

# Microhabitat selectivity shapes the seascape ecology of a carnivorous macroalgae-associated tropical fish

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**ABSTRACT:** Habitat quantity and quality can be key drivers for the distribution and abundance of animals in heterogeneous landscapes. Macroalgal meadows are often a prominent component of tropical marine ecosystems, yet we have little understanding of how dynamic shifts in this habitat type may affect patterns of fish biodiversity. We examined whether a tropical carnivorous wrasse, *Xenojulis margaritaceus*, was a macroalgal specialist that responded to changes in canopy habitat structure across space and time. Field surveys revealed that *X. margaritaceus* exclusively occupied macroalgal meadows, where it foraged for invertebrate epifauna on a range of macroalgal genera such as *Sargassum* and *Lobophora*. During summer, *X. margaritaceus* preferentially occupied the canopy-forming macroalgae *Sargassum*. *Sargassum* canopy height, percent cover of understory algae and the abundance of strong competitors and roving predators provided the best predictors for the abundance of *X. margaritaceus* abundance across the seascape. Despite seasonal shifts in habitat use to include more understory algae during winter, *X. margaritaceus* displayed significant declines in abundance from summer to winter according to the extent of seasonal canopy habitat loss within each meadow. We conclude that carnivorous fishes can be dependent on tropical macroalgal meadows, where they may be vulnerable to a loss of canopy habitat quality arising from local factors and climatic forcing.

**KEY WORDS:** Habitat quality · Specialisation · Seasonality · *Sargassum* meadow · *Xenojulis margaritaceus*

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## INTRODUCTION

Habitat selection by animals is typically motivated by their specific needs for food and shelter, amidst pressure from density-dependent interactions such as competition and predation (Jones 2001, Morris 2003a, Resetarits 2005). Accordingly, shifts in the availability of preferred microhabitats can drive the spatial and temporal dynamics of populations and communities over space and time, which is critical to understand for adaptive fisheries conservation and management (Morris 2003b, Boyce et al. 2016, Fulton et al. 2016). In tropical marine ecosystems, we know the abundances of some fish species are tightly linked with the availability of specific hard

corals they use exclusively for food; such species become locally extinct when their preferred corals are lost (Munday 2004, Wilson et al. 2006). Density-dependent competition for reduced habitat quantity and/or quality can also manifest as a sub-lethal loss of body condition and/or poor recruitment into the adult population (Pratchett et al. 2004, Feary et al. 2007, Wilson et al. 2016). Such strong dependency on live hard corals is of obvious concern for tropical fish communities subject to mass coral bleaching events. Less well recognised, however, is the potential sensitivity of tropical fishes to the loss of other habitat types, such as macroalgal meadows (Wilson et al. 2010, Lim et al. 2016, Eggertsen et al. 2017, Tano et al. 2017).

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Canopy-forming macroalgae are key primary producers that can form extensive meadow habitats along tropical coastlines around the world (Glenn et al. 1990, Ateweberhan et al. 2005, Fulton et al. 2014). The benthic coverage and canopy height of tropical fleshy macroalgae can vary in complex ways to produce a mosaic of varying habitat quantities and qualities among and within meadows (Wilson et al. 2014, Lim et al. 2016). Macroalgal habitat quality refers to certain levels of canopy height, density and type (genus of habitat-forming macroalgae), which fish species may prefer to occupy (Wilson et al. 2014, Lim et al. 2016). Variations in macroalgal quantity and quality have been linked to sea temperature, which makes these habitats vulnerable to thermal anomalies and climate change (Glenn et al. 1990, Ateweberhan et al. 2005, Fulton et al. 2014). Recent research has highlighted the consequences of variation in macroalgal habitats for a browsing herbivorous fish, which displayed a 50% decrease in abundance with a 41% decline in cover of its preferred *Sargassum* canopy habitat (Lim et al. 2016). While there is an obvious trophic dependency of herbivorous fish on macroalgae, canopy macroalgae also support an abundance of diverse epifauna for carnivores to consume (Edgar & Aoki 1993, Martin-Smith 1994, Tano et al. 2016). As such, there is potential for carnivorous fishes to exhibit strong linkages to macroalgal habitat quantity and quality across the seascape (Fulton et al. 2016, Wilson et al. 2017).

