



# Optimising Seagrass Conservation for Ecological Functions

Christopher J. Henderson,<sup>1,2,3\*</sup> Tim Stevens,<sup>1</sup> Shing Y. Lee,<sup>1,4</sup>  
Ben L. Gilby,<sup>2,3</sup> Thomas A. Schlacher,<sup>2,3</sup> Rod M. Connolly,<sup>1</sup> Jan Warnken,<sup>1</sup>  
Paul S. Maxwell,<sup>5</sup> and Andrew D. Olds<sup>2,3</sup>

<sup>1</sup>Australian Rivers Institute—Coasts and Estuaries and Griffith School of Environment, Griffith University, Gold Coast Campus G24, Parklands Drive, Southport, Queensland 4222, Australia; <sup>2</sup>School of Science and Engineering, University of the Sunshine Coast, Maroochydore, Queensland 4558, Australia; <sup>3</sup>The ANIMAL Centre—Health, Ecology and Conservation Research, University of the Sunshine Coast, Maroochydore, Queensland 4558, Australia; <sup>4</sup>Simon FS Li Marine Science Laboratory, School of Life Sciences, and Earth System Science Programme, The Chinese University of Hong Kong, Shatin, Hong Kong SAR, China; <sup>5</sup>Healthy Land and Water, PO Box 13086, George Street, Brisbane, Queensland 4003, Australia

## ABSTRACT

Animals are central to numerous ecological processes that shape the structure and function of ecosystems. It follows that species that are strongly linked to specific functions can represent these functions spatially and hence be useful in conservation planning. Here we test this notion of ‘functional species surrogacy’ for the conservation of seagrass meadows that have been impacted by stressors. We measured algal herbivory and herbivorous fish assemblages across a range of seagrass meadows in the Moreton Bay Marine Park, Queensland, Australia. We determined the suitability of herbivorous fish to act as a surrogate for the function of algal herbivory and modelled the abundance of this surrogate, and thus herbivory, in

seagrass meadows to compare the spatial distribution of this function within existing reserves. We used underwater video systems to determine the abundance of all herbivorous fish species in seagrass meadows. The abundance of the dusky rabbitfish (*Siganus fuscescens*) was the best predictor of algal herbivory in seagrass meadows, supporting the suitability of this species as a functional surrogate. The distribution of dusky rabbitfish, and therefore the ecological function of herbivory, was not well represented in the Moreton Bay Marine Park protected areas. Only 7% of the equivalent area of seagrass meadows protected in marine reserves were found to have high abundances of dusky rabbitfish. We demonstrate that the abundance of functionally important herbivores can be suitable as a surrogate for herbivory in seagrass conservation. Our findings show that data on the spatial distribution of ecological functions can alter priorities for reserve design, and we suggest that our functional approach to species surrogacy is likely to improve conservation performance in seagrass ecosystems.

**Key words:** coastal ecosystems; conservation prioritisation; herbivory; seagrass; surrogate species; fish.

Received 16 July 2018; accepted 8 January 2019;  
published online 4 February 2019

**Electronic supplementary material:** The online version of this article (<https://doi.org/10.1007/s10021-019-00343-3>) contains supplementary material, which is available to authorized users.

**Author Contributions** CH, TS, SYL, BG, PM, and AO conceived the idea; CH and BG performed the research; CH, TS, SYL, BG, and JW analysed the data; and CH, TS, SYL, BG, TS, RC, and AO wrote the paper.

Data for this article can be found at <https://zenodo.org/record/2535950#.XDZ22vxx3OR>.

\*Corresponding author; e-mail: chender1@usc.edu.au

## MANUSCRIPT HIGHLIGHTS

- Herbivory positively correlated with the abundance of one harvested fish species.
- Dusky rabbitfish were a suitable herbivory surrogate in seagrass meadows.
- Herbivory was maximised outside of reserves, altering priorities for management.

## INTRODUCTION

Animals perform a diversity of ecological processes that shape the structure and function of all ecosystems (Lundberg and Moberg 2003; Ripple and others 2014; Mellin and others 2016). The types, distributions, and rates of ecological functions have, however, been altered in many landscapes by humans (Estes and others 2011; McCauley and others 2012; Tschamtker and others 2012). Amongst others, humans have modified the dispersal of seeds by birds (Lundberg and others 2008), pollination of flowers by insects (Lowenstein and others 2015), and consumption of plants by herbivores (Poore and others 2012; Atwood and others 2015; Duffy and others 2015). Thus, protecting species that perform pivotal ecological functions is recognised as a key consideration in conservation (Possingham and others 2005).

Arguably, a central objective of reserves (for example, national parks, marine protected areas, hunting closures) should be to maintain, or enhance, ecosystem function (Mace 2014; Althaus and others 2017). Yet, data on ecological functions are rarely used in the design of existing reserves (Klein and others 2009; Hunter Jr and others 2016). Poor consideration of functional criteria could result, *inter alia*, from functions being difficult, expensive, or time-consuming to measure, and from uncertainty about the ecological roles of species (Carwardine and others 2009; Schlacher and others 2014; Stephens and others 2015).

