***Sargassum* epifaunal communities vary with canopy size, predator biomass and seascape setting within a fringing coral reef ecosystem**

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ABSTRACT: Tropical seascapes are comprised of a range of patch habitat types, yet we have only a partial understanding of how local patch condition and seascape position may influence patterns of marine biodiversity, particularly for invertebrate taxa. We investigated how the epifaunal abundance and biomass of tropical *Sargassum* varied with canopy size (volume, total length and dry weight), local patch conditions (macroalgal composition, canopy structure and invertivorous fish biomass) and seascape setting (nearshore, lagoon and back reef) within the Ningaloo fringing reef ecosystem, Australia. A total of 49431 epifauna, dominated by crustaceans and molluscs, were extracted from the thalli of 81 tropical *Sargassum polycystum* individuals. Epifaunal abundance and biomass were most strongly correlated with host *Sargassum* canopy volume and dry weight, respectively. Epifaunal abundance and biomass also varied significantly among separate *Sargassum* meadow patches, with a significant interaction between canopy size and seascape position. Considerable site-level variations in epifaunal biomass density (mg per g *Sargassum* dry weight) were best predicted by either seascape context or local invertivorous fish biomass. *Sargassum* within meadows furthest from the back reef tended to have the highest epifaunal biomass (dominated by molluscs), while meadows closest to the back reef were dominated by crustacea. *Sargassum* within meadows with a high local abundance of invertivorous labrids and serranids tended to have the lowest epifaunal biomass. Strong *Sargassum* canopy size–epifauna relationships indicate that even small differences in canopy extent have major flow-on effects for the trophic function of tropical marine ecosystems by affecting the epifaunal secondary productivity available to higher-order consumers, such as fishes.

KEY WORDS: Tropical macroalgae · Epifauna · Invertivorous fish · Crustacea · Mollusca · Biomass · Patch habitat

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1. INTRODUCTION

Tropical seascapes can be composed of a range of habitat-forming organisms that create patches of coral, seagrass, mangroves, and macroalgae embedded within a matrix of carbonate reef and sand. Emerging evidence indicates that local conditions can interact with the seascape position of these biogenic patch habitats to shape spatial patterns of tropical marine biodiversity and ecosystem function (Berkström et al. 2013, Hensgen et al. 2014, van Lier et al. 2018). For in-

stance, the local abundance of macroalgal-associated fishes has been linked to within-patch habitat complexity and proximity to nearby patches of coral, seagrass and/or macroalgal habitat (Berkström et al. 2013, van Lier et al. 2018). The extent to which these within-patch and seascape effects operate at lower trophic levels (e.g. small-bodied invertebrates), however, remains poorly understood.

Epifauna are invertebrates (typically 0.5–10 mm long) that occupy the living canopy of other organisms, such as macroalgae and corals (Edgar 1990a, Edgar &

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Aoki 1993, Kramer et al. 2017). Often extremely abundant with rapid rates of turnover (growth and mortality), the productivity of these epifauna can support large populations of higher-order consumers, such as fishes, and underpin major pathways of energy and nutrient transfer in marine ecosystems (Edgar & Aoki 1993, Taylor 1998, Kramer et al. 2017). In marine ecosystems, epifaunal communities have been documented within abiotic substrata (rubble and sand) as well as within the canopy of corals, seagrasses and macroalgae (Stella et al. 2010, Kramer et al. 2014, Tano et al. 2016). Current evidence suggests that epifaunal abundance and diversity may be highest within macroalgal microhabitats, including both erect canopy-forming taxa as well as turf communities of the epilithic algal matrix (Kramer et al. 2017), which are targeted by a range of invertivorous reef fishes (Kramer et al. 2015, Wenger et al. 2018).

Canopy-forming macroalgae of the genus *Sargassum* are widespread along coastlines of the world, where they can form extensive meadow habitats. *Sargassum* meadows are increasingly being recognised as an integral component of tropical marine ecosystems, where they support primary production and provide habitat for a diversity of juvenile and adult fishes (Fulton et al. 2019). Canopy structure and composition of tropical *Sargassum* meadows and their associated reef fish communities can vary strongly over space and time due to local environmental conditions and seascape context (Ateweberhan et al. 2009, Fulton et al. 2014, van Lier et al. 2018). Moreover, limited evidence suggests tropical *Sargassum* canopies can contain a range of epifaunal invertebrates, which may vary in abundance according to macroalgal canopy size (Leite & Turra 2003, Wenger et al. 2018) and the presence of invertivorous fishes (Edgar & Aoki 1993). However, we lack an understanding of the relative importance of these local factors alongside seascape context for shaping the relative abundance of *Sargassum* epifauna, which are likely to be a key trophic resource for many higher-order consumers found within tropical macroalgal meadows (Berkström et al. 2013).