In this study, we examined how a tropical carnivorous wrasse responds to marked changes in both habitat structure and epifaunal prey across a seasonally dynamic mosaic of macroalgal meadows. Our study species, *Xenojulis margaritaceus*, is nominally considered a macroalgal specialist that consumes benthic invertebrates (Randall & Adamson 1982, Kuitert 2002). If confirmed as a macroalgal habitat specialist, we hypothesise that *X. margaritaceus* abundance can be predicted by changes in macroalgal habitat quality across space and time. To test this hypothesis, we used a combination of field and lab-based evidence to explore the relative importance of habitat quantity, quality and biotic interactions for explaining variations in *X. margaritaceus* abundance among macroalgal meadows. Observations of foraging behaviour and gut content analysis were combined with detailed surveys of macroalgal epifauna across a major seasonal change in canopy habitat structure. Together, this evidence was used to assess the extent to which the changing abundance of a carnivorous fish across a tropical seascape may be explained by microhabitat specialisation and/or trophic dependence.

## MATERIALS AND METHODS

### Study region

Field surveys of fish density were conducted in the Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, Western Australia (Fig. 1). The fringing reef ecosystem at Ningaloo encloses a shallow (<6 m depth) lagoon with a complex network of hard coral patches and macroalgal meadows embedded within a matrix of sand-covered limestone pavement (Kob-



Fig. 1. Study region, indicating all macroalgal meadow sites surveyed in this study (green), as well as coral-dominated sites (dots) surveyed within the adjacent fringing coral reef (pink) within the Maud Recreation Zone of Ningaloo Marine Park, Western Australia

ryn et al. 2013). Macroalgal meadows typically consist of 20–80% benthic cover of canopy-forming brown macroalgae (principally *Sargassum*, with some *Sargassopsis*) during the summer months, which seasonally decline during winter (typically down to 0–40% benthic cover); an understory of other macroalgae (mostly *Lobophora*, *Padina*, *Dictyota* and *Dictyopteris*) typically varies in benthic cover from 0 to 40% in response to this canopy change (Fulton et al. 2014, Wilson et al. 2014, Lim et al. 2016). Coral-dominated habitats on the lagoon edge (known as 'back reef') are on average composed of 40% dead coral, 25% live coral (mostly plating and corymbose *Acropora*), 25% abiotic substratum (limestone pavement, sand, rubble) and 10% macroalgae (Lim et al. 2016). A total of 33 sites were surveyed during the austral summer (February–March) in 2016, which included 29 macroalgal meadow sites (25 located within the lagoon and 4 on the back reef; Sites 1–27, 31 and 33), and 4 coral-dominated reef sites (Sites 28, 29, 30 and 32) to confirm that *Xenopus margaritaceus* was restricted to the macroalgal meadow habitats (Fig. 1, and see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m590/p187\\_supp.pdf](http://www.int-res.com/articles/suppl/m590/p187_supp.pdf)). Within the constraints of the prevailing weather conditions, we haphazardly surveyed 25 of the same sites during the austral winter (August) of the same year (Table S1), which is typically when there is a seasonal decline in canopy-forming macroalgae across this region (Fulton et al. 2014, Lim et al. 2016). All sites were of similar shallow depth (mean  $\pm$  SE = 3.7  $\pm$  0.2 m).

### Fish abundance among macroalgal meadows

Fish abundance and habitat composition were surveyed on scuba or snorkel using the stationary point-census method of Noble et al. (2013). Each census involved laying a 5 m tape measure in a straight line, waiting on the edge for 3 min to allow the fish to return to normal behaviour and then recording the species and estimated total length (TL, to nearest cm) of all target fish that were present within the 5 m diameter cylinder and within 2 m above the benthos. Target species included *X. margaritaceus*, as well as fish that were their putative predators and competitors (Table S2). Following each visual fish survey, the habitat at the base of the survey cylinder was characterised in terms of percent cover composition, canopy height and density of canopy-forming macroalgae, and vertical relief of the hard substratum, which are relevant to fish occupying these macroalgal mead-