In cases where a particular function can unequivocally be attributed to a species (or group of species), the distribution and abundance of this species can serve as a surrogate for the function in conservation planning (Olds and others 2014; Berger and others 2015; Lindenmayer and others 2015). Surrogate species have been used widely, and across many landscapes, to represent biodiversity, habitats, and ecosystems in conservation (Leslie 2005; Rodrigues and Brooks 2007; Caro 2010). Functionally important species have been employed as surrogates in terrestrial conservation

for decades, but few proxies appear to work well, and consistently, across multiple ecosystems and landscapes (Cardinale and others 2006; Stephens and others 2015). However, although it remains difficult to employ the same surrogates across multiple ecosystems, there are a number of examples where suitable surrogates have been used successfully in the management of a number of ecosystems (Lindenmayer and others 2015). The function of herbivory is a key process in the sea, especially on coral reefs, in kelp forests and seagrass meadows, where it plays a critical role in maintaining the health of these ecosystems (Valentine and others 1997; Mumby and others 2006; Olds and others 2012c; Poore and others 2012). Herbivorous fishes have been used as surrogates for the ecological function of herbivory on coral reefs (Edwards and others 2010; Brown and Mumby 2014; Olds and others 2014; Berger and others 2015), but this functional approach to species surrogacy (that is, where an individual species is a surrogate for a function) has not been tested in other coastal ecosystems (for example, estuaries, sandy beaches, seagrass meadows, kelp forests) (Ling and others 2009; Unsworth and Cullen 2010; Schlacher and others 2015; Gilby and others 2017a).

Seagrass meadows are key ecosystems in many marine systems, providing nursery areas for many fish, supporting fisheries production, and containing significant stocks of blue carbon globally (Heck and others 2003; Fourqurean and others 2012; Cullen-Unsworth and others 2014). Seagrass meadows are, however, also in global decline (Orth and others 2006; Hughes and others 2009; Waycott and others 2009; Unsworth and others 2015), resulting from human pressures and the excessive growth of epiphytic and drift algae (Waycott and others 2009; Maxwell and others 2014). Herbivores can control detrimental impacts to seagrass by grazing down algae that reduces the light availability to seagrass meadows (Heck and Valentine 2006; Whalen and others 2013; Duffy and others 2015), and hence, herbivory is a pivotal function in seagrass meadows (Vergés and others 2014; Maxwell and others 2017). Direct or indirect herbivory on seagrass blades, however, remains dominated by macro-herbivores and invertebrates, with very few fish herbivores having direct negative effects on the biomass of a seagrass meadow (Heck and Valentine 2006). Herbivory on algae is, however, rarely considered in seagrass conservation (Unsworth and Cullen 2010; Saunders and others 2017), even though herbivorous fish do often benefit from conservation in many different systems (Prado and

others 2008; Henderson and others 2017b). Functionally important herbivores might be suitable as surrogates for this ecological function and could be used to improve conservation planning for seagrass meadows (Henderson and others 2017b), but this hypothesis has not been tested with empirical data.

Although herbivory in seagrass meadows can be focused on epiphytic algae, macroalgae, and even seagrass blades, and is completed by different grazer types ranging from macrograzers (for example, turtles and dugongs, Aragones and Marsh 2000) to fish grazers (for example, siganids and sparids, Pages and others 2014) and mesograzers (for example, amphipods and shrimp, Ebrahim and others 2014), our focus here is on algae grazing by herbivorous fish species. One of the key conservation benefits of marine reserves is the removal of fishing pressure, with this likely impacting the functions that many fish provide (Olds and others 2012c). Here we test whether a herbivorous fish species could be used as a functional surrogate in the context of conservation planning in a subtropical bay (Moreton Bay, Queensland, eastern Australia) that contains seagrass meadows inside and outside of reserves. These reserves were designed to protect 'function', but no empirical data are available to support this tenet for seagrass meadows (Bennett and others 2009; Gibbes and others 2014). Consequently, we (1) identify a suitable surrogate for herbivory on algae in seagrass meadows; (2) determine the spatial distribution of the functional surrogate, and thus algal herbivory, in seagrass meadows across the bay; (3) test how well existing marine reserves conserve the spatial distribution of the surrogate of this important ecological function; and (4) put forward recommendations on how the reserve network could be modified to better represent ecological functions in seagrass meadows.

## METHODS

### Study Seascape

Moreton Bay is a large (c. 1500 km<sup>2</sup> in area) subtropical embayment on the south-east coast of Queensland, Australia. The Moreton Bay Marine Park consists of a number of different protection zones, ranging from zero restrictions to complete marine national park zones (hereafter referred to as marine reserves), where no extraction of any resource is allowed. It supports a heterogeneous seascape that includes seagrass meadows, mangroves forests, coral reefs, and several marine reserves that are closed to fishing (Stevens and

Connolly 2005; Olds and others 2012b; Gibbes and others 2014). We measured algal herbivory rates and surveyed herbivorous fish assemblages in 10 subtidal seagrass (*Zostera muelleri*) meadows in the bay: five were located in no-take marine reserves and five in areas open to fishing (Figure 1). Approximately a quarter of all seagrass meadows (c. 208 km<sup>2</sup> in area) in the Moreton Bay Marine Park is located within marine reserves (c. 52 km<sup>2</sup> in area). All ten sites were sampled three times, in the austral winter (August 2014), spring (November 2014), and summer (February 2015), to encompass the typical range of temperature variation in Moreton Bay. The ten sampled seagrass meadows varied in size (< 1–16 km<sup>2</sup>) and shape; however, all were considered to be individual meadows as they were separated by either deep channels, other habitats or small islands. Although the size and shapes of meadows varied, we used the same methods for sampling herbivory and fish in each, with twelve replicate algal assays in each meadow per season and BRUVS separated by a minimum of 200 m.

Previous studies in Moreton Bay have identified that fish abundance and diversity in seagrass meadows are positively influenced by the size and spatial context of individual meadows (that is, their spatial proximity to mangrove forests and coral reefs) and are impacted by the strong east–west gradient in water quality (that is, salinity, turbidity, nutrient concentrations) (Henderson and others 2017a; Olds and others 2017; Skilleter and others 2017). Sampling sites were selected to be representative of the full spectrum of variation in these environmental attributes. Due to variation in the seascape and environmental variables that each meadow experiences, seagrass meadow characteristics were not always similar; however, they were all dominated by *Zostera muelleri*. Seascape variables were calculated in ArcGIS (ESRI) by quantifying the area of each seagrass meadow as well as the proximity of meadows to other seagrass, and to coral reefs and mangrove forests (Table 1). Benthic habitat maps and marine park zoning were sourced from the then Queensland Department of Environment and Resource Management. Water quality data were sourced from Healthy Land and Water (EHMP 2016), which conducts monthly monitoring of water quality in Moreton Bay. We obtained data on salinity, turbidity, and temperature and interpolated (using inverse distance weighting) these metrics to each site from data collected across the entire study area (Table 1).

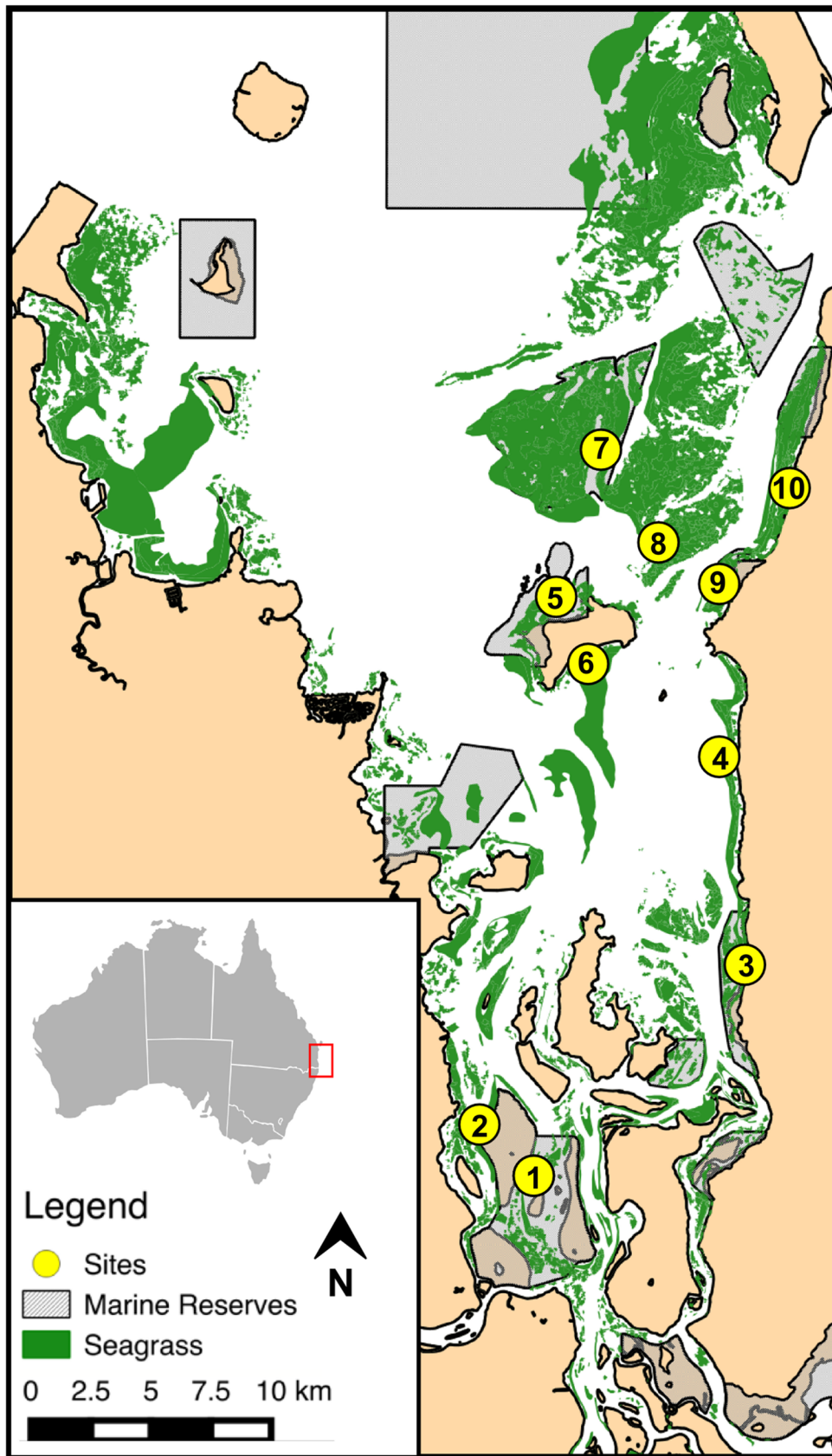


Figure 1. Seagrass meadows, marine reserves, and sampling sites in Moreton Bay, Australia.

**Table 1.** Environmental Attributes that Might Shape Seagrass Herbivory and Affect the Abundance of Herbivores in Seagrass Meadows in the Study Area

Environmental attributes	Description	Underlying ecological hypothesis
Seagrass area	The area of the seagrass in each meadow	Larger seagrass meadows support more herbivorous fishes in Moreton Bay (for example, Henderson and others 2017a)
Seagrass isolation	The distance of each seagrass meadow to the nearest neighbouring seagrass meadow	Seagrass meadows that are nearer to other seagrass support more herbivorous fishes in Moreton Bay (for example, Connolly and Hindell 2006)
Mangrove isolation	The distance of each seagrass meadow to the nearest mangrove forest	Seagrass meadows that are nearer to mangroves support more herbivorous fishes in Moreton Bay (for example, Skilleter and others 2017)
Coral reef isolation	The distance of each seagrass meadow to the nearest coral reef	Seagrass meadows that are nearer to coral reefs support more herbivorous fishes in Moreton Bay (for example, Unsworth and others 2008)
Conservation status	The conservation status of each seagrass meadow (that is, no-take marine reserves or open to fishing)	Marine reserves promote the abundance of herbivores, and the ecological function, of herbivory in seagrass meadows (for example, Valentine and others 2008)
Herbivore abundance	The abundance of herbivores will alter the rates of herbivory.	A greater abundance of herbivores will result in more herbivory in seagrass meadows (Best and Stachowicz 2012)
Predator abundance	The abundance of piscivores, which are known to prey on herbivorous fishes, at each seagrass meadow	Predators can shape herbivore assemblages in seagrass meadows through top-down effects on fish (for example, Heck and Valentine 2007)
Temperature	The temperature of the water at each seagrass meadow	Water temperature affects the composition of fish assemblages in seagrass meadows—fish abundance is often positively correlated with water temperature (for example, Nagelkerken 2009)
Turbidity	The turbidity of the water at each seagrass meadow	Water clarity affects the composition of fish assemblages in seagrass meadows—fish abundance is often positively correlated with water clarity (for example, Nagelkerken 2009)
Salinity	The salinity of the water at each seagrass meadow	Salinity affects the composition of fish assemblages in seagrass meadows—fish abundance is often positively correlated with salinity (for example, Bell and others 1988)

## Herbivory Experiments

We quantified spatial variation in relative algal herbivory rates by measuring the consumption of macroalgae (*Catenella nipae*) (following Gilby and others 2015). We used this algae in our herbivory assays for three reasons: (1) this species is a major food source for numerous herbivorous fishes that are common in the seagrass meadows of Moreton Bay (Olds and others 2012a; Davis and others 2014; Ebrahim and others 2014); (2) it has been used successfully to index herbivory in similar experiments in seagrass meadows, and on coral reefs (Maxwell and others 2014; Gilby and others 2015); and (3) it does not occur naturally in seagrass meadows, which ensures consistency in the nov-

elty of algal assays among sampling sites, and eliminates the potential bias that would result from deploying other macroalgae species that are naturally abundant at some sites and absent from others (Pillans and others 2004; Hoey and Bellwood 2011; Yabsley and others 2016). However, some species may prefer this algal type over others, resulting in a possible overestimation of algal herbivory by some species and an underestimation by others that may prefer other algal types. Twelve replicate algal assays were placed in each of the 10 seagrass meadows, and herbivory was measured as the reduction in algae weight over 72 h of deployment, with this being replicated in each season. Algal assays were placed in the middle, or close to the middle of seagrass meadows to reduce any confounding edge

effects that may be experienced. Although herbivory on algae in seagrass meadows is often caused by a number of types of grazers (Ebrahim and others 2014; Maxwell and others 2015), this study is focusing on the impact of grazing on algae by fishes and hence deployments were placed in meadows for a suitable period of time to reflect this. Herbivory on macroalgae was not filmed across the 72 h of deployment, as camera battery life did not allow for this. Deployments were long enough to measure reductions due to fish consumption (based on visual observations), but short enough to avoid complete depletion (Ebrahim and others 2014; Gilby and others 2015; 2017b).

## Fish Surveys

The species composition and abundance of fishes in each seagrass meadow were surveyed with baited remote underwater video stations (BRUVS). BRUVS consisted of a GoPro HD video camera attached to a 5-kg weight and were baited with 0.5 kg of pilchards (*Sardinops sagax*) fixed 0.5 m in front of the camera. BRUVS are effective for surveying herbivorous fishes, and stations that are baited with pilchards perform as well as, or better than, unbaited stations, or units that are baited with algae (Harvey and others 2007; Gilby and others 2016b). The use of BRUVS also allows for the abundance and diversity of predatory fish species to be determined, as predatory fish species can shape the abundance and distribution of herbivores throughout seagrass meadows (Heck and Valentine 2007). We deployed eight replicate BRUVS, for 1 h in each seagrass meadow, in each season of the study, giving a total video sampling time of 240 h for the study (Henderson and others 2017a). All BRUVS were deployed over seagrass, positioned in water depths of 1–1.5 m at low tide, and spaced at least 200 m apart to avoid sampling the same individual more than once (Gilby and others 2017a). Fish abundance, species richness, and assemblage composition was quantified from video footage using the standard Max N statistic (Willis and Babcock 2000; Harvey and others 2007).

## Data Analysis

Generalised additive mixed models (GAMMs) were used to identify potential surrogates for the ecological function of algal herbivory in seagrass meadows. We first tested whether, and how, herbivory was related to the abundance of herbivorous fishes in seagrass, or the environmental attributes of individual meadows (that is, their seascape context or water quality). This approach was then

used to examine whether the abundance of functionally important herbivores (that is, species that were significantly correlated with algal herbivory) was correlated with variation in seascape (seagrass area, proximity to seagrass, mangrove forests, coral reefs) and water quality variables (salinity, turbidity, and temperature) among seagrass meadows. Analyses were conducted with the *mgcv* (Wood 2012) and *MuMIn* (Bartoń 2013) packages in R. Model overfitting was reduced by running all possible combinations of no more than four variables and using no more than four model knots (that is, individual polynomial functions that combine to smooth GAMMs) (Zuur and others 2009). To evaluate whether surrogate species could be used to improve spatial conservation planning for ecological functions in seagrass meadows, we developed species distribution models (SDMs) for the abundance of functionally important herbivores (that is, species that were significantly correlated with herbivory) in seagrass meadows. SDMs were based on best fit GAMMs and were visualised using ArcGIS (Lentini and Wintle 2015). Seagrass meadows were then ranked based on the modelled abundance of functionally important herbivores, and we used ArcGIS to compare the distribution of functionally important seagrass meadows (that is, those that support abundant herbivores) to the position of reserves in Moreton Bay Marine Park.

## RESULTS

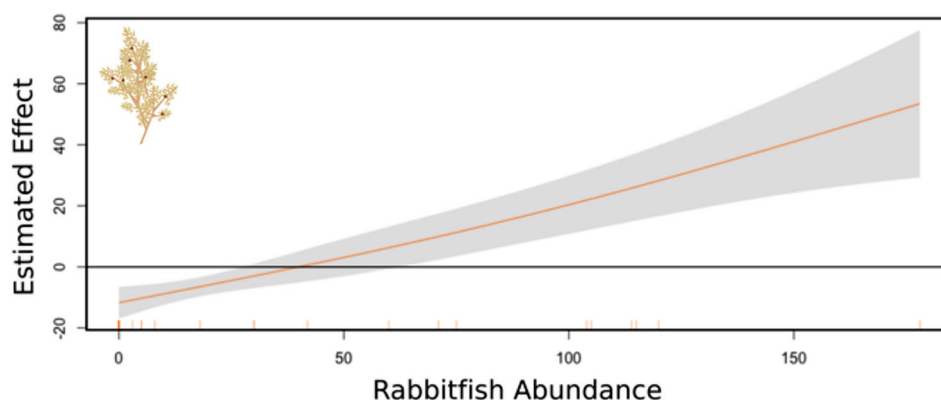
### Identifying Surrogates for Algal Herbivory in Seagrass Meadows

Algal herbivory varied significantly between seasons ( $p = 0.001$ ) and seagrass meadows ( $p = 0.045$ ). However, herbivory was not higher in marine reserves than in fished areas ( $p = 0.099$ ). Herbivory on algal assays was highest at seagrass meadows that were closer to oceanic input and was maximised over the summer months (Table S1). Baited remote underwater videos recorded three different herbivorous fish species: the dusky rabbitfish (*Siganus fuscescens*), sabretooth blenny (*Petroscirtus variabilis*), and a fan-bellied leatherjacket (*Monacanthus chinensis*). The most abundant herbivore throughout the study was the dusky rabbitfish (1083 individuals), followed by the fan-bellied leather jacket (713 individuals) and the sabretooth blenny (87 individuals). Generalised additive mixed models for algal herbivory in seagrass meadows showed that the abundance of a single herbivorous fish species, the dusky rabbitfish, was the only factor in the best fit model (Table 2). The

**Table 2.** Best fit Generalised Additive Mixed Models (GAMMs) Relating: (a) Algal Herbivory to Herbivore Abundance, and the Environmental Attributes of Seagrass Meadows; and (b) Herbivore Abundance to the Environmental Attributes of Seagrass Meadows

Best fit models	$R^2$	df	AICc
(a) Algal herbivory Dusky rabbitfish ( $I = 1.00, p < 0.001$ )	0.58	5	267.4
(b) Herbivore abundance *Temp. ( $I = 0.95, p < 0.001$ ) + Sal. ( $I = 0.85, p = 0.001$ ) + Seagrass ( $I = 0.81, p = 0.04$ )	0.61	6	305.6
Temp. ( $I = 0.95, p < 0.001$ ) + Sal. ( $I = 0.85, p = 0.001$ ) + Seagrass ( $I = 0.81, p = 0.04$ ) + Status ( $I = 0.29, p = 0.14$ )	0.64	7	306.7

\*Spatial distribution model based on the following: rabbitfish abundance =  $-604 + 11.51(\text{salinity}) + 10.18(\text{temp}) + 0.98(\text{seagrass patch area})$ . Important values and factor significance are included in parentheses. (Larger values indicate stronger correlation with fish abundance.)



**Figure 2.** Generalised additive mixed model (GAMM) relating the distribution of algal herbivory to the abundance of dusky rabbitfish (*Siganus fuscescens*) in seagrass meadows. No other species or environmental attributes were significantly correlated with spatial variation in herbivory. Shaded regions indicate 95% confidence intervals. Algae illustration courtesy of [www.ian.umces.edu](http://www.ian.umces.edu).

amount of recorded algal herbivory correlated positively with the abundance of dusky rabbitfish in seagrass meadows ( $R^2 = 0.58$ , Figure 2). Importantly, the abundance of no other species or environmental variables were present in the best fit model for herbivory. The other two herbivorous fish species, sabretooth blenny ( $p = 0.06$ ) and fanbellied leatherjacket ( $p = 0.87$ ), did not have significant correlations with the recorded herbivory in seagrass meadows.

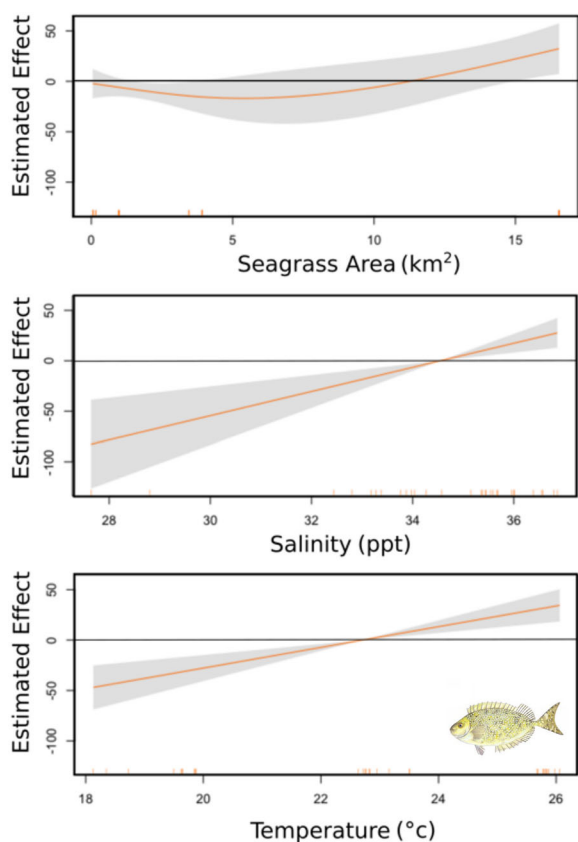
The best fit model on the abundance of dusky rabbitfish recorded on BRUVS in seagrass meadows was positively correlated with seagrass area, salinity, and water temperature ( $R^2 = 0.61$ , Figure 3, Table 2). This was the best fit model assessing the abundance of rabbitfish, with two other models within 2AICc values also being recorded. Dusky rabbitfish were most abundant over large seagrass meadows (that is, area  $\geq 16 \text{ km}^2$ ) in fully marine parts of the bay (that is, salinity  $> 35 \text{ ppt}$ ), during spring and summer (that is, water temperature  $> 23^\circ\text{C}$ ) (Table 3). No other environmental

variable was significantly correlated with rabbitfish abundance in seagrass meadows (Table 2).

### Using Surrogates to Conserve Algal Herbivory in Seagrass Meadows

The distribution of dusky rabbitfish, and therefore the ecological function of macroalgal herbivory in the seagrass meadows of Moreton Bay, was clustered over meadows outside of marine reserves (Figure 4). We calculated the top ten seagrass meadows based on the modelled abundance of dusky rabbitfish; these are referred to as functionally important seagrass meadows (Figure 4, Table S2). One quarter of the seagrass in Moreton Bay is currently included in marine reserves ( $51 \text{ km}^2$ , Figure 4), but these reserves protect only 7% of the ten highest ranked (in terms of herbivory rates) meadows ( $4/51 \text{ km}^2$ ). The top ten ranked meadows encompass the same area of seagrass that is currently protected within Moreton Bay (that is,  $52 \text{ km}^2$ ), but seagrass meadows that are currently

protected inside the existing reserves are not important areas for macroalgal herbivory. (That is, protected meadows were ranked between fifteenth and twentieth in terms of rabbitfish abundance.) In



**Figure 3.** Generalised additive mixed models (GAMMs) relating the distribution of dusky rabbitfish (*Siganus fuscescens*) to significantly important environmental attributes. Shaded regions indicate 95% confidence intervals. Fish illustration courtesy of [www.efishalbum.com](http://www.efishalbum.com).

our surveys, the top ten seagrass meadows accounted for 37% of all counted rabbitfish (1126/3032 individuals) and comprised only 25% of the total area of seagrass in the system (53/208 km<sup>2</sup>) (Figure 4, Table S2). The model results had a significant relationship with the survey results ( $R^2 = 0.539$ , Figure S4).

## DISCUSSION

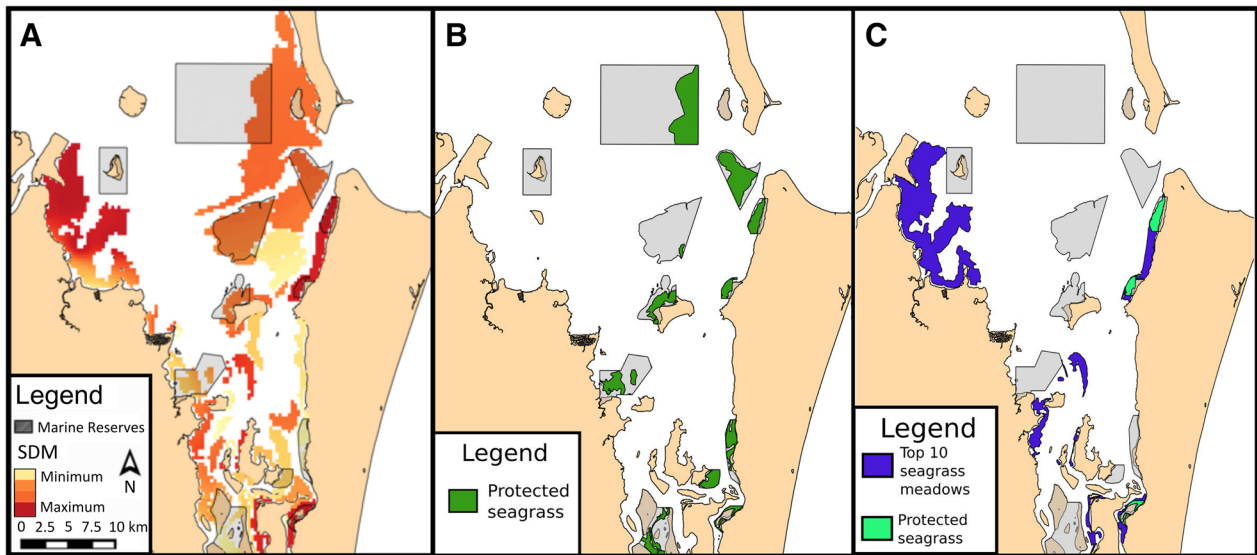
Conservation areas generally aim to protect, maintain, and enhance biodiversity, populations, and ecological functions (Estes and others 2011; Mace 2014; Pressey and others 2014). It is, however, often not clear whether reserves are successful at promoting the functioning of ecosystems (Possingham and others 2005; Olds and others 2012c; Brown and Mumby 2014). We show that functionally important herbivorous fishes, which are responsible for the bulk of algal herbivory within seagrass meadows, can be adopted as surrogates to conserve the ecological function of herbivory in seagrass landscapes (Henderson and others 2017b). Our findings also demonstrate that the preservation of algal herbivory can lead to different priorities for seagrass conservation, than the protection of biodiversity through simple representation of ecosystems in marine reserve networks.

The abundance and distribution of herbivorous fishes is an adequate proxy for herbivory on coral reefs (Edwards and others 2010; Olds and others 2014; Beger and others 2015), but this has not been tested for other marine habitats (Caro 2010; Hunter and others 2016). Our results show that spatial patterns in a single species of herbivorous fish can accurately predict rates of algal herbivory in seagrass meadows. This species, the dusky rabbitfish, is a common roving herbivore that feeds on a range

**Table 3.** Environmental Characteristics for Each Meadow Surveyed in the Study

Meadow number	Salinity (psu)			Temperature (°C)			Seagrass meadow size (km <sup>2</sup> )
	Winter	Spring	Summer	Winter	Spring	Summer	
1	35.68	33.18	28.8	18.13	23.51	25.85	0.0666
2	35.36	32.8	27.64	18.35	23.5	26.06	0.0486
3	35.38	33.27	32.44	18.73	23.16	25.67	3.921
4	35.54	33.38	35.15	19.5	22.95	25.69	3.921
5	36	33.98	36.86	19.62	22.83	25.82	0.158
6	35.96	33.76	36.01	19.64	22.82	25.77	3.447
7	35.67	34.57	36.55	19.64	22.75	25.98	16.54
8	35.59	33.87	36.39	19.86	22.77	25.79	16.54
9	35.45	34.04	36.57	19.88	22.72	25.82	0.975
10	35.44	34.27	36.79	19.85	22.63	25.87	0.975