To better understand the likely drivers of tropical macroalgal epifaunal community structure, we used an extensive network of *Sargassum*-dominated meadows within a fringing coral reef ecosystem to determine (1) to what extent epifaunal abundance (in terms of number of individuals) and biomass are correlated with different measures of host *Sargassum* canopy size (total length, volume and dry weight), (2) whether epifaunal community structure varies with seascape position (nearshore, lagoon and back reef)

and (3) if local conditions of within-patch macroalgal composition and invertivorous fish biomass can predict spatial variations in *Sargassum* epifaunal community structure.

2. MATERIALS AND METHODS

2.1. Study location

Ningaloo Reef is a World Heritage site in the eastern Indian Ocean that comprises >290 km of fringing coral reef encompassing a shallow lagoon dominated by >30 000 hectares of brown macroalgal meadows dominated by tropical members of the canopy-forming genus *Sargassum* (Kobryn et al. 2013, Fulton et al. 2014). While the taxonomy of *Sargassum* remains to be fully resolved for this tropical region, our collections were focused on the most common morphotype in these meadows which we believe matches the description for *Sargassum polycystum* (Huisman 2019). For this study, which focused on spatial variation in the *Sargassum* epifaunal community, we selected 9 distinct *Sargassum* meadow patches separated by a minimum of 300 m and spread across the 3 distinct seascape positions of nearshore (sites typically within 50 to 300 m of the shoreline and embedded within ancient reef pavement covered in a layer of sand an average of 1–3 cm thick), lagoon (>500 m from shoreline and embedded within pavement-sand matrix) and back reef (embedded within pavement-sand surrounded by fringing coral reef), within a 6 km² section of the Maud Region of the Ningaloo Marine Park near Coral Bay, Western Australia (Fig. 1). These seascape positions are relevant to many coastlines where *Sargassum* meadows occur alongside coral reefs in the Pacific (e.g. New Caledonia), Indian (e.g. Ningaloo and Tanzania) and Atlantic (e.g. Brazil) Oceans, as well as the Red Sea (Berkström et al. 2013, Tano et al. 2016, Fulton et al. 2019). The macroalgal meadow study sites were an average of 26 210 m² ($\pm$ 10 605 m² SE) in area (van Lier et al. 2018), embedded within a pavement-sand matrix in shallow water (2–6 m deep), and were subject to similar site-level mean sea temperatures ($27.3 \pm 0.1^\circ\text{C}$) during the 4 wk field survey and collection period.

2.2. *Sargassum* epifauna sampling

During the late austral summer (February to March) of 2018, we collected 9 entire *S. polycystum* individuals and their epifauna at each of the 9 study

Fig. 1. Nine *Sargassum*-dominated study sites at 3 seascape positions (nearshore, lagoon, back reef) within the Maud Recreation Zone near Coral Bay, Ningaloo Reef, Western Australia

sites. Since canopy size can be a key predictor for epifaunal abundance (Edgar 1990b), we haphazardly sub-sampled a cross section of *Sargassum* canopy sizes at each site. To do this, a 15 m line transect across the centre of each study site was used to select the *S. polycystum* individuals closest to the 5 m mark that fell within each of 3 height classes (>60, 30–60 and <30 cm). These height classes corresponded to the top, middle and bottom third of mean canopy sizes recently recorded for this region across sites, years and seasons (Wilson et al. 2014, van Lier et al. 2018). We repeated this procedure at the 10 and 15 m points on the same line transect to collect a total of 9 *S. polycystum* individuals per site (3 per size class). For each selected *S. polycystum* individual, a SCUBA diver gently and fully enclosed the entire *S. polycystum* thallus and

associated epifauna with a canvas bag, then cut the stipe just above the holdfast before immediately sealing the canvas bag to reduce the risk of epifauna escape. All collected samples were brought back to the research vessel within 30 min and transported in a cooler to the Coral Bay Research Station for processing within 4 h of collection.

Post-collection processing of *S. polycystum* individuals involved immersion in cold freshwater for 10 min before gently shaking and then dislodging all of the chilled epifauna from their *S. polycystum* host with a salad spinner. All of the cold freshwater containing the epifauna was then passed through a 125 µm stainless steel sieve so the retained particles could be washed into a labelled zip bag and frozen at –20°C for transport to The Australian National University for further analysis. After all the freshwater was removed from the *S. polycystum* individual, a range of metrics were taken for each host canopy: total extended length from stipe end to tip (to nearest cm), total volume (to nearest millilitre measured via displacement of freshwater in a measuring cylinder) and total wet weight (g). *S. polycystum* individuals were then dried in an oven at 60°C for 48 h to obtain a canopy dry weight (to nearest 0.1 g).