ows (Wilson et al. 2014, Lim et al. 2016). Percent cover benthic composition was measured as the distance occupied (to the nearest cm) by different habitat categories (macroalgae to genus, coral to functional growth form, sand, rubble and pavement) along a 5 m line transect bisecting each cylinder. Wherever canopy-forming macroalgae occurred, canopy height was measured (to nearest cm) as the vertical distance between the substratum and the naturally floating canopy at 1 m intervals along the same 5 m line transect, beginning at 0 m ( $n = 6$  transect<sup>-1</sup>). Density of canopy-forming macroalgae was quantified as the number of holdfasts within a 0.5  $\times$  0.5 m quadrat at the same 1 m intervals ( $n = 6$  transect<sup>-1</sup>). Vertical relief of the hard substratum was recorded using a numerical score from 0 to 5 adapted from Polunin & Roberts (1993) and Gratwicke & Speight (2005), where: 0 = flat, 1 = low relief (<10 cm depth/height of concavities/convexities), 2 = low-moderate relief (10–30 cm), 3 = moderate relief (30–60 cm), 4 = high-moderate relief (60–100 cm), and 5 = high relief (>100 cm). These paired surveys of fish and habitat took 7 to 12 min each, and were repeated 6 times at each site. Replicate cylinders were distributed haphazardly so that a minimum of 5 m separated the edges of adjacent cylinders and the habitat edge. At the start of each day, each observer conducted visual checks of their size estimates using stationary benthic objects, which indicated no significant difference between estimated and actual sizes (paired *t*-test:  $t_{100} = 0.98$ ,  $p = 0.33$ ).

### Microhabitat use

Microhabitat use by *X. margaritaceus* individuals was determined in summer and winter using instantaneous focal surveys (Fulton et al. 2001). This involved the observer swimming a non-overlapping haphazard path throughout a site, and recording for each individual encountered: fish TL (to nearest cm), behaviour during first 3 s of observation (Table S3) and the microhabitat type directly below the fish (rubble, sand, pavement, macroalgae to genus, coral to functional growth form). A minimum of 75 microhabitat observations were collected in summer for *X. margaritaceus* at each of 3 sites (Sites 33, 21 and 12). This was repeated in winter, although due to a general drop in abundance of *X. margaritaceus* at these sites, only 21 microhabitat observations were obtained for Site 21.

Microhabitat selectivity was explored using the electivity indices of Vanderploeg & Scavia (1979),

which were calculated as:  $E_i^* = [W_i - (1/n)] / [W_i + (1/n)]$ , where  $n$  is the number of microhabitat categories;  $W_i$  is the selectivity coefficient for microhabitat category  $i$ , calculated as  $W_i = (r_i/p_i) / (\sum_i r_i/p_i)$ , where  $r_i$  is the proportional use and  $p_i$  the proportional availability of the microhabitat category  $i$  at each site. Values of 0 indicate use of a microhabitat at roughly equal to availability (neutral selection), while positive and negative values indicate preference and avoidance for a microhabitat type, respectively. Electivity indices were averaged across the 3 sites to explore patterns of microhabitat association within the lagoon.

### Trophic resource use

Trophic resource use of *X. margaritaceus* was determined through (1) direct feeding observations recorded during the instantaneous focal surveys of microhabitat use in the wild (Table S3), and (2) gut contents of collected fish specimens, which were compared to the availability of potential prey within the macroalgae and benthic epilithic algal matrix (EAM, which is a mixture of algae, sediment, detritus and invertebrates). Twelve *X. margaritaceus* specimens of a range of sizes (45–116 mm TL) were collected during the austral summer in 2016 using a fine monofilament barrier net, then euthanized and preserved on ice within 1 h of capture before being frozen for transport back to the Australian National University for analysis. Individuals were collected from a single macroalgal meadow site (Site 33) to enable comparisons of dietary preferences relative to the prey availability at the same site, without disturbing our seasonal surveys of abundance changes at our other sites. In the laboratory, gut contents were carefully removed from the anterior half of the gut to minimise the effects of digestion bias in our estimates of the presence of hard and soft-bodied dietary items. Gut contents were spread as a single layer in a Petri dish in a square shape, and a 10×10 grid was overlaid that had 40 random squares visible for evaluation, following Bellwood et al. (2006). Using a stereo dissecting microscope with 10–40× magnification, the dominant dietary items (i.e. prey type occupying the largest proportional planform area) present within the 40 random squares were identified and then grouped into 10 functional categories: micro-Crustacea (<5 mm diameter, which included Amphipoda, Copepoda, Isopoda, Ostracoda, Tanaidacea), macro-Crustacea (>5 mm, principally Brachyura), micro-Bivalvia (<5 mm), micro-Gastro-

