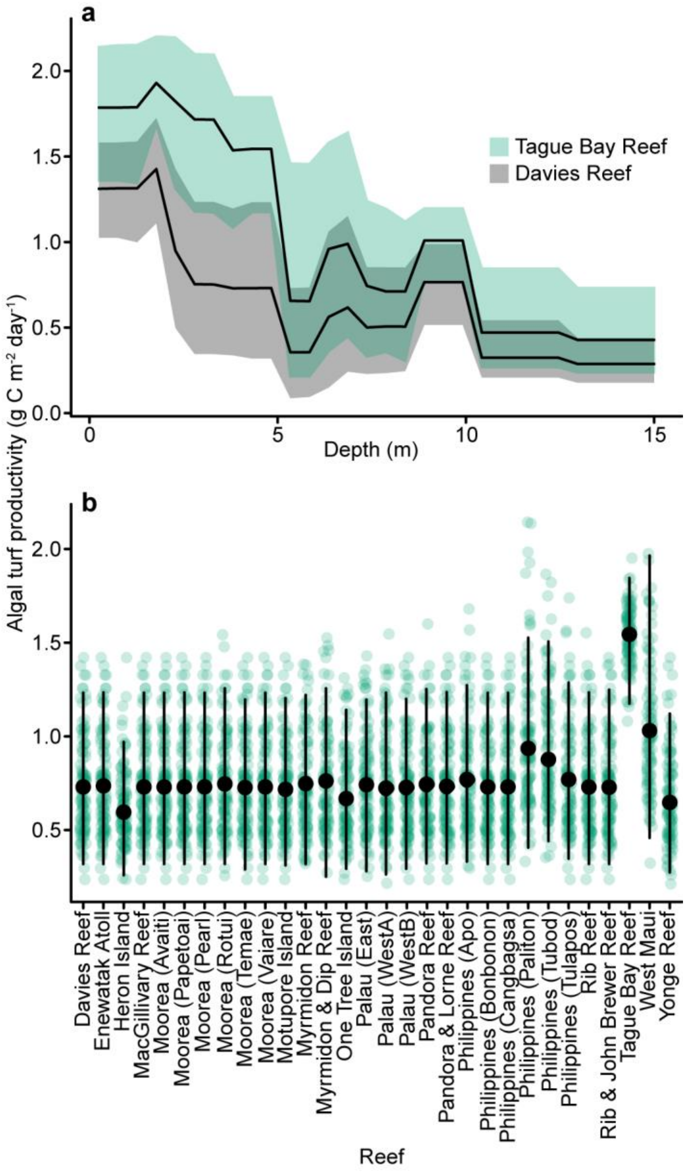

Figure 3 Partial dependency plots of the relationship between algal turf productivity and the key explanatory variables that accounted for more variability than expected: a) water depth and b) study site. All other variables were kept at their mean values and the most common category of categorical variables were used for plots (note in panel (a) that Davies Reef and

Tague Bay Reef were both equally common in the dataset [n = 55]). The black line (a) and the black points (b) represent the median predicted values, the coloured ribbons (a) and the point ranges (b) denote the 95% highest density intervals, and the green points (b) represent 100 randomly selected predicted values for each reef based on an extreme gradient boosted regression tree model (n = 1000 model iterations).

The relationship between algal turf turnover rates and standing biomass was inverse in nature. Turnover rates appear to be very high at low standing biomass levels but decreased markedly across the range of algal turf biomass levels examined (Fig. 4). However, the most precipitous decrease occurred at the lowest algal turf biomass levels (<10 g C m^{-2}), with turnover rates decreasing by more than half across this range alone (Fig. 4). This pattern suggests that algal turf productivity rates and standing biomass levels do not scale linearly, with a marked decrease in the ability of turfs to replace existing biomass as standing biomass increases.

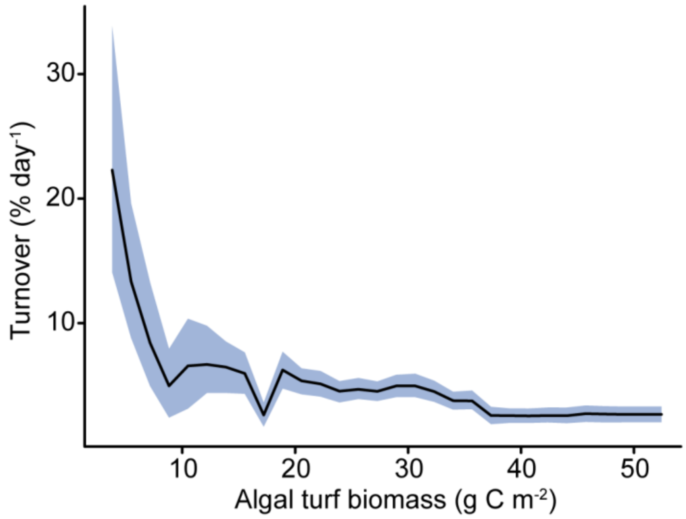

Figure 4 Partial dependency plot of the relationship between algal turf turnover and the key explanatory variable (standing algal turf biomass). All other variables were kept at their mean values and the most common category of categorical variables were used for the plot. The black line denotes the median predicted values, while the coloured ribbon denotes the 95% highest density intervals, based on an extreme gradient boosted regression tree model (n = 1000 model iterations).

3.3 *Methodological considerations*

There were marked differences in the sediment loads accumulated in algal turfs on natural substrata compared to conditioned algal turf-covered coral blocks (Fig. 5a). Sediment loads were more than 10-fold higher in natural algal turfs (2031.1 [1292.9 – 3238.4] g m^{-2}; median ± 95% highest posterior density intervals) relative to algal turfs on coral blocks (188.9 [68.5 – 527.9] g m^{-2}) (Fig. 5a; Table S2). The Bayesian model used to test these differences revealed that substratum type did influence sediment load as the 95 % credibility intervals did not overlap one (Table S2). There was no evidence that site had any effect on these sediment loads (Table S2). The differences in accumulated sediment loads translated to clear differences in algal turf productivity when we used a second Bayesian model to predict potential algal turf productivity on each substratum (Fig. 5b). Predicted potential algal turf productivity was more than two-fold higher on conditioned coral blocks (0.44 ± 0.02 mm day^{-1}) relative to natural substrata (0.19 ± 0.01 mm day^{-1}). Together, these results suggest that algal turfs grown on coral blocks/tiles accumulate lower sediment loads, potentially yielding higher algal turf productivity rates.

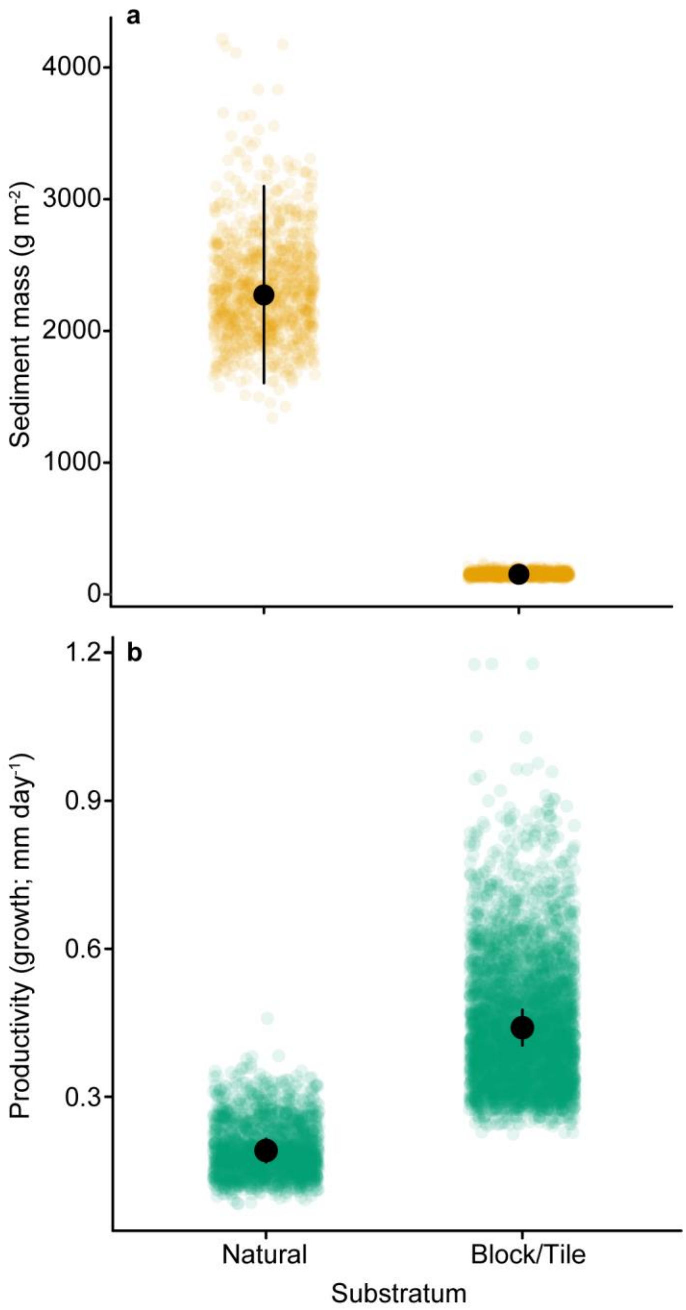

Figure 5 Differences in a) sediment loads, and b) estimated productivity, of algal turfs growing on natural substrata and coral blocks. Black points and range represent the mean predicted values and 95% credibility intervals; coloured dots represent 1000 random draws from the posterior distribution of Bayesian models to show the uncertainty around the estimates. The sediment data was sourced from (Tebbett et al., 2018a).

4.0 Discussion

Algal turfs are a key component of coral reef ecosystems and can underpin their high productivity (Adey and Goertemiller 1986; Hatcher 1988; Steneck 1997) and fuel herbivorous trophic pathways (Russ and St. John 1988; Kelly et al. 2017; Morillo-Velarde et al. 2018). While algal turf productivity may be shaped by a range of factors (e.g. Carpenter 1985; Klumpp and McKinnon 1989; Roff et al. 2019), of the factors we considered, water depth was by far the most important in structuring this productivity on coral reefs. Moreover, our consideration of algal turf turnover revealed that algal turf productivity and standing biomass do not scale linearly together in a one-to-one relationship. This suggests that the efficiency of algal turf productivity decreases as standing biomass increases, i.e. higher biomass reduces the capacity of algal turfs to replace existing biomass. However, it is important to note that in undertaking this meta-analysis we also revealed a distinct paucity of data on algal turf productivity rates from many coral reef regions around the world. Furthermore, we highlighted that the methods employed to assess algal turf productivity on reefs may have shaped our understanding of this process. The implications of these methodological limitations need to be carefully considered when quantifying algal turf productivity on coral reefs in the future.

4.1 *Productivity*

4.1.1 *Depth*

The depth at which algal turfs exist on coral reefs clearly has a marked influence on their productivity. In this respect, our meta-analysis strongly supports the conclusion of previous studies that have highlighted a decrease in turf productivity with depth (e.g. Klumpp and McKinnon 1989; Carpenter 1990; Russ 2003), as well as variation in other qualities of algal turf communities such as turf yield-to-herbivores, cover and community composition

(Brokovich et al. 2010; Fricke et al. 2014; Magalhães et al. 2015). The clear decline in algal turf productivity as water depth increases is likely to be driven by a variety of key factors including light availability (Brokovich et al. 2014; Fricke et al. 2014; Roberts et al. 2019), wave-driven hydrodynamic activity (Fulton and Bellwood 2005), herbivory rates (Cooper et al. 2019) and algal turf sediment loads (Purcell 2000), that all correlate with water depth on coral reefs to varying extents. Of these factors, light availability is likely to be one of the most important. This is because, the rate of algal turf productivity is constrained as light levels decrease because algal turf photosynthesis rates are closely tied to irradiance levels (Carpenter 1985; Klumpp and McKinnon 1989). Interestingly, previous studies have highlighted that algal turfs are well adapted to high light intensity as rates of photosynthesis increase steadily with irradiance levels, showing few signs of photo-inhibition (Carpenter 1985; Klumpp and McKinnon 1989). This lack of photo-inhibition may underpin how algal turf communities maintain their highest productivity levels at the shallowest water depths.

While depth mediated light availability appears to shape algal turf productivity rates directly (Carpenter 1985; Klumpp and McKinnon 1989), it may also influence productivity rates indirectly by shaping the community composition of algal turfs. Specifically, different algal species make up the algal turf community across depth gradients, potentially due to different tolerances for light levels (Anderson et al. 2005; Fricke et al. 2014; Magalhães et al. 2015). In addition, herbivory is known to decrease substantially as depth increases (Brokovich et al. 2010; Cooper et al. 2010), and this factor can also shape the community composition of algal turfs (Scott and Russ 1987; Hixon and Brostoff 1996; McClanahan 1997). This is important because the nature of algal turf communities, in terms of the species that inhabit them, as well their structure and diversity, is likely to influence biomass and productivity levels, as per-unit biomass and productivity differs between algal species and functional groups (Rogers and Salesky 1981; Steneck and Dethier 1994; Bruno et al. 2006;

but see Williams and Carpenter 1990). As such, variation in algal turf community composition across depth/light gradients could also influence net productivity rates.

4.1.2 *Site effects*

Apart from factors associated with the depth at which algal turfs exist, there was some variability in productivity among sites. There are two notable points that can be drawn from these results. Firstly, there appeared to be remarkably little variation in algal turf productivity among the vast majority of reef sites. This suggests that the broader scale factors that vary among reefs such as temperature, light intensity and nutrient inputs may not have a substantial influence on algal turf productivity for many reefs. However, secondly, algal turf productivity from the Tague Bay Reef site was approximately two-fold higher than all other sites. These data suggest that a factor, or factors, operating at Tague Bay Reef led to far higher productivity levels at this site. Tague Bay, is located on Saint Croix in the Caribbean, and it has been suggested that Caribbean reefs function quite differently from other reef systems due to factors such as lower species and functional diversity, geographic isolation, and more severe anthropogenic impacts (Bellwood et al. 2004; Roff and Mumby 2012; Bruno et al. 2019; Siqueira et al. 2019). Unfortunately, determining which factors may be accounting for these higher productivity levels is difficult, as Tague Bay is the only site from the Caribbean in our dataset, and all productivity values at this location were quantified on the same experimental substrata, using the same methods. Therefore, it is unclear if these productivity estimates were driven by a methodological difference between the studies at this site vs other studies, a factor associated with the reef in Tague Bay, or a broader Caribbean phenomenon.

4.2 *Turnover*

Turnover was clearly related to algal turf biomass, highlighting a loss of productivity efficiency as biomass increased. Importantly, variation in algal turf biomass is associated with variation in the length and density of turf filaments (i.e. an alteration of the algal turf canopy structure) (Purcell 2000; Tebbett and Bellwood 2020), as well as the community composition of algal turfs (Scott and Russ 1987; Hixon and Brostoff 1996; Harris et al. 2015). Essentially, algal turfs exist on a gradient from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs) (Goatley et al. 2016; Tebbett and Bellwood 2020). SPATs are maintained by the constant grazing pressure of herbivorous fishes, as well as other herbivorous organisms, which remove algae, reduce sediment loads (Carpenter 1986; Steneck 1997; Goatley et al. 2016; Steneck et al. 2018; Humphries et al. 2020), and constrain the community of algal species to ones that tolerate high grazing (Sammarco 1983; Scott and Russ 1987; Hixon and Brostoff 1996; McClanahan 1997). However, when the strength of herbivory is reduced, through factors such as herbivore removal (Heenan et al. 2016; Steneck et al. 2018), or the accumulation of sediments that weaken herbivore feeding pressure (Tebbett et al. 2017b; McAndrews et al. 2019), this can result in an increase in algal turf length/biomass (Goatley and Bellwood 2013; Fong et al. 2018; Humphries et al. 2020) and/or changes in algal taxonomic composition (Scott and Russ 1987; Hixon and Brostoff 1996), resulting in LSATs.

Across this gradient in algal turf condition from SPATs to LSATs, a number of aboitic factors within the turf canopy varies, including flow speeds and mass transfer (Carpenter and Williams 1993, 2007), light levels available for photosynthesis via self-shading (Williams and Carpenter 1990) and sediment loads (Purcell 2000; Latrille et al. 2019). As turf biomass increases this suite of factors may act together to reduce productivity in the basal portion of the turf community because these factors limit light and the exchange of nutrients. This results in a turf community that is reliant on the apical portion of filaments for most of the production, i.e. the filament sections that are above the sediment layer and exposed to high water flow and light. As such, reductions in algal turf turnover rates may be driven by changes in the conditions within the turf community as biomass increases.

In addition to the abiotic factors described above, the community composition of the algal turf may be related to the productivity efficiency of the entire turf community as per-unit productivity rates can differ between algal species (Rogers and Salesky 1981; Steneck and Dethier 1994; Bruno et al. 2006; but see Williams and Carpenter 1990). However, unfortunately, our understanding of the specific nature of the relationships between sediment accumulation, canopy structure, productivity and algal turf community composition are currently limited (reviewed in Tebbett and Bellwood [2019]), making it difficult to determine the relative importance of community composition changes, compared to abiotic conditions within the turf canopy, in driving variation in turnover. However, exploring these relationships in more detail offers fertile ground for further future research.

4.3 *Methodological considerations and future studies*

Despite evidence that algal turf coverage has increased on coral reefs in recent decades (Toth et al. 2014; Holbrook et al. 2016; Ellis et al. 2019; Kennedy et al. 2020; Koester et al. 2020), and algal turfs are likely to be an abundant benthic covering on coral reefs in the future (Bellwood et al. 2019a; Tebbett and Bellwood 2019), the paucity of available data on their productivity is concerning. Unfortunately, beyond the foundations laid by the pioneering research of formative reef scientists (e.g. Carpenter 1986; Klumpp and McKinnon 1992; Steneck 1997; Russ and McCook 1999) there appears to have been remarkably little quantification of algal turf productivity in-situ on coral reefs within the last three decades, within the scope of our meta-analysis. It is important to note that this result is not because of our search parameters and paper filtering methods, as the same units of measure (g C m^{-2} day^{-1}) are just as applicable to studies of productivity today as they were historically. Unfortunately, the exact reason behind the limited quantification of algal turf productivity in-situ on coral reefs in recent decades is unclear. It may be due to logistics (limited access to respirometery chambers or field time/access). However, it probably reflects a shift in emphasis, with attention focussed on documenting declines rather than understanding the system.

Regardless of the reasons behind the limited quantification of algal turf productivity, the amount of available data is sobering. Especially, considering the extent to which coral reef research has grown recently, the technological advances that have assisted this research, the strength and frequency of environmental disturbances (e.g. global coral bleaching events) that are now shaping this ecosystem (Cheal et al. 2017; Hughes et al. 2018; Williams et al. 2019), and the inevitable increase in algal turf area on reefs (Bellwood et al. 2019a; Tebbett and Bellwood 2019; Vercelloni et al. 2020). If we are to understand the functioning of coral reef systems into the future, it appears to be a logical imperative to enhance our knowledge about the productivity of one of the most widespread primary producers; algal turfs. To stimulate further research into the quantification of algal turf productivity on coral reefs, this may require the development of new technologies that are both relatively cheap and easy to use in the field (see below for further discussion), as well as greater collaboration between research groups with access to such technologies, or with access to areas where turf productivity has not been quantified. In addition, exploring potential links between algal turf productivity and other reef processes, that are viewed as inherently valuable (e.g. fishable biomass [Lau et al. 2019; Woodhead et al. 2019]), may help highlight the importance of turfs on coral reefs, and in-turn, encourage the study of turfs in other research fields.