Total abundance of epifauna collected from each *S. polycystum* individual was quantified by defrosting the epifauna and fixing them in a 10 % formalin-seawater solution for 1 h, before rinsing in seawater for identification and enumeration under a stereo-microscope with 40× magnification. To allow estimation of epifaunal biomass in terms of ash-free dry weight (AFDW), we used the sieve method proposed by Edgar (1990c), which involved passing the now-fixed epifauna samples through a nested series of sieves (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.7 and 0.5 mm stainless steel mesh sizes) that fractionated the epifauna by body size. Epifauna retained on each sieve were then identified to 6 taxonomic groups following Edgar (1990c): crustaceans, molluscs, echinoderms, polychaetes, foraminifera and other animals; epifaunal abundance was determined by counting all individuals per taxonomic group per sieve size. For epifauna retained on sieve sizes of ≤4.0 mm, we used the empirically derived equations of Edgar (1990c) to estimate the total AFDW of each taxonomic group in the sample. For all epifauna > 5.6 mm, we empirically measured the dry weight and ash weight of each taxonomic group (following 48 h in a 60°C oven or 2 h in a 500°C muffle furnace, respectively) to estimate AFDW by subtracting the ash weight from dry weight.

2.3. Macroalgal and invertivorous fish surveys

Macroalgal benthic composition within each site was estimated underwater by SCUBA divers deploying 6 replicate 10 m line transects run in series and separated by a minimum of 5 m. Along each transect, the relative percentage cover of macroalgal genera was estimated by recording the distance occupied under the line (to nearest 5 cm). *Sargassum* canopy structure was also assessed in terms of holdfast density (number within a 0.5×0.5 m quadrat) and vertical canopy height (maximum length when manually extended along a ruler to nearest cm) at 2 m intervals (starting at 0 m) to yield 6 replicate measures of each canopy metric per 10 m line transect, following Wilson et al. (2014).

Invertivorous fishes have been identified as common in tropical macroalgal meadows and include species in the 4 diverse families of the Labridae (excluding the Scarinae), Lethrinidae, Mullidae and Serranidae (Wilson et al. 2010, van Lier et al. 2018, Fulton et al. 2019). We estimated the biomass of these fish families within our 9 study sites using the point-census cylinder survey method of Noble et al. (2013). This involved the same observer on SCUBA recording the estimated total length (cm) of all target fishes within 6 replicate 5 m diameter cylinders that were haphazardly spread within each site so as to be separated by at least 5 m from each other. Mean site-level biomass of each fish family was then calculated by converting the total length (cm) of all individuals to an estimated mass (g) using published length-weight relationships for each species (Kulbicki et al. 2005, Froese & Pauly 2019).

2.4. Data analyses

To examine which measures of *Sargassum* canopy size may best predict variation in epifaunal total abundance and biomass, we used least-squares regression to model the relationships between 3 metrics of *Sargassum* canopy size (total length, volume and dry weight) and either total epifaunal abundance or total epifaunal biomass (AFDW) per *S. polycystum* individual. Initial analyses indicated that most relationships were significant and non-linear (see Fig. A1 in the Appendix), so they were linearised via natural log-log transformations for subsequent analyses.

Epifaunal community structure among sites was then explored in terms of both individual abundance and biomass of the 6 taxonomic groups of epifauna (as dependent variables), with the fixed factor of sea-

scape position (nearshore, lagoon or back reef) and random factor of site (nested in seascape position) in a 2-way multivariate permutational analysis of covariance (PERMANCOVA). *Sargassum* canopy size was included as a covariate (logged volume for epifaunal abundance, logged dry weight for epifaunal biomass). These PERMANCOVAs were performed with Type 1 sum of squares and a maximum of 9999 permutations of resemblance matrices based on the modified Gower (base 2) dissimilarity measure applied to either $\log_{10}(x + 1)$ (abundance) or fourth-root (biomass) transformed data that were used to reduce skew across the dependent variables (Anderson et al. 2006, 2008). Post-hoc explorations of significant terms were explored with threshold-metric multi-dimensional scaling (tmMDS) ordinations of the site-seascape group centroids. Ordination structure in epifaunal individual abundance and biomass was explored with principal components analysis (PCA), optimised with vector overlays to indicate the degree of Pearson's correlation between the epifaunal variables and the ordination structure.