poda (<5 mm), Foraminifera, worms, sediment, amorphous organic matter (AOM), macroalgae and other (egg masses, unidentified fragments), following Bellwood et al. (2006).

Prey availability was determined for a range of abundant macroalgal genera and EAM at the same site where the fish specimens were collected. Six EAM samples and 6 whole macroalgal samples of each of *Sargassum*, *Padina*, *Dictyopteris* and *Lobophora* were collected at 6 random points (generated by Excel RAND function) located >1 m apart along a 30 m line transect at Site 33 in summer 2016. Winter samples of *Sargassum* and *Lobophora* were also collected at the same site ( $n = 6$  each). EAM samples were collected by scraping EAM into 100 ml plastic containers with a dive knife and sealing with a plastic zip-lock bag. Macroalgal collection involved placing a zip-lock bag carefully over an entire macroalgal specimen, then carefully levering the holdfast off the substratum using a dive knife and sealing the bag immediately to trap all associated epifauna (Christie et al. 2009). Excess water was carefully poured off after an overnight settling period, then the entire samples were frozen for transport to the Australian National University for detailed analysis. Epifauna associated with the macroalgae were extracted by washing and shaking the defrosted macroalgae vigorously with saline water in the plastic bag, and then pouring this water through a 120 µm mesh filter. This was repeated 2–3 times per specimen to ensure all epifauna were dislodged, which Norton & Benson (1983) found to effectively remove the majority of all motile epifauna. Macroalgal epifauna and EAM infauna were individually picked out from the sediment and detritus under a dissecting microscope, and identified into the same prey categories used to assess the fish gut contents. Wet volumes of the host macroalgae were then measured to the nearest ml via water displacement in a measuring cylinder, after the initial removal of water from the macrophyte sample using a salad spinner.

### Data analyses

Site-level differences in summer fish abundance and habitat were explored using permutational multivariate ANOVA (PERMANOVA). Coral-dominated sites were excluded from the analysis, as *X. margaritaceus* was entirely absent from this habitat type. In the first instance, separate PERMANOVAs with site as a random factor were conducted for the variables: (1) *X. margaritaceus* juvenile ( $\leq 4$  cm TL, based on

juvenile colouration; Kuitert 2002) and adult densities, (2) habitat composition and structure, (3) putative competitor fish density and (4) putative predator fish density. For the fish variables, resemblance matrices were constructed using a modified Gower (base 2) dissimilarity measure (which emphasises a doubling in abundance as a major change in community structure) on square-root transformed data (Anderson et al. 2006). Habitat composition and structure included all measured habitat variables (canopy height and density, with associated coefficients of variation, percent cover of each benthic category, and vertical relief). Due to the different measurement scales of the habitat variables (% , cm, cm<sup>2</sup>), habitat data were normalized against the mean for each variable across all sites, then constructed into a resemblance matrix using Euclidean distance (Anderson et al. 2008). Abiotic substratum types (pavement, sand, rubble) were excluded, as they were strongly inversely correlated with macroalgal cover ( $r = -0.98$ ). Several minor understory macroalgae (*Turbinaria*, *Hormophysa*, *Hydroclathrus*, *Sporochnus*, *Udotea*, *Caulerpa*, *Halimeda*, *Penicillus*, *Codium*, *Galaxaura*, *Jania*, *Laurencia*, *Asparagopsis* and *Hypnea*) were combined into 'other macroalgae', as together they represented an average of 1.4% of total benthic cover. Similarly, sponges and seagrass (*Halophila*) were grouped as 'other biota'. Predators were piscivorous species that were classified as mobile or ambush predators based on their predominant hunting strategy; 'strong' or 'weak' fish competitors were classified according to whether they consumed high or low amounts of the same micro-invertebrate prey as *X. margaritaceus* (Lieske & Myers 1994, Kuitert 2002, Bellwood et al. 2006; Table S2).