**Figure 4.** Spatial distribution models (SDMs) illustrating the distribution of: **(A)** algal herbivory in seagrass meadows (calculated from best fit GAMMs for herbivore abundance, Table 2); **(B)** seagrass meadows that are protected in marine reserves; and **(C)** functionally important seagrass meadows (that is, meadows that supported abundant herbivores and high rates of algal herbivory), in the Moreton Bay Marine Park.

of algal types across a number of ecosystems, including fleshy macroalgae on coral reefs (Gilby and others 2017b), filamentous algae that grows in seagrass meadows (Capper and others 2006) and indirectly feeds on epiphytic algae through the consumption of seagrass (Chelsky Budarf and others 2011). All other species of herbivorous fish recorded in this study feed predominantly on epiphytic algae and either correlated poorly with rates of algal herbivory or their low abundance, small size and likely small influence would result in them not being an ecologically suitable proxy for this function in seagrass meadows (Gilby and others 2016a). This suggests that seagrass meadows in the study area may have a low diversity of functionally important herbivorous fishes (Gilby and others 2016a), possibly resulting in limited functional redundancy (that is, few species perform the same ecological role), which may lead to negative effects when functionally important fishes are also a target for commercial fisheries (Ebrahim and others 2014; Henderson and others 2017b). Low diversity and limited functional redundancy has been reported from other subtropical seagrass meadows, where herbivory is also dominated by very few species (Pages and others 2014; Vergés and others 2014).

Here we show that when conservation planning is focused on macroalgal herbivory by fishes, the priorities for marine reserve design can differ to those of conventional approaches that seek to

protect biodiversity and conserve representative areas of marine ecosystems (Beger and others 2015; Lentini and Wintle 2015). Our spatial distribution models predict that herbivory is not uniformly distributed in seagrass meadows across Moreton Bay, and demonstrate that it is greatest in large meadows (for example, area > 16 km<sup>2</sup>) that are also well connected with the ocean (that is, salinity > 35 ppt). Most seagrass meadows that sustain high rates of herbivory are not, however, prioritised for conservation; marine reserves protect 25% of all seagrass in Moreton Bay, but only 7% of the top ten seagrass meadows with the highest abundance of rabbitfish. The network of marine reserves in Moreton Bay could, therefore, be refined to better represent the ecological function of herbivory in seagrass meadows (Ebrahim and others 2014; Maxwell and others 2015; Saunders and others 2017). Our models predict highest rates of herbivory in seagrass in both the western and eastern areas of the Bay, and we suggest that these locations would make suitable targets for the conservation of ecological functions in seagrass meadows.

We recorded the highest rates of herbivory in large seagrass meadows, often double that of anywhere else, with these large meadows having strong links to the open ocean, and a demonstrated capacity to withstand chronically poor conditions from flood disturbances (Gibbes and others 2014; Maxwell and others 2014; Roelfsema and others 2014). These ecological features underpin the

habitat values of seagrasses for many fish species, both in Moreton Bay (Ebrahim and others 2014; Henderson and others 2017b; Skilleter and others 2017) and elsewhere (Heck and others 2003; Connolly and Hindell 2006; Nagelkerken and others 2015). They also modify the spatial distribution of herbivorous fishes, particularly parrotfish (Scaridae), rabbitfish (Siganidae), and sea bream (Sparidae), and the ecological function of herbivory in many seagrass landscapes (Unsworth and others 2007; Valentine and others 2008; Gullström and others 2011; Pages and others 2014). To improve the conservation of ecological functions in seagrass meadows, we therefore require empirical data to describe how seagrass area, cover, community composition, seascape context, and meadow persistence combine to structure the spatial distribution of functionally important herbivorous fishes in coastal seascapes, and to represent herbivory in coastal conservation planning (Duffy and others 2015; Henderson and others 2017b).

Our results here offer a suitable tool that can be implemented more broadly into spatial conservation planning and decision-making; however, our results do not consider other important ecological functions, such as sediment trapping and nutrient processing, or the effects of mega-herbivores (for example, turtles and dugong) (Maxwell and others 2017), but our approach could easily be used to incorporate these ecological functions in seagrass conservation. We suggest that when functionally important herbivores can be identified in seagrass meadows, they should be protected from harvesting in areas where fishing pressure is high, and used as surrogates to better integrate the function of herbivory into seagrass conservation. These findings offer new insight that can be used to improve seagrass conservation globally, and support the wider use of surrogates to conserve important ecological functions.

## ACKNOWLEDGEMENTS

We thank the three anonymous reviewers and the editor for their comments on this manuscript. We thank the staff of the Moreton Bay Research Station and K. Finlayson, E. Bell, N. Harcla-Goody, and B. Meteyard for field assistance. The Australian Rivers Institute and the Griffith University School of Environment funded the project.

**Data Accessibility** Data for this paper are archived in the University of the Sunshine Coast Research Bank.

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