Possible environmental predictors of site-level variation in the relative biomass of the 6 taxonomic groups of *Sargassum* epifauna were explored with best-subsets model selection using distance-based linear models (DistLM) and the Akaike information criterion corrected for finite sample sizes (AICc) to select the most parsimonious model(s), following Burnham & Anderson (2002). We first converted the matrix of dependent data (being epifaunal biomass per taxonomic group) into biomass per *Sargassum* canopy dry weight ($\text{mg epifauna g DW}^{-1}$) to take account of general canopy size effects on epifaunal biomass. This standardised epifaunal biomass was then arranged into a modified Gower (log base 2) resemblance matrix, following a fourth-root transformation to correct for skew. An environmental predictor matrix was assembled, comprising site means for 3 groups of possible predictors: invertivorous fish biomass (per each of the 4 families), *Sargassum* canopy structure (canopy height, holdfast density, percent cover canopy and understory taxa, taxonomic genera richness and Pielou's evenness) and seascape context (meadow patch area, distance to fringing reef, distance to nearest neighbouring meadow and depth). The most parsimonious environmental model for predicting *Sargassum* epifaunal biomass across the 9 study sites was chosen as the one with the fewest variables within 2 AICc of the top model, which was then visualised by a distance-based redundancy analysis (dbRDA) ordination with the best predictor environmental vectors as an overlay. All

analyses were performed in PRIMER (v.7.0.13) with the Permanova+ add-on (Anderson et al. 2008).

3. RESULTS

A total of 49431 epifauna individuals were extracted from 81 *S. polycystum* individuals, which represented an estimated total biomass of 18619.4 mg (AFDW) of epifauna from 6119.8 g (dry weight) of tropical *Sargassum* canopy biomass. Total abundance and biomass of epifauna per *S. polycystum* individual varied significantly with all 3 measures of *Sargassum* canopy size (Fig. 2). Pearson's correlation was highest for epifaunal abundance against *Sargassum* canopy volume (Fig. 2B); correlations were generally lower for epifaunal biomass–canopy relationships, being highest for *Sargassum* canopy dry weight (Fig. 2F).

Half of the total epifaunal abundance (50.0%) consisted of crustaceans (mainly Amphipoda, Har-

pacticoida and Isopoda), a third (33.4%) were molluscs (mainly Gastropoda), and the remainder comprised foraminifera (9.1%), echinoderms (2.6%, mostly Ophiuroidea), polychaetes (1.9%) and a mixture of other animals (2.7%, including Nematoda). In biomass terms (estimated as AFDW that excludes skeletal tissues such as shells), however, molluscs were the dominant group (77% of the overall total), followed by crustaceans (20%). Considerable variation was apparent at the sample level, with little apparent structure in either epifaunal abundance or biomass as related to seascape position across all of the taxonomic groups (Figs. 3 & 4), perhaps with the exception of crustaceans and molluscs being more abundant in the back reef *S. polycystum* samples (Fig. 3A,B) that also tended to be at the larger end of the canopy size spectrum across the entire collection (Fig. 2A–C).

Both epifaunal individual abundance and biomass varied significantly among sites, with a significant

Fig. 2. Log-log plots of the relationship between different measures of *Sargassum* canopy size (total length, volume, and dry weight) and either (A–C) epifaunal abundance (total individuals per *S. polycystum*) or (D–F) epifaunal biomass (ash-free dry weight, AFDW, per *S. polycystum*) collected from 9 study sites at 3 seascape positions (nearshore, lagoon, and back reef) in the Maud region of Ningaloo Reef during summer 2018

Fig. 3. Principal component analysis (PCA) of epifaunal abundance on 81 individual *S. polycystum* collected from 9 sites ($n = 9$ samples per site) at 3 seascape positions (nearshore, lagoon, and back reef; $n = 3$ sites per position) in Ningaloo during summer 2018. (A) Total epifaunal abundance, and (B) vector overlay of epifaunal taxonomic groups strongly correlated with the ordination structure, and (C) ordinations optimised with bubbles scaled to relative abundance of each epifaunal group

interaction between *Sargassum* canopy size and seascape position after taking into account the significant covariance between canopy size and epifauna (Table 1, Fig. 2). Whilst the largest *Sargassum* canopy sizes were sampled in the back reef, there

was high variability among sites that created considerable overlap among all 3 seascape positions (Fig. 5). Focusing on this site-level variation, best-subsets model selection revealed 2 competing models that could provide the best predictors for epifauna

Fig. 4. PCA of epifaunal biomass on 81 individual *S. polycystum* collected from 9 sites ($n = 9$ samples per site) at 3 seascape positions (nearshore, lagoon, and back reef; $n = 3$ sites per position) in Ningaloo during summer 2018. (A) Total epifaunal biomass, and (B) vector overlay of epifaunal taxonomic groups strongly correlated with the ordination structure, and (C) ordinations optimised with bubbles scaled to relative biomass of each epifaunal group

nal community biomass structure (Table 2), which were based on either invertivorous fish biomass (Fig. 6A,C) or seascape context (Fig. 6B,D). In general, *Sargassum* at sites characterised by a high biomass of mullid fishes had higher epifaunal biomass

for a given canopy size, while a lower epifaunal biomass (particularly molluscs; Fig. 6C) tended to be found in sites characterised by a high biomass of labrid, serranid and lethrinid fishes (Fig. 6A,C). Distance to fringing reef was the best single seascape

Table 1. Summary of PERMANCOVA of *Sargassum* epifaunal (A) individual abundance and (B) biomass across 3 seascape positions (fixed) and 9 study sites (random, nested in seascape) in the Maud region of Ningaloo Reef during summer 2018, with log *Sargassum* canopy size included as a covariate in terms of either (A) volume or (B) dry weight according to the best predictors for the canopy size–epifauna relationships (see Fig. 2). Significant terms ($p < 0.05$) are highlighted in **bold**

Source	df	SS	MS	Pseudo- <i>F</i>	p-value
(A) Epifaunal individual abundance					
<i>Sargassum</i> canopy volume	1	16.125	16.125	55.990	<0.01
Seascape	2	1.139	0.569	1.024	0.454
Site (Seascape)	6	3.445	0.574	3.064	<0.01
<i>Sargassum</i> canopy volume × Seascape	2	1.129	0.564	3.012	<0.05
<i>Sargassum</i> canopy volume × Site	6	1.812	0.302	1.612	0.079
Residual	63	11.807	0.187		
Total	80	35.456			
(B) Epifaunal biomass					
<i>Sargassum</i> canopy dry weight	1	13.127	13.127	18.134	<0.01
Seascape	2	1.865	0.932	0.506	0.827
Site (Seascape)	6	11.365	1.894	4.873	<0.01
<i>Sargassum</i> canopy dry weight × Seascape	2	2.817	1.409	3.623	<0.01
<i>Sargassum</i> canopy dry weight × Site	6	3.301	0.550	1.415	0.115
Residual	63	24.491	0.389		
Total	80	56.967			

predictor for epifaunal community structure (accounting for >47% of the total variation along dbRDA1), with a trend of increasing epifaunal biomass (particularly molluscs) with increasing distance of the patch from the coral back reef (Fig. 6B). Depth and distance to the nearest neighbouring *Sargassum* meadow appeared to play a smaller overall role (8% of total variation along dbDRA2) in explaining spatial variations in epifaunal canopy-specific biomass (Fig. 6B,D).

Table 2. Summary of best-subsets selection of distance-based linear models for predicting site-level variation in biomass of *Sargassum* epifauna. The most parsimonious models within 2 Akaike information criterion (AICc) units of the top model are indicated in **bold**

Model	AICc	deltaAICc	r ²
Invertivorous fish biomass	2.413	–	0.635
Seascape context	3.103	0.69	0.606
Canopy structure	88.001	85.59	0.885

Fig. 5. Threshold-metric multi-dimensional scaling (tmMDS) ordination of site-level group centroids for *Sargassum* epifaunal (A) abundance and (B) biomass collected at 3 seascape positions (nearshore, lagoon, back reef; $n = 3$ sites per position) within Ningaloo during summer 2018. Bubble sizes are proportional to site-level mean *Sargassum* canopy (A) volume or (B) dry weight to explore the significant canopy seascape interaction (see Table 1)

4. DISCUSSION

Our study found 3 key results that significantly increased our understanding of invertebrate biodiversity patterns within tropical seascapes containing macroalgal meadows. First, we found an overarching positive correlation between epifaunal community structure and *Sargassum* canopy size, although the best canopy size metric varied for the measures of epifaunal individual abundance and biomass. Second, we found epifaunal community structure varied significantly among *Sargassum* meadow patches, with a prominent interaction between host canopy size and seascape position. Third, the local biomass of invertivorous fish and the position of macroalgal meadows within the seascape provided some of the best predictors for site-level variations in *Sargassum*

epifaunal community structure (Fig. 7). Given that epifauna are a critical trophic link between the macroalgal production base and higher-order consumers such as fishes, our evidence suggests distinct differences in the trophodynamics of these tropical ecosystems across relatively fine spatial scales

(<2 km). Moreover, the strong links between epifaunal biomass and canopy size, and the sensitivity of *Sargassum* canopy growth to sea temperature (Fulton et al. 2014, 2019), suggest climate change is likely to influence flows of primary to secondary production in macroalgae-dominated systems.

Fig. 6. Distance-based redundancy analysis (dbRDA) ordination of the most parsimonious best-subsets models for predicting site-level variation in epifaunal biomass across 3 seascape positions (nearshore, lagoon and back reef) in terms of (A) invertivorous fish biomass and (B) seascape context, with optimisations showing bubble sizes scaled to site-level epifaunal biomass for both crustacea and molluscs for each model (C and D, respectively). Vector overlays indicate invertivorous fish family and seascape metric most strongly correlated with each ordination structure

Fig. 7. Conceptual diagram showing the relationship between macroalgal canopy volume/dry weight and epifaunal abundance/biomass at within-patch scale, and how seascape contexts and the presence of invertivorous fishes affect epifaunal community structure at seascape scales

Strong correlations between epifaunal abundance and *Sargassum* canopy size, such as those found in this study, may arise through habitat amount effects that can govern the size and diversity of ecological communities (Fahrig 2013). However, the differing metrics of canopy size relevant to either individual abundance or biomass of epifauna suggest some nuanced effects related to habitat microstructure. For instance, epifaunal abundance was most strongly correlated with canopy volume (rather than canopy length or biomass), which may point to the importance of overall surface area and microniches for colonisation by mobile animals on fresh *Sargassum* (Carvalho et al. 2018). Indeed, canopy macroalgal meadows have already been found to harbour more epifauna than other macrophyte habitats, such as seagrass meadows (Tano et al. 2016, Belattmania et al. 2018), the epilithic algal matrix (EAM; Kramer et al. 2012, 2014) or the understory macroalgae (Wenger et al. 2018), due to their complexity and higher volumetric canopy structure. An increased epiphyte load, which increases the structural complexity and surface area of the overall macroalgal canopy, has also been found to support a greater abundance of epifauna (Martin-Smith 1993, Leite & Turra 2003). Our late-summer samples at Ningaloo showed a very low occurrence level of *S. polycystum* epiphytes (total of 53.65 g epiphytes across 6119.8 g *S. polycystum*, dry weight). Epiphyte loads on tropical *Sargassum* can change dramatically with season (Martin-Smith 1993, Lefevre & Bellwood 2010), and such seasonal effects should be a priority for future research in this area. We found epifaunal biomass, however, was most strongly correlated with *Sargassum* canopy dry weight in the Ningaloo sam-

ples, which is consistent with prior studies of epifaunal biomass on tropical and temperate *Sargassum* (Mukai 1971, Edgar & Aoki 1993, Edgar & Klumpp 2003, Leite & Turra 2003). Notably, Pearson's correlations for epifaunal biomass–canopy relationships were generally lower than for epifaunal abundance–canopy relationships, which may arise from biomass estimates of epifauna larger than 5.6 mm that represent a greater amount of biomass (59.14 %) relative to their individual abundance (0.86 %) of the total epifaunal community. Nonetheless, we found significant positive correlations between the amount of epifauna and *Sargassum* canopy size, which is emerging as a common scenario in

tropical *Sargassum* communities (Martin-Smith 1993, Wenger et al. 2018).

Epifaunal communities inhabiting *Sargassum* canopies in Ningaloo were dominated by 2 key taxonomic groups: crustaceans and molluscs. Peracarid crustaceans (amphipods and isopods), harpacticoid crustaceans and gastropod molluscs were the main taxonomic groups contributing to total epifaunal abundance (83.4 %) and biomass (94 %), followed by ophiuroid echinoderms and polychaetes. Our findings are congruent with previous studies indicating that crustaceans and molluscs are the most abundant mobile epifauna on *Sargassum* in tropical and temperate biomes around the world (Table 3). Indeed, studies of epifauna living within turf algae of the EAM (immediately adjacent to corals) or scleractinian corals found crustaceans were most abundant, followed by molluscs, annelids, foraminifera, and nematodes (Stella et al. 2010, Kramer et al. 2012, Kramer et al. 2014). Depending on seascape setting (explored further below), these 2 taxonomic groups may be the most abundant drivers of trophodynamics and nutrient cycling within these macroalgal-dominated ecosystems. Notably, our estimates of total epifaunal density (individual number per g *Sargassum* dry weight) were ~3-fold lower than the average from other studies of tropical and temperate *Sargassum* epifauna (Table 3). A previous estimate from a single *Sargassum* meadow at Ningaloo, which was an order of magnitude higher than our estimate (148 individuals per g canopy dry weight; Wenger et al. 2018), provides some insight into the possible source of these differences. Wenger et al. (2018) used 0.12 mm as the finest mesh size while processing

Table 3. Studies of *Sargassum*-associated epifaunal composition around the world. Epifaunal density is presented as the individual number per gram of *Sargassum* dry weight. The top 3 most abundant taxa (if present) are listed. Most studies used a 0.5 mm mesh size, and studies using 0.1 to 0.3 mm mesh size are marked with an asterisk. *Sargassum* wet weight in some studies was converted to dry weight by following Brey et al. (2010)

Epifaunal density	Most abundant taxa	Focal region	Source
(A) Tropical			
13	Crustaceans > Molluscs > Foraminifera	Ningaloo Reef, Australia (23° 1' S)	Present study
8	Crustaceans > Molluscs > Polychaetes	Northeast Queensland, Australia (18° 1'–18° 4' S)	Edgar & Klumpp (2003)
31*	Crustaceans > Polychaetes > Molluscs	The Great Barrier Reef, Australia (19° 1' S)	Martin-Smith (1993)
12	Crustaceans > Molluscs > Polychaetes	Red Sea, Saudi Arabia (21° 2' N)	Ba-Akdah et al. (2016)
148*	Foraminifera > Crustaceans > Molluscs	Ningaloo Reef, Australia (23° 1' S)	Wenger et al. (2018)
66*	Molluscs > Crustaceans > Polychaetes	Flamengo Bay, Brazil (23° 3' S)	Leite & Turra (2003)
1	Crustaceans > Polychaetes > Molluscs	Lazaro and Tabatinga, Brazil (23° 3' S)	Tanaka & Leite (1998)
Mean density $\pm$ SE: 39.9 $\pm$ 19.8			
(B) Temperate			
97	Crustaceans > Platyhelminthes > Molluscs	Tomiooka Peninsula, Japan (32° 3' N)	Edgar & Aoki (1993)
4	Crustaceans > Molluscs > Polychaetes	El Jadida shoreline, Morocco (33° 2' N)	Belattmania et al. (2018)
74*	Crustaceans > Polychaetes > Molluscs	Sydney & Illawarra, Australia (34° 2'–34° 4' S)	Lanham et al. (2015)
3*	Crustaceans > Molluscs > Annelids	Southeast New South Wales, Australia (34° 3'–34° 8' S)	Marzinelli et al. (2016)
31	Molluscs > Crustaceans	West and south coast, Portugal (37° 1'–37° 4' N)	Engelen et al. (2013)
14	NA	North coast, Portugal (41° 4'–41° 5' N)	Veiga et al. (2014)
2	Crustaceans > Molluscs > Polychaetes	Galician coast, Spain (42° 1'–42° 2' N)	Gestoso et al. (2012)
6	Molluscs > Crustaceans > Nematodes	Galician coast, Spain (42° 2' N)	Gestoso et al. (2010)
Mean density $\pm$ SE: 28.9 $\pm$ 13.0			

their *Sargassum* epifauna, which captured an extremely abundant foraminifera fauna that were subsequently found to not be major prey targets for a *Sargassum*-associated invertivorous fish (Wenger et al. 2018). While there are some wide variations across studies using similar mesh collection sizes, there is a generally higher mean epifaunal density on tropical versus temperate *Sargassum* (Table 3). This fits with the notion that production of the ectothermic epifaunal community is higher in warmer sea temperatures (Edgar 1990c).

Consumers can exert strong top-down pressure on prey to shape relative abundance and biomass across space and time. Macroalgal meadows can be important foraging grounds for invertivorous fishes (Edgar & Aoki 1993, Wilson et al. 2014, Tano et al. 2016), which have been found to specifically target mobile epifauna on macroalgae like *Sargassum* (Edgar & Aoki 1993, Wenger et al. 2018), with varying effects. For instance, one study found no significant decrease in epifaunal abundance on *Sargassum* canopies caged to exclude fish foraging activity (Martin-Smith 1993). In contrast, Edgar & Aoki (1993) found that predation by an invertivorous wrasse (Labridae) tended to remove larger epifauna from macroalgae in mesocosm experiments, which freed up resources (through competitive release) for smaller epifauna that subsequently increased in

abundance. In other words, it appears predation could drive an increase in the abundance and productivity of *Sargassum* mobile epifauna, which may help explain why higher epifaunal biomass was often found in meadows with greater invertivorous fish biomass at Ningaloo. The biomass of common invertivorous fish species has been positively correlated to *Sargassum* canopy structure (Wilson et al. 2014, Wenger et al. 2018), with at least one invertivorous fish species found to preferentially target epifaunal crustaceans and molluscs on tropical *Sargassum* (Wenger et al. 2018). Given that invertivorous fishes have previously been shown to vary in abundance with seascape position (van Lier et al. 2018), some of the seascape effects on epifauna condition may arise from these predation effects. Such linkages of invertivorous fishes, epifauna and *Sargassum* in Ningaloo provide a hint of how secondary and higher production may be supported by the underlying *Sargassum* canopy habitat at Ningaloo and across seascapes dominated by *Sargassum* meadows around the world (Fulton et al. 2019). This is clearly a key research front for future work in this arena, requiring empirical study of epifauna–fish interactions and microhabitat foraging preferences to help resolve the relative importance of bottom-up (canopy structure) and top-down influences on macroalgal epifauna.

Our study reveals that local conditions of mean *Sargassum* canopy size can vary considerably over fine spatial scales to provide one of the primary explanations (indicated by the significant interaction term) for variations in epifaunal community structure in a range of seascape contexts. At Ningaloo, *Sargassum* canopy size was not consistent across all meadows, creating a complex mosaic of high/low canopy density, height and cover across meadows spread across the seascape (Wilson et al. 2014, Lim et al. 2016, Wenger et al. 2018). While this was largely irrespective of seascape position, we did find a tendency for higher maximum *Sargassum* canopy size in back reef positions, where the *Sargassum* meadows were embedded among the fringing coral reef. Once these canopy size effects were taken into account, however, seascape position did provide further explanations for spatial variations in *Sargassum* epifaunal community structure. In particular, distance to the back reef provided one of the key predictors for differences in epifaunal community structure at Ningaloo. This was largely because of a shift in the relative dominance of the 2 major epifaunal taxa: crustaceans dominated the *Sargassum* epifauna in macroalgal meadows close to coral reef (i.e. back reef sites), while epifaunal molluscs predominated in nearshore and lagoonal macroalgal meadows. This is significant because these 2 invertebrate groups may have very different levels of growth (secondary production) to support consumption by higher-order consumers like fishes using different strategies for consumption and processing of these 2 prey types (Wainwright 1988, Edgar 1990a,b,c, Kramer et al. 2015). If so, then adjacent macroalgal meadows separated by relatively fine spatial scales (100s of metres to a few kilometres) may have remarkably different trophodynamics.

Strong canopy–epifauna relationships such as those revealed here indicate some broader consequences for the conservation and management of diverse and productive tropical seascapes. Across the range of canopy sizes examined here, which span a typical range of *Sargassum* canopy sizes that have been observed across sites, seasons and years in this region (Wilson et al. 2014, van Lier et al. 2018), we can see that even small reductions in canopy extent can translate to much lower epifaunal abundance with flow-on effects for associated species and overall ecosystem function. A reduction in *Sargassum* canopy from disturbance or seasonal effects is likely to trigger a trophic cascade in reduced productivity at higher trophic levels, with variable consequences across the seascape. The non-linear nature of these

effects suggests a particularly severe reduction in epifaunal abundance for canopies below 30 to 60 cm height at Ningaloo. Indeed, similar reductions in canopy size due to seasonal cycles in *Sargassum* phenology have been linked to major declines in the abundance of macroalgal-dependent fishes (Lim et al. 2016, Wenger et al. 2018). Besides a reduction in the overall abundance of epifauna with canopy reductions, there may also be a loss of certain taxa (e.g. shifts in the gammarid crustacean epifauna over seasonal *Sargassum* canopy cycles; Kodama et al. 2020) that are key components in nutrient cycling and trophic flows. A major cause for concern is that one of the key stressors of climate change—sea temperature—is a primary determinant of *Sargassum* canopy growth in tropical reef settings around the world (Fulton et al. 2019). Alongside disturbances like marine heatwaves and cyclones (Fulton et al. 2019) which can dramatically reduce *Sargassum* canopy size in a short time, these climatic effects can drive a bottom-up collapse of trophic flows to higher-order consumers, including fish species that underpin productive tropical fisheries linked to the livelihoods of millions of people across the tropical world (Robinson et al. 2019, Fulton et al. 2019). As such, we suggest that tropical macroalgal canopy conditions should be a key metric in habitat-based fisheries management and spatial approaches to conservation that seek to encompass a representative cross-section of biodiversity across a range of seascape settings. The thermal thresholds that may underpin major shifts in epifaunal abundance and production should be a key priority for future experimental work and targeted multi-season and multi-year field studies.

Acknowledgements. We thank Maria Eggertsen, David Ellis, Rosalie Harris, Joshua van Lier and Adrienne Nicotra for field assistance and helpful discussions; and 2 anonymous reviewers for helpful comments on an earlier draft. Funding was provided by the Research School of Biology at The Australian National University, the Ministry of Education Taiwan, and a Joyce W. Vickery Scientific Research Award from The Linnean Society of NSW.

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Appendix

Fig. A1. Relationship between different measures of *Sargassum* canopy size (total length, volume, and dry weight) and either (A–C) epifaunal abundance (total individuals per *S. polycystum*) or (D–F) epifaunal biomass (ash-free dry weight per *S. polycystum*) collected from 9 study sites at 3 seascape positions (nearshore, lagoon, and back reef) in the Maud region of Ningaloo Reef, Australia, during summer 2018