To determine which habitat, competitor or predator variables may best predict variations in the summer abundance of *X. margaritaceus* across all 29 macroalgal meadow sites, a best subsets model selection process was conducted using distance-based linear modelling (DistLM). This method considered all possible combinations of habitat predictors, and the most parsimonious model was selected as the one with the fewest variables within 2 Akaike information criterion corrected for finite samples (AICc) points of the lowest AICc of all possible models, following Burnham & Anderson (2002). The relative importance of each habitat predictor was also explored by summing the AICc model weights across all models containing that variable. Variations in *X. margaritaceus* densities were visualised for the most parsimonious model using a distance-based redundancy analysis (dbRDA) ordination.

Seasonal changes in fish and habitat composition for the subset of 21 macroalgal meadow sites re-surveyed in winter were examined using PERMANOVA, with site and season as random and fixed factors, respectively, for the same 4 groups of fish and habitat variables examined for the summer data (details above). All PERMANOVAs were conducted using Type III sum of squares and a maximum of 9999 permutations, and run in Primer (version 6.1.16) with Permanova+ (version 1.0.6).

Variations in the epifaunal prey available for *X. margaritaceus* foraging within a macroalgal meadow during summer were examined with analysis of similarity (ANOSIM), following Clarke & Gorley (2006). Epifauna substratum type (*Sargassum*, *Lobophora*, *Dictyopteris*, *Padina* and EAM) was a fixed factor, and we used 9999 permutations of a Bray-Curtis resemblance matrix constructed from the  $\text{Log}_{10}(x + 1)$  transformed volumetric density of 9 epifauna functional groups (as described for gut content analysis above, minus the macroalgae group). Seasonal changes in the epifaunal community on the *Sargassum* and *Lobophora* macroalgal hosts was also examined via ANOSIM, with substratum type nested within season as a fixed factor and 9999 permutations on the same type of resemblance matrix and data transformation. To explore potential dietary preferences, proportional consumption of prey types by *X. margaritaceus* was compared to proportional prey abundance on *Sargassum* and *Lobophora*, their preferred feeding microhabitats (following Manly et al. 2002). Proportions of prey available to a foraging *X. margaritaceus* were calculated from the number of epifaunal individuals within a category divided by the total number of epifauna found on each *Sargassum* or *Lobophora* sample. These were then averaged across all samples for each epifaunal host macroalgal genus. Availability of sediment and algae was calculated as the mean percentage cover of each category from the benthic line transects conducted at Site 33 in each of summer and winter. The only exception was availability of AOM, which was not quantified in the epifauna or benthic surveys.

## RESULTS

### Fish abundance among macroalgal meadow habitats

*Xenajulis margaritaceus* were found exclusively within macroalgal meadows over both summer and winter, and were never observed in coral-domi-



nated habitats (Fig. 2). While the distribution of juveniles overlapped with adults (Fig. 2A), they were generally rare across all sites in both summer (mean  $\pm$  SE:  $0.08 \pm 0.02$  fish  $20 \text{ m}^{-2}$  site $^{-1}$ ) and winter ( $0.23 \pm 0.05$ ). Significant differences in *X. margaritaceus* densities were apparent among macroalgal sites during summer (pseudo- $F_{28,145} = 3.51$ ;  $p < 0.001$ ), with mean densities ranging from 0 to 3.8 ind.  $20 \text{ m}^{-2}$  site $^{-1}$  (Fig. 2A). Significant variation was also evident in habitat structure and composition (pseudo- $F_{28,145} = 5.21$ ,  $p < 0.001$ ; Fig. 2B,C), as well as the abundance of their fish predators (pseudo- $F_{28,145} = 4.76$ ,  $p < 0.001$ ; Fig. 2D) and competitors (pseudo- $F_{28,145} = 4.94$ ,  $p < 0.001$ ; Fig. 2D). Best-subsets model selection indicated that a combination of 6 predictors (canopy height, strong competitors, mