Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem

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Abstract

Environmental drivers of seaweed biomass were investigated at Ningaloo, Western Australia, a coral reef ecosystem with negligible anthropogenic influences on seaweeds from fishing, farming, or eutrophication. Periodic surveys of benthic macroalgae occupying seaweed-dominated beds within the lagoon at two locations (Coral Bay, Tantabiddi) were made during winter, spring, and late summer over a 26 month period. Canopy-forming *Sargassum* spp. biomass fluctuated over a seasonal growth–decay cycle, with highest values in the warm summer months (up to 1013 g fresh weight 0.25 m^{-2} at Coral Bay) and lowest values in winter (down to 155 g fresh weight 0.25 m^{-2} at Tantabiddi). Conversely, prominent understory seaweed genera *Dictyopteris* and *Lobophora* reached peak biomass in winter, when the *Sargassum* spp. canopy was lowest. *Sargassum* spp. biomass variation could be attributed largely to time (52%), location (21%), and site (26%), with low variation within individual seaweed beds (1%). Statistical analysis of the influence of five environmental variables (temperature, light, wind-driven upwelling, rainfall, significant wave height) indicated that location and sea temperature (1 month antecedent to biomass) provided the best explanation for *Sargassum* spp. biomass fluctuations. While sea temperature is a key driver of seaweed temporal dynamics, heterogeneity at the kilometer scale suggests that spatial context is also important. Given the important role of seaweeds in many ecosystem processes, this strong biophysical coupling between *Sargassum* spp. biomass and sea temperature suggests that thermal climate change will significantly affect coral reef productivity and biodiversity.

Canopy-forming seaweeds are important components of both tropical and temperate reef ecosystems, where they are key primary producers, competitors with other benthic organisms (e.g., smaller seaweeds, corals), and facilitators of food and complex habitat for numerous species (Thomsen et al. 2010; Wilson et al. 2010). While seaweeds naturally occur on and around coral reefs, the occurrence of phase shift events involving a habitat cascade from coral- to seaweed-dominated states has led to suggestions that large seaweeds are a threat to coral reef biodiversity (Mumby et al. 2007; Hughes et al. 2010; Graham et al. 2011). Consequently, increasing attention has been directed towards the drivers of canopy-forming seaweed biomass on coral reefs in order to understand and manage this important aspect of ecosystem diversity, productivity, and resilience (Hughes et al. 2010; Graham et al. 2011; Mumby et al. 2013).

Seaweed biomass fluctuations have been linked to both biotic (competition, herbivory) and abiotic (light, temperature, wave action, nutrients) factors that can vary in importance according to regional setting. For instance, in systems where herbivore faunas are largely intact, changes in fleshy seaweed biomass have been linked predominantly to a combination of sea temperature, wave energy, light, and/or gradients in grazing pressure (Glenn et al. 1990;

Ferrari et al. 2012; Mumby et al. 2013). When herbivores are removed, however, nutrient inputs and other bottom-up factors can become the primary drivers of fleshy seaweed biomass (Schaffelke and Klumpp 1998; Burkepile and Hay 2006; Ferrari et al. 2012). As such, seaweed biomass can be highly contingent on levels of anthropogenic affects, such as increased nutrient runoff from coastal development and overharvesting. While seasonal seaweed fluctuations have been explored for a range of coral reef locations (Glenn et al. 1990; Ateweberhan et al. 2005; Lefevre and Bellwood 2010), very few studies have investigated such fluctuations in the absence of major anthropogenic influences (Hughes et al. 2010; Graham et al. 2011).

Ningaloo Reef, a 290 km fringing coral reef located along the northwest coast of Western Australia, provides a unique system to explore natural environmental drivers of seaweed seasonality for several reasons. The aridity of the adjacent coastline and lack of any major river catchments produces minimal terrestrial runoff into the Ningaloo system, with the seasonal rainfall (200–300 mm per annum) captured largely by subterranean karst limestone along Cape Range peninsula (Cassata and Collins 2008). Relatively low density human settlement and a predominantly recreational fishery that does not target herbivores (Sumner et al. 2002) has maintained a seemingly intact herbivorous fish and urchin fauna at Ningaloo (Johansson et al. 2010;

Verges et al. 2011). Within this setting, a vast network of discrete seaweed beds dominated by the canopy-forming *Sargassum* are found throughout the shallow fringing reef lagoon, which collectively comprise up to 110 of the 760 km² of subtidal habitats within Ningaloo (Johansson et al. 2010; Kobryn et al. 2013). Notably, these lagoonal seaweed beds experience minimal grazing pressure from herbivores (Johanssen et al. 2010; Verges et al. 2011) and limited nutrient input from oceanic upwelling (Hanson et al. 2005; Wyatt et al. 2013). As such, Ningaloo Reef provides an ideal ecosystem in which to explore the influence of environmental drivers on fluctuations in fleshy seaweed biomass on a coral reef.

Tropical *Sargassum* is known to respond seasonally to different environmental variables according to the regional setting (Glenn et al. 1990; Vuki and Price 1994; Ateweberhan et al. 2005), so a suite of environmental forcing factors could be driving fluctuations in seaweed biomass within the Ningaloo Reef lagoon. Focusing on the lagoonal seaweed-dominated beds and using a quantitative modeling approach, our aims were to examine which environmental forcing factor(s), if any, can best explain seasonal changes in the benthic biomass of canopy-forming seaweeds (*Sargassum* spp.) within the Ningaloo Reef lagoon across the growth and decay cycles (the latter being defined as biomass lost from the benthic attached thalli via physical detachment and/or decomposition) and explore whether understory benthic seaweeds respond to seasonal changes in *Sargassum* spp. canopy biomass over time and space.

Methods

Benthic seaweed surveys—Periodic surveys of benthic macroalgae were conducted at three seaweed-dominated bed sites (separated by 1–5 km) at each of two locations (approximately 120 km apart) within the Ningaloo lagoon (Tantabiddi 21°53′15″S, 113°59′02″E and Coral Bay 23°12′30″S, 113°46′18″E; Fig. 1) to measure temporal variation in both canopy-forming *Sargassum* spp. and understory macroalgal biomass across the 26 month period between July 2010 and August 2012. These locations were chosen for their positions north (Tantabiddi) and south (Coral Bay) of Point Cloates (near Ningaloo Station; Fig. 1), which is thought to be a pivotal boundary for surface circulation, sea temperature, and upwelling patterns along the Ningaloo coast (Woo et al. 2006; Lowe et al. 2012). Each survey consisted of scuba divers haphazardly placing six replicate quadrats (0.25 m²) on the benthos within each submerged bed site (between 1 to 5 m in depth), and harvesting all attached macroalgae (larger than 1 cm) within each quadrat by detaching individuals from the reef by hand and placing them into a site-specific numbered calico cloth bag. Processing of these harvest samples involved an initial washing of each sample in freshwater to remove sediment and epizooids (preserved for future study) and then sorting all macroalgae into genus-level or higher categories, which were weighed to the nearest 0.1 g after removing any excess water by shaking. All algal identifications were made by the same person (TW) throughout the study who drew on available texts and/or
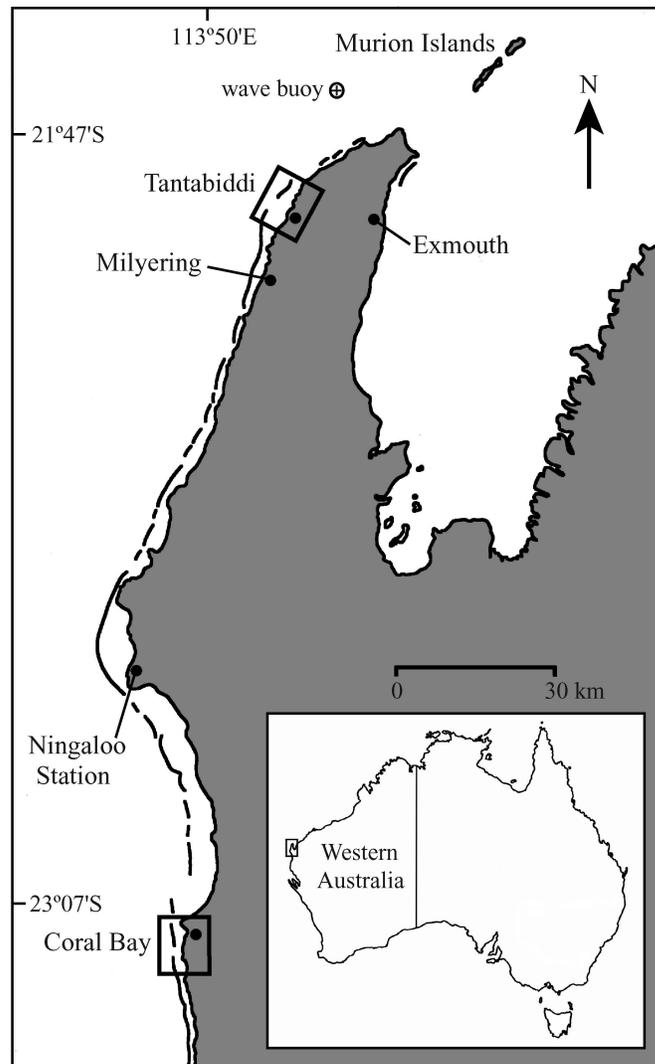

Fig. 1.   Study locations (bounding boxes, Tantabiddi and Coral Bay), nearby township of Exmouth, and relevant weather stations (Ningaloo Station, Milyering, wave buoy) along Ningaloo reef (broken outline), Western Australia (box on inset map).

consultation with local taxonomic experts using photographs and pressings taken from harvest samples. This procedure was repeated at each of the same meadow sites during winter (July–August), spring (November–December), and late summer (February). Care was taken not to reharvest previous microsites by haphazardly dispersing harvest replicates around each large meadow site while avoiding previous harvest scars. For statistical analysis, the seaweed biomass measurements for each quadrat were pooled at the level of genus.

Environmental variables—Available data on monthly variation in five variables that have previously been linked to seaweed seasonality (sea temperature, rainfall, light, wind-driven upwelling, significant wave height; Glenn et al. 1990; Ateweberhan et al. 2005; Mumby et al. 2013) were collected for the Ningaloo region to compare against the periodic surveys of macroalgal biomass. Sea temperature

was recorded at each location via submersible temperature loggers sampling at 30 min intervals at 3–5 m depth within the lagoon, which were periodically downloaded and replaced every 3–12 months at each of the two locations (SBE39, Sea-Bird Electronics and Sensus Ultra, ReefNet; both types were routinely calibrated by Australian Institute of Marine Science staff). Monthly rainfall totals (mm) were extracted from the Australian Government Bureau of Meteorology public database for measurements taken at Ningaloo Station (No. 5020; 10 m elevation; 22°41′51″S, 113°40′29″E) located on the coast between our locations (Fig. 1). Daily values for photosynthetically active radiation (PAR; μmol s^{-1} m^{-2}) and wind velocity (m s^{-1}) were based on Australian Institute of Marine Science data from the Ningaloo weather station at Milyering (10 m elevation; 22°01′58″S, 113°55′01″E), which is also located on the coast between our two study locations (Fig. 1). We used monthly average PAR in our analyses, which was calculated from the cumulative PAR received each day per month. We used wind data (from the Milyering station noted above) to explore the possible role of wind-driven upwelling, which can produce seasonal nutrient increases within the Ningaloo lagoon (Hanson et al. 2005; Wyatt et al. 2013). This involved a weighted index of how monthly winds aligned with the upwelling-favorable conditions of southwesterly winds exceeding 3 m s^{-1} (Woo et al. 2006; Lowe et al. 2012). Because the monthly mean wind velocity was always above 3.5 m s^{-1} during our survey periods, our wind-driven measure of upwelling index weighted the monthly mean wind direction, the latter being designated as 1 when blowing from the southwest (225°, most upwelling favorable) and scaling this down to zero as the direction tended towards the upwelling unfavorable directions of southeast (135°) or northwest (315°) and setting all values between 315° and 135° as zero (Woo et al. 2006; Lowe et al. 2012). Finally, we obtained daily significant wave heights (H_s, m, daily means and overall maximum) based on measurements by an offshore wave-rider buoy (21°41′58″S, 114°05′55″E) maintained by the Department of Transport, Western Australia (Fig. 1). Monthly means were calculated from the daily values for all variables (except monthly totals for rainfall) for the period May 2010–August 2012 to allow for antecedent analyses of up to 2 months prior to the first macroalgal harvest in July 2010 and were chronologically aligned with biomass measurements across the sampling period.

Statistical analyses—We explored the level at which variation occurred in the biomass of canopy-forming seaweeds within the genus *Sargassum* using hierarchical variance partitioning (Chevan and Sutherland 1991), a modified version of generalized linear modeling (Mac Nally 2000), to calculate the percentage distribution of independent effects across different model levels and variables. We then used generalized additive mixed models (GAMM; Burnham and Anderson 2002) and a full subsets approach (Zuur et al. 2009) to infer the effects of different environmental variables on the biomass of canopy-forming *Sargassum* through time. This modeling approach provided a flexible and unconstrained method for fitting ecological

responses in the predictor variable while incorporating random effects (Zuur et al. 2009). We fitted all possible model combinations for up to four variables, which included location plus any of the five environmental variables (sea temperature, rainfall, PAR, wind-driven upwelling index, maximum significant wave height), with the latter set at three levels of antecedence (monthly value taken at 0, −1, or −2 months prior to when seaweed biomass measured) to explore time lags in seaweed biomass responses to environmental change (Luning and tom Dieck 1989; Glenn et al. 1990; Vuki and Price 1994). Given that different measures of wave height may be autocorrelated, we chose to analyze just maximum significant wave height as the most likely agent of seaweed canopy pruning and dislodgment (Thomsen and Wernberg 2005). Due to the spatial scale of the environmental data (available only at the location level or higher), we fitted models with site as a random effect nested within location. Larger models of more than four variables were not fitted because of both the available degrees of freedom and the logistical constraints of fitting an excessive number of model combinations. Model fits across the 4094 possible combinations of variables were compared using the Akaike information criterion corrected (AICc) for finite sample size to minimize the probability of model overfitting (Burnham and Anderson 2002). Number of knots (the joining points between adjacent polynomial curves) were also restricted in the model spline fits (k = 3) to produce conservative models and avoid overfitting (Zuur et al. 2009); increasing the number of knots in the final models was explored and found not to increase overall accuracy or substantially alter the GAMM outputs. Best models were selected based on being within 2 AICc of the minimum AICc value across all resolved models (indicted by the arithmetic difference between a model AICc and the minimum AICc for all models, denoted ΔAICc) and having the lowest number of model terms, following Burnham and Anderson (2002). To explore the relative importance of each variable, we summed the weighted AICc values across all possible models. The above procedure (excluding the fitting of environmental variables) was repeated to explore the response of four understory macroalgae groups (*Lobophora*, *Dictyopteris*, *Dictyota*, Others) to changes in *Sargassum* canopy biomass through time. We also used the above model selection process to explore the potential for different environmental variables to explain *Sargassum* spp. biomass fluctuations within each of the Tantabiddi and Coral Bay locations. All model fitting was completed using R statistical software (version 3.0.1; R Development Core Team) with the library "mgcv," with graphical presentations produced in Sigmaplot (version 9; Statsoft Pacific).

Results

Mean biomass of canopy-forming *Sargassum* spp. varied up to 18-fold over the 26 month survey period, with cyclical troughs and peaks in mean *Sargassum* biomass from winter to late summer coinciding with the lowest and highest annual values of several environmental variables, including PAR, surface winds, and sea temperature (Fig. 2). Consid-
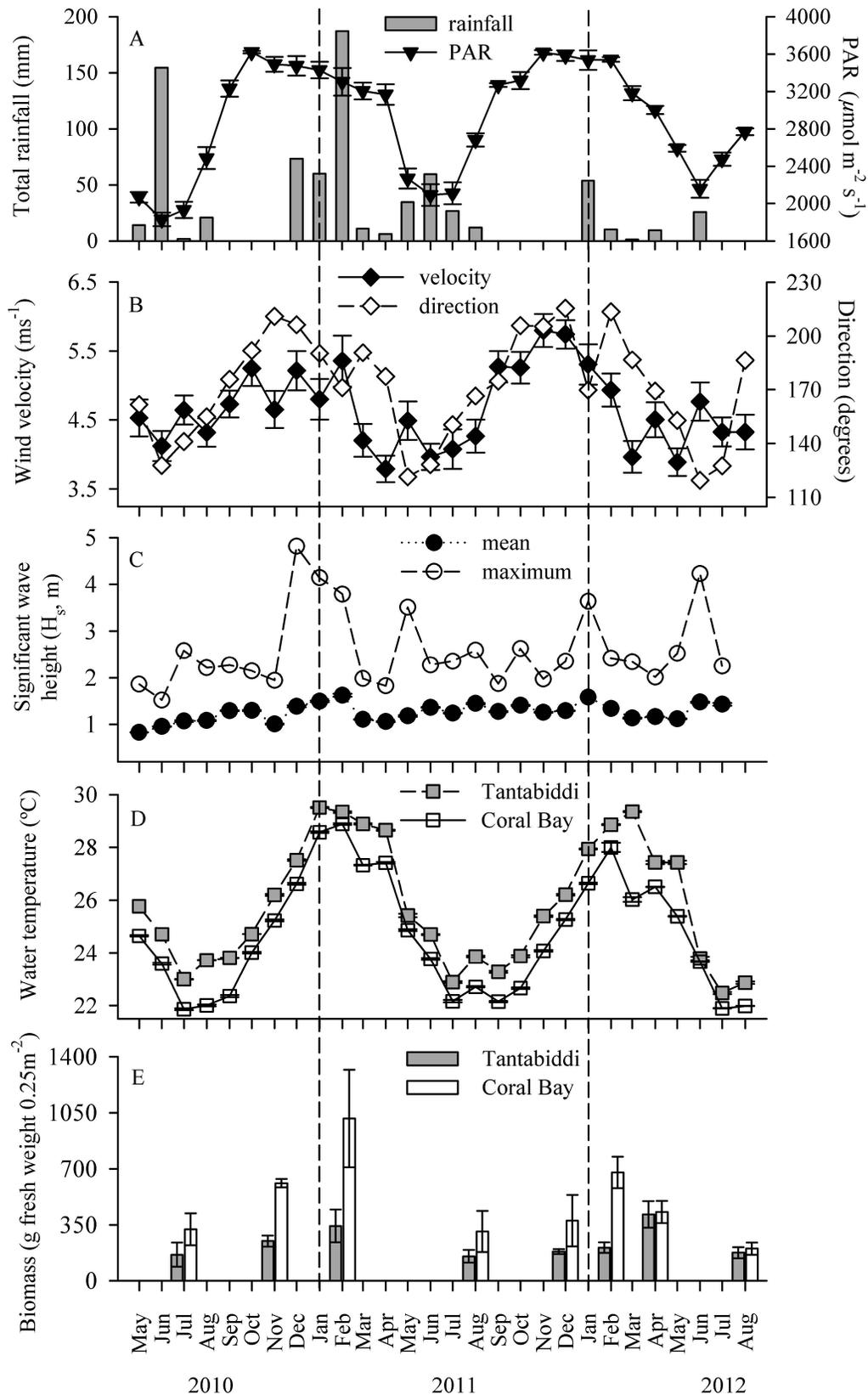
Fig. 2. Temporal variation in the environmental variables of (A) rainfall and PAR, (B) surface winds, (C) surface wave height, (D) sea temperature (at 3–5 m depth), and (E) biomass of canopy-forming *Sargassum* spp. over 26 months at two locations (Tantabiddi and Coral Bay) within the Ningaloo lagoon. Mean monthly values are based on daily environmental means, except monthly totals for rainfall. Mean *Sargassum* spp. biomass is based on site-level biomass at each survey period (*n* = 3 per location). Errors are standard errors of the mean.

Table 1. Seasonal change in mean biomass (g fresh weight 0.25 m^{-2}) of canopy-forming *Sargassum* spp. across (a) growth and (b) decay phases at three sites within two locations (Tantabiddi and Coral Bay) within the Ningaloo lagoon. Growth (positive values) is the difference in mean site biomass from winter (July–August) to late summer (February) the following year, while decay (negative values) is the difference from late summer to winter of the same year. Percent change in biomass relative to the standing biomass in the prior winter (growth) or prior summer (decay) are indicated in parentheses.

Location	Tantabiddi			Coral Bay		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
(a) Growth						
Jul 2010–Feb 2011	79.4(26)	447.8(189)	242.5(172)	129.9(18)	394.0(201)	1546.8(271)
Aug 2011–Feb 2012	37.5(16)	12.0(9)	112.8(119)	164.9(30)	532.8(176)	407.3(451)
(b) Decay						
Feb–Aug 2011	−155.6(104)	−356.2(72)	−289.0(75)	−312.3(37)	−286.2(49)	−1513.6(94)
Feb–Aug 2012	−31.6(12)	−25.4(17)	−91.1(44)	−528.8(76)	−675.4(81)	−219.6(44)

erable spatial and temporal variation was evident in the timing and magnitude of *Sargassum* spp. biomass growth and decay across sites and locations (Table 1), with higher monthly summer temperatures and peak *Sargassum* spp. biomass in February 2011 relative to lower summer temperatures and biomass in February 2012 (Fig. 2D,E). Peaks in mean biomass at sites in Coral Bay (1013.2 ± 304.5 and 677.4 ± 98.4 g fresh weight 0.25 m^{-2} across sites in February 2011 and 2012, respectively) tended to be 195–224% higher than sites at Tantabiddi (343.3 ± 101.9 and 208.8 ± 33.2 g fresh weight 0.25 m^{-2}). Hierarchical partitioning revealed the variation attributed to replicate quadrats (0.25 m^2) was low (1%), with the majority attributed to time (52%), location (21%), and site (26%). While seasonal changes were apparent in several environmental variables (Fig. 2A–D), AICc indicated that the best-fit GAMM incorporated location and mean monthly sea temperature at 1-month antecedence to best explain *Sargassum* spp. biomass variation over time (Table 2a; Fig. 3A). Other levels of antecedence and environmental variables (e.g., upwelling, PAR, wave height) or combinations of these variables ranked markedly lower across all the fitted models (Table 2a; Fig. 3B). Location-specific analyses confirmed sea temperature as the best explanatory variable for *Sargassum* spp. biomass fluctuations, with the only difference being the level of antecedence at each location: −2 months at Tantabiddi and −1 or 0 months at Coral Bay (Table 3). Monthly mean sea temperature conditions varied over a 7°C range at both locations (Fig. 2D), but Coral Bay (overall monthly mean of 24.7°C) was generally cooler than Tantabiddi (25.8°C).

Fluctuations in understory macroalgal biomass occurred asynchronously to *Sargassum* spp. canopy biomass, with understory biomass peaks occurring during winter to early summer each year (Fig. 4). For example, during winter months (July–August), when *Sargassum* spp. canopy biomass was lowest, understory genera, such as *Lobophora* (Fig. 5A) and *Dictyopteris* (Fig. 5B), increased in biomass three to six times from summer levels. However, these patterns were extremely variable over space, with changes in understory biomass following markedly different trajectories at Tantabiddi and Coral Bay (Fig. 4). Accordingly, hierarchical partitioning revealed that high levels of variation were attributed to the spatial factors of location (30%) and site (38%), with relatively little attributed to the understory genus groups of *Dictyopteris* (14%), *Lobophora* (8%), *Dictyota* (4%), and Others (6%). Indeed, when *Sargassum* spp. canopy biomass was lowest, a collection

Table 2. Summary of the best restricted (k = 3 knots) GAMMs for predicting (a) *Sargassum* spp. biomass variation within the Ningaloo lagoon relative to environmental variables, and (b) the relationship between *Sargassum* spp. and understory macroalgae biomass. The best-fit *Sargassum* environment model (indicated in bold) was selected from combinations of location and five environmental variables (including sea temperature [T] and upwelling index [U]) at varying antecedence (0, −1, and −2 months prior to biomass). The best-fit *Sargassum* understory model (indicated in bold) was selected from combinations of location and four understory macroalgae groups (*Lobophora*, *Dictyopteris*, *Dictyota*, Others). Site was included as a random effect. Note the clear reduction in AICc and weight for the next best and subsequent models that fell 2 ΔAICc outside of the best-fit GAMMs (following Burnham and Anderson 2002).

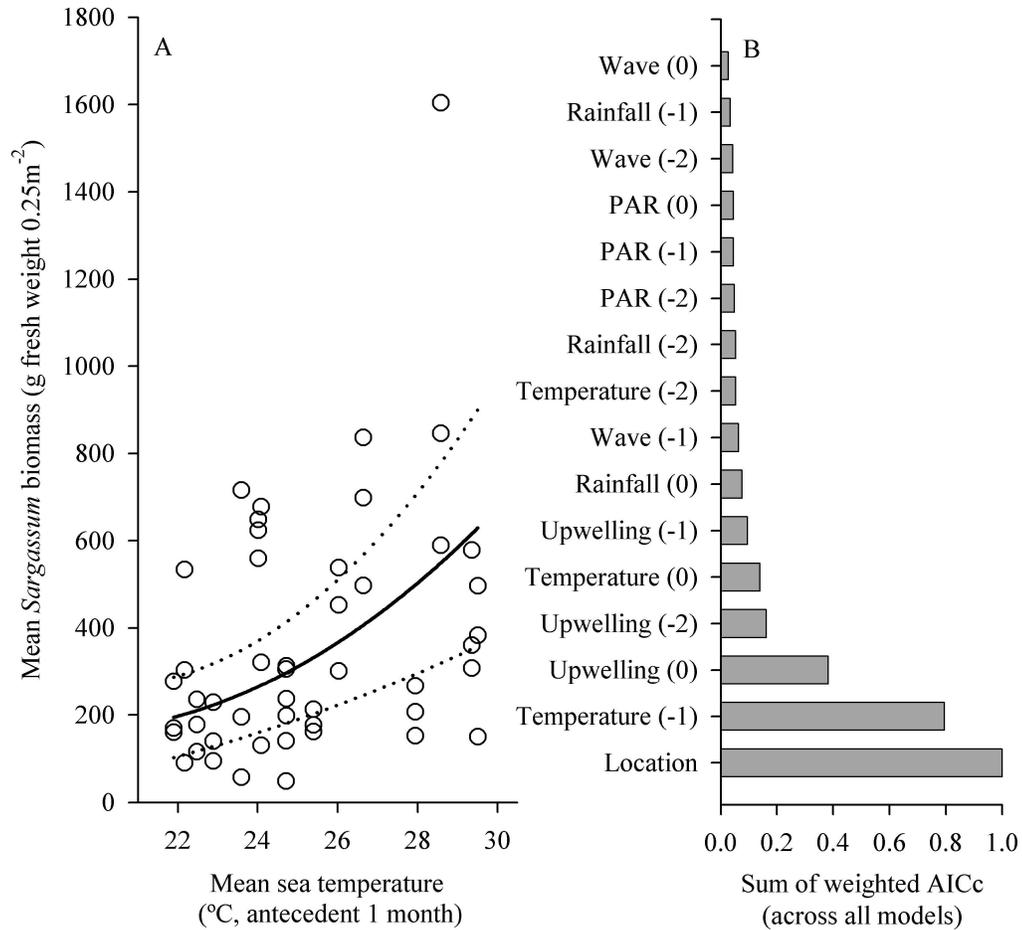| Model terms+intercept	df	AICc	ΔAICc	Weight	R^2
(a) *Sargassum* environment					
Location+T$_{-1}$+6.238	**6**	**81.57**	**0**	**0.535**	**0.54**
Location+T$_{-1}$+U$_{-2}$+6.205	8	84.90	3.33	0.040	0.56
(b) *Sargassum* understory					
Location+*Lobophora*+*Dictyopteris*+6.129	**8**	**678.4**	**1.28**	**0.219**	**0.23**
Lobophora+*Dictyopteris*+Others+5.792	9	680.7	3.50	0.072	0.23

Fig. 3. Association between environmental variables and *Sargassum* spp. biomass across two locations within the Ningaloo lagoon during 2010–2012: (A) Mean biomass of *Sargassum* spp. relative to sea temperature (1 month prior) based on fitted parameter estimates $\pm$ 95% confidence limits (dotted lines) from the best GAMM (Table 2a) with significant intercept (*t*-test, $t = 76.24$, df $= 47$, $p < 0.01$) and model terms (location *t*-test, $t = 6.42$, df $= 4$, $p < 0.01$, T_{-1} $F_{1,1} = 32.94$, $p < 0.01$). (B) Relative importance of possible variables (antecedence indicated as $0 =$ same month, $-1 = 1$ month prior, $-2 = 2$ months prior) as indicated by the sum of weighted AICc for each variable across all possible models.

of *Lobophora*, *Dictyopteris*, and Other genera interchanged dominance of the understory at Tantabiddi (Fig. 4A), while *Lobophora* displayed the highest understory biomass at Coral Bay throughout the survey period (Fig. 4B). Likewise, temporal patterns were highly variable, with *Lobophora* winter biomass peaks only occurring in some years at each location (Tantabiddi 2010, Fig. 4A; Coral Bay 2011, Fig. 4B). Consequently, the best-fit GAMM relating components of the understory biomass to *Sargassum* spp. canopy biomass included location alongside *Lobophora* and *Dictyopteris* to describe relatively little of the total variation (Table 2b; Fig. 5). Notably, *Lobophora* was always present, even when *Sargassum* spp. biomass was high (Figs. 4, 5A).

Discussion

Multiple environmental factors can drive the seasonal phenology of seaweeds (De Wreede 1976; Luning and tom Dieck 1989; Mohring et al. 2013). However, temperature often has an overriding influence on ectothermic biological

Table 3. Summary of the best restricted (k = 3 knots) GAMMs for predicting *Sargassum* spp. biomass variation within the Ningaloo lagoon relative to environmental conditions at each of two locations: (a) Tantabiddi and (b) Coral Bay. The best *Sargassum*-environment models for each location (indicated in bold) were selected from combinations of five environmental variables (including sea temperature [T] and upwelling index [U]) at three levels of antecedence (0, -1 month, and -2 months prior to biomass survey). Site was included as a random effect. Note the clear reduction in AICc and weight for the subsequent models that fell 2 ΔAICc outside of the best-fit GAMMs (following Burnham and Anderson 2002).

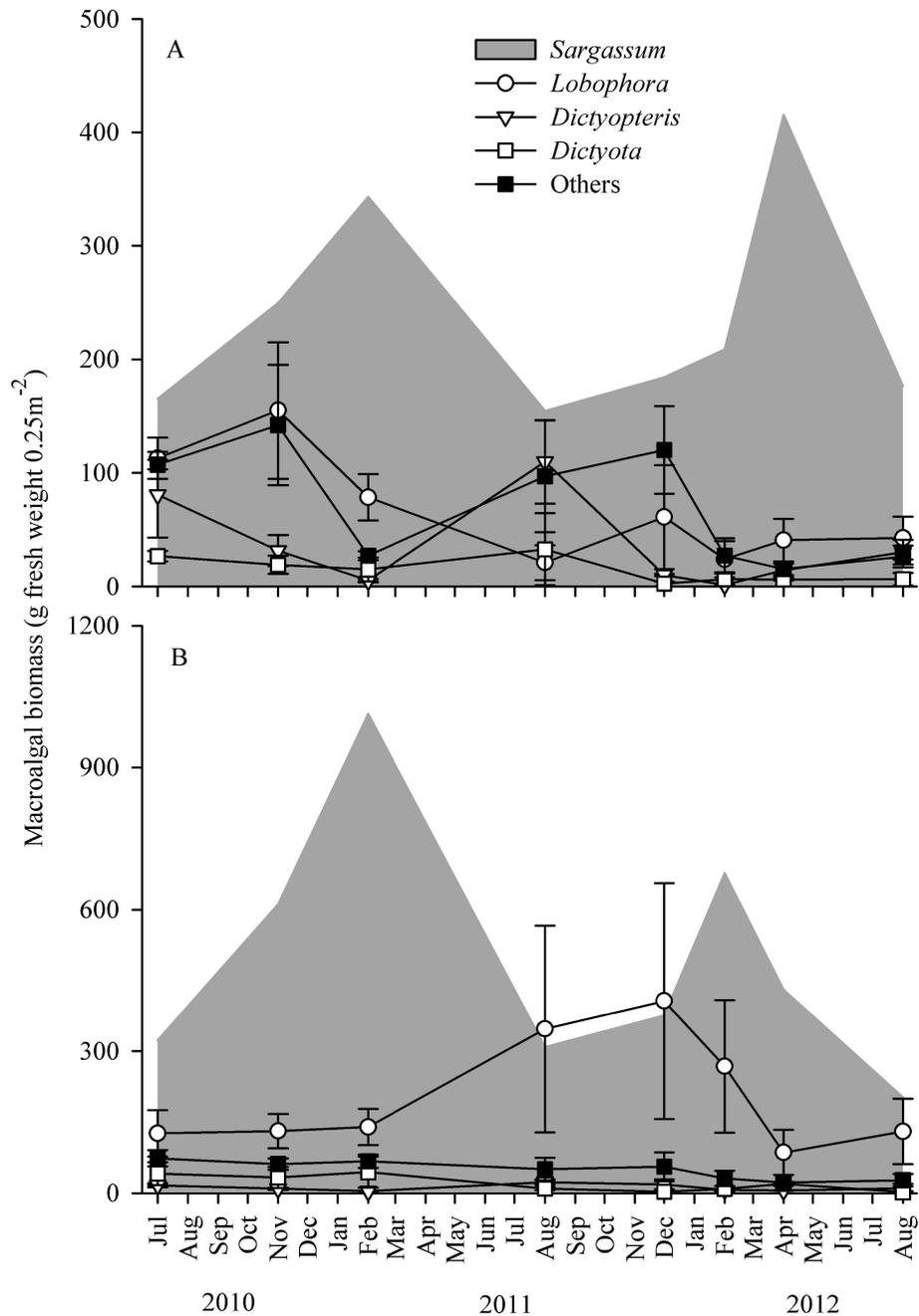| Model terms+intercept	df	AICc	ΔAICc	Weight	R^2
(a) Tantabiddi					
T_{-2}+237.2	**4**	**102.4**	**—**	**0.346**	**0.55**
T_{-1}+237.2	4	106.3	3.90	0.117	0.32
(b) Coral Bay					
T_{-1}+492.9	**4**	**119.5**	**—**	**0.528**	**0.79**
T_0+492.9	**4**	**120.0**	**0.51**	**0.409**	**0.41**
U_{-2}+517.2	4	123.8	4.25	0.063	0.89

Fig. 4. Temporal variation in understory seaweed biomass relative to canopy-forming *Sargassum* spp. (gray shading) across the two locations of (A) Tantabiddi and (B) Coral Bay within Ningaloo lagoon. Mean understory biomass was calculated from site-level values for each survey period ($n = 3$ per location, per time). Errors are standard errors of the mean.

activity via a direct effect on metabolic and photosynthetic rates that underpin growth, reproduction, and decay (Luning and tom Dieck 1989; Vuki and Price 1994; Mohring et al. 2013). We found that temperature is a key driver of seasonal fluctuations in *Sargassum* biomass within lagoonal seaweed beds at Ningaloo to produce peaks in biomass at the end of the Austral summer (February). Indeed, levels of peak *Sargassum* canopy biomass closely tracked interannual variation in sea temperature, with

warmer summer temperatures and larger biomass in 2011 and cooler summer temperatures and smaller biomass in 2012 across both locations. However, the magnitude of biomass fluctuations was strongly dependent on the location of seaweed-dominated beds across the northern and central sections of Ningaloo, with generally cooler sea temperatures and higher overall biomass in Coral Bay relative to Tantabiddi. While we find temperature to be an important determinant of seaweed biomass fluctuations
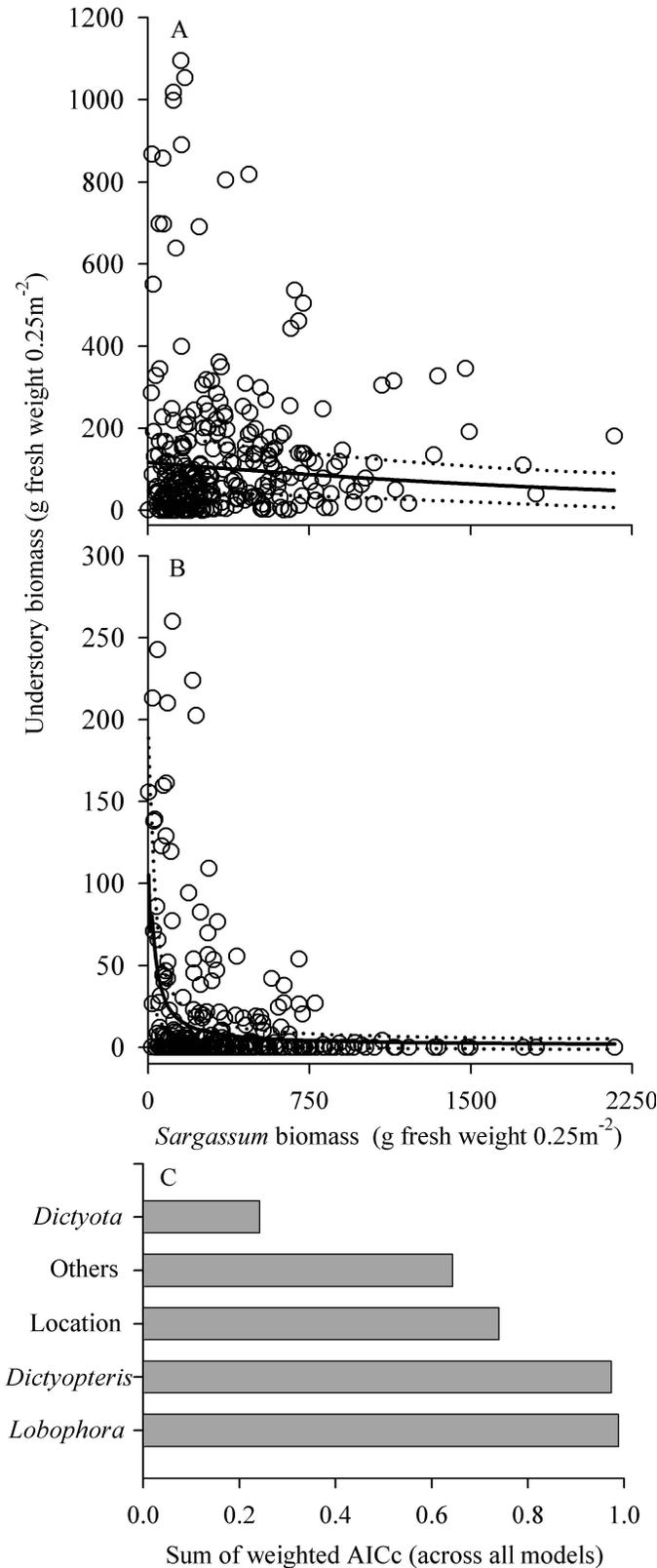
over time (both across and within regions), the presence of higher *Sargassum* biomass at a cooler location suggests that a range of factors other than those considered here may be determining regional levels of standing biomass. Asynchronous cycles and a complex interchange of different genera within the macroalgal understory also occurred in location-specific patterns in response to changing *Sargassum* canopy biomass. While our findings support the hypothesis that temperature is a primary driver of seaweed seasonality in many tropical reef systems (Glenn et al. 1990; Martin-Smith 1993; Ateweberhan et al. 2005), Ningaloo yields a unique perspective on the drivers and consequences of *Sargassum* seasonality within a coral reef ecosystem experiencing wide ranges in sea temperature.

Tropical seaweed seasonality relative to environmental conditions can vary in region-specific ways, with some tropical *Sargassum* reaching peak biomass in cooler months of the year (De Wreede 1976; Ateweberhan et al. 2005) and others peaking in the warm summer months (Glenn et al. 1990; Martin-Smith 1993; Lefevre and Bellwood 2010). *Sargassum* phenology within Ningaloo lagoon appears to follow a similar pattern to that seen on the Great Barrier Reef, where warming temperatures trigger increased *Sargassum* growth rates via thermal increases in metabolism and photosynthesis before hitting a peak at which reproduction occurs and the plants rapidly decay (Martin-Smith 1993; Vuki and Price 1994; Lefevre and Bellwood 2010). We found that sea temperature conditions 1-month prior to the standing biomass, in concert with the spatial factor of location, provided the single best explanation for *Sargassum* biomass variation throughout two full growth–decay cycles at Ningaloo. Such prevalence of a single forcing factor could be a reflection of the high variation in sea temperature at Ningaloo, where the 7°C range in mean monthly sea temperatures (at both locations) exceeds that recorded for *Sargassum* beds in the Caribbean (3.9°C; Ferrari et al. 2012), Hawaii (5°C; Glenn et al. 1990), the southern Red Sea (5.7°C; Ateweberhan et al. 2005), and the central Great Barrier Reef (6.7°C; Lefevre and Bellwood 2010). Such temperature effects were strongly dependent on spatial context in our study, with roughly half of the *Sargassum* biomass variation attributable to spatial factors. Most notably, Coral Bay tended to have over 100% greater *Sargassum* biomass than Tantabiddi during the summer peak. Sea temperatures at Coral Bay were noticeably cooler (approximately 1°C) than Tantabiddi throughout the year, which seems to run counter to the otherwise positive correlation between temperature and peak *Sargassum* biomass at Ningaloo.

←

and fitted parameter estimates of 95% confidence limits (dotted lines) from the best (Table 2) with significant intercept (*t*-test, $t = 104.8$, df = 280, $p < 0.01$) and model terms (location *t*-test, $t = 6.96$, df = 4, $p < 0.01$; *Lobophora* $F_{1,1} = 5.47$, $p < 0.01$, and *Dictyopteris* $F_{2.3,2.3} = 13.48$, $p < 0.001$). (C) Relative importance of variables including four groups of understory macroalgae, as indicated by the sum of weighted AICc for each variable across all possible models.

Fig. 5. Biomass of understory macroalgae relative to the *Sargassum* spp. canopy across two locations within the Ningaloo lagoon during 2010–2012. Mean biomass of understory macroalgae within the genera (A) *Lobophora* and (B) *Dictyopteris* relative to *Sargassum* spp. canopy biomass based on spline fits

We suggest further work examining the role of environmental variation at the finer patch scale, including variables such as bed depth, local bathymetry, and position relative to tidal channels, to further clarify the role of environment at various spatial scales.

Strong temporal variation was apparent in several other environmental factors at Ningaloo that have been linked to seaweed biomass on coral reefs, such as wave-driven water movement, light, and nutrients (Schaffelke and Klumpp 1998; Ferrari et al. 2012; Mumby et al. 2013). All of these variables were found to be markedly poor descriptors of Ningaloo seasonal *Sargassum* fluctuations, presumably because they are not limiting or their variation is not significantly large enough to be drivers in this regional setting. For instance, seasonal cycles in rainfall had little apparent effect on seaweed biomass at Ningaloo, which is likely due to the subterranean karst system trapping most of the potential terrestrial runoff (Cassata and Collins 2008). Likewise, possible oceanic inputs of nutrients from seasonal wind-driven upwelling onto Ningaloo reef (Woo et al. 2006; Lowe et al. 2012; Wyatt et al. 2013) did not seem to translate directly to levels of seaweed biomass within the lagoon. While increased nitrogen can boost seaweed primary production under some circumstances (Schaffelke and Klumpp 1998; Burkepile and Hay 2006), it is possible that the majority of oceanic nitrogen inputs are being captured by corals on the reef front and flat before it can reach lagoonal *Sargassum* meadows (Muscatine and D'elia 1978; Wyatt et al. 2013). Likewise, PAR levels fluctuated in similar seasonal cycles throughout the year (largely due to day length), but this may not be a limiting factor for canopy-forming species at Ningaloo occupying shallow water (1–5 m) of consistently low turbidity (Cassata and Collins 2008). However, it is difficult to judge the relative role of these factors without known environmental tolerances of *Sargassum* populations to these variables. We suggest further investigation into the specific thresholds of tropical *Sargassum* populations to these and other factors, such as sediment load (Kawamata et al. 2012), to clarify their relative role and seasonal importance in future quantitative models.

Ecological processes can also influence variation in fleshy macroalgal biomass on reefs. Chief among these is herbivory, which can be a primary top-down control of seaweed biomass on many coral reefs (McCook 1996; Burkepile and Hay 2006; Ferrari et al. 2012). However, at Ningaloo, browsing herbivore biomass is low during periods of both peak (Johansson et al. 2010) and trough (Verges et al. 2011) *Sargassum* canopy states, with very low rates of grazing per individual thallus of *Sargassum* within lagoonal seaweed beds (Verges et al. 2011), suggesting that temporal shifts in herbivory are unlikely to be a major determinant of seasonal fluctuations in *Sargassum* biomass. Indeed, seasonal changes in herbivorous grazing rates on *Sargassum* on the Great Barrier Reef were found to occur in the reverse pattern (i.e., highest rates of biomass removal during summer canopy peak; Lefevre and Bellwood 2010). Density-related population processes, such as mortality and recruitment of new seaweed individuals, could also be possible drivers of biomass although unlikely given the perennial persistence of individual holdfasts and generally low levels of recruitment observed in such persistent *Sargassum* beds (Vuki and Price 1994; Kendrick and Walker 1995).

Environmental forcing of *Sargassum* canopy biomass could have wider implications for coral reef biodiversity at Ningaloo. Within the seaweed-dominated beds, understory seaweed genera tended to fluctuate in biomass according to changes in the *Sargassum* canopy throughout time. Competition for light and space are thought to be key factors in such understory–canopy interactions, with the intensity of this competition linked to the morphology, physiology, and relative biomass of the competitor groups (Wernberg et al. 2005; Ferrari et al. 2012). Vastly different trajectories of canopy–understory biomass change occurred over space and time, and these, in part, may be due to the different magnitude of *Sargassum* canopies across locations. At Coral Bay, where the highest levels of canopy biomass occurred, *Lobophora* consistently dominated the understory, while at Tantabiddi sites with low canopy biomass year-round, there was interchange in understory dominance among three seaweed groups. In a pattern analogous to other tropical and temperate seaweed assemblages (Wernberg et al. 2005; Ferrari et al. 2012), the canopy state of *Sargassum* is pivotal for Ningaloo seaweed bed diversity. However, considerable spatial variation among beds of similar canopy biomass suggests that local recruitment processes and small-scale environmental variations (Kendrick and Walker 1995; Ferrari et al. 2012) warrant further investigation.

Besides competition, habitat-forming seaweeds such as *Sargassum* can also facilitate many species that, in turn, are likely to be affected by environmental forcing of canopy structure. For instance, epibiont seaweeds and invertebrates are known to change in diversity and population size in proportion to the nature of the *Sargassum* canopy (Dean and Connell 1987; Lefevre and Bellwood 2010). Likewise, a broad diversity of reef fishes are found to occupy seaweed-dominated beds at certain canopy states (Wilson et al. 2010; Terazono et al. 2012). In many cases, the juvenile stages of these fishes settle into seaweed beds during the summer peak in *Sargassum* canopy biomass (Wilson et al. 2010; Terazono et al. 2012). Presumably, this complex seaweed habitat provides a number of benefits to juvenile fish, such as protection from predators and provisioning of prey, similar to that provided by sea grass and mangroves to many marine organisms (Verweij et al. 2006; Nagelkerken et al. 2008). Being a potential nursery, the biophysical coupling of *Sargassum* canopy development and decay to sea temperature could influence the success or failure of seasonal fish recruitment if a timing mismatch occurs. Given concerns over the future range and magnitude of sea surface temperatures in the Indian Ocean (Lough and Hobday 2011), it appears that thermal climate change could alter the time of year when *Sargassum* canopy changes occur at Ningaloo. If such shifts in seaweed phenology result in seasonal misalignments between species (e.g., canopy decay occurs prior to fish recruitment), this could jeopardize the many *Sargassum*-dependent species and processes that occur within coral reef ecosystems.

Such climate-related concerns could also extend to the role of seaweed-dominated beds in shaping the broader produc-

tivity of Ningaloo. The magnitude of biomass change across growth and decay phases of the *Sargassum* canopy suggests that these seaweed beds provide an important source of primary productivity and nutrient flow within the Ningaloo ecosystem. Coral reefs, including Ningaloo, are typically oligotrophic systems with relatively low nutrient inputs fueling insipient primary production (Webb et al. 1975; Wyatt et al. 2013). While corals and their zooxanthellae symbionts are known to be highly productive under these nutrient-poor conditions, much of this gross primary production is held within the corals themselves (Smith and March 1973; Muscatine and D'elia 1977). Within this coral reef ecosystem, therefore, the annual production and decay of *Sargassum* biomass could represent a considerable component of the total net primary production available to a wide range of reef organisms. Our measured fluxes of *Sargassum* during the decay phase (up to 6 kg fresh weight m^{-2}; Table 1) is a substantial amount of primary biomass, considering that these seaweed beds cover up to 110 km^2 of the Ningaloo lagoon (Kobryn et al. 2013). When detached from the substratum in autumn–winter, this *Sargassum* biomass can take a number of pathways that include the formation of floating rafts, deposition of wrack onto intertidal habitats, and/or sinking wrack that can disperse throughout subtidal habitats (Duarte and Cebrian 1996; Yatsuya 2009; Stimson 2013). Such transport of seaweed biomass could provide substantial spatial subsidies of primary production to other parts of the system (Duarte and Cebrian 1996; Vanderklift and Wernberg 2008; Stimson 2013). Indeed, floating *Sargassum* rafts can persist for 4–14 weeks and travel considerable distances in that time (Yatsuya 2009), emphasizing the potential role that rafts could play in the transport of nutrients and primary productivity to biomes both internal and external to Ningaloo Reef.

Biophysical coupling between sea temperatures and habitat-forming seaweeds such as *Sargassum* points to a wider vulnerability of coral reef ecosystems, such as Ningaloo, to climate change. Given that the major contributions of *Sargassum* to primary productivity and coral reef biodiversity are affected by the timing and magnitude of *Sargassum* biomass production and decay, the ecosystem benefits of *Sargassum* are ultimately linked to thermal climate. Small-scale environmental variations are likely to play a key role in these cycles given the strong variation at multiple spatial scales revealed in this study. We suggest future work exploring the specific thresholds in key environmental parameters (e.g., temperature, PAR, sediment, nutrients) that affect rates of *Sargassum* growth, reproduction, and decay. Exploring to what extent these thresholds are crossed at small to large spatial scales (particularly among discrete beds and locations) will help refine future quantitative models of environmental forcing of *Sargassum* biomass on coral reefs.

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