Furthermore, it must be noted that our understanding of algal turf productivity to-date appears to have been shaped substantially by the methods used, especially the use of experimental substrata, and their interactions with sediments. Overwhelmingly, artificial tiles or coral blocks have been used to quantify in-situ algal turf productivity (>92 % of observations in our dataset used these methods). Such tiles or blocks can be readily deployed, removed and quantified, and offer exact replicate units. However, these surfaces only represent 'potential productivity' at a location as they are not natural. Indeed, experimental surfaces such as coral blocks accumulate far lower sediment loads than the natural surrounding reef substratum (Fig. 5). This may be due to: 1) the elevation of tiles/blocks above the substratum making them more exposed to hydrodynamic activity, 2) 'edge effects' and/or 3) enhanced fish grazing (Duran et al. 2018; Latrille et al. 2019; Tebbett et al. 2020). The influence of these factors is likely to be relatively consistent across tiles, meaning that the patterns of algal turf productivity reported in prior studies are valid in relative terms. However, in terms of absolute productivity levels, we may have systematically overestimated productivity values for coral reef algal turfs. There is a clear need to estimate algal turf productivity on natural reef substrata more widely.

In terms of estimating algal turf productivity in-situ on natural reef substrata this may involve the use of specially designed incubation chambers (e.g. Miller et al. 2009; Tait and Schiel 2010; Murphy et al. 2012; Dellisanti et al. 2020), boundary layer approaches (McGillis et al. 2011; Takeshita et al. 2016), or PAMs (Silveira et al. 2015). Indeed, the use of the Community In Situ Metabolism 'CISME' units appears to offer a particularly promising avenue for future research (Murphy et al. 2012; Dellisanti et al. 2020). However, it must be noted that the methods outlined above can be limited by constraints associated with expense, technical difficulties, and time. All would hamper our ability to quantify productivity efficiently across broader spatial scales. To address this issue, and expand this research field further, such methods may be used to establish relationships between easily measured universal traits (sensu Bellwood et al. 2019b), such as algal turf length/density or accumulated sediment load, and algal turf productivity rates. Essentially, mechanistic relationships could be established between these traits and algal turf productivity, allowing for the estimation of productivity from more-easily, and cheaply, measured universal traits (as for the length and biomass production relationships established in reef fishes e.g. Morais and Bellwood [2020]). If such relationships were established, this would allow productivity on natural reef substrata to be widely estimated and studied, allowing more nuanced insights into the functioning of coral reefs going forward.

5.0 *Conclusions*

In this study we identified water depth and standing algal turf biomass as important drivers that shape algal turf productivity and turnover on coral reefs, respectively. This strongly supports the conclusions of past studies (e.g. Klumpp and McKinnon 1989; Carpenter 1990; Russ 2003). However, we also uncovered potential limitations in our understanding of these ecosystem processes, and our approaches to measuring them. This comes at a time when climate change is changing the status-quo for coral reefs (Hughes et al. 2017; Williams et al. 2019), and when more people than ever before are depending directly on the productivity that coral reefs provide (Newton et al. 2007; Teh et al. 2013; Hicks et al. 2019). Into the future it appears likely that people will have to inceasingly depend on algal turf-covered reefs (Bellwood et al. 2018; Tebbett and Bellwood 2019), particularly as many reefs already support algal turf cover of >50% (Vroom 2011; Harris 2015; Aued et al. 2018; Bierwagen et al. 2018; Emslie et al. 2019). As such, renewed research into the quantification of algal turf productivity, particularly on natural reef substratum, will be important. This research will help us to understand how coral reefs will function in the future and the extent to which they can continue to provide the services that people require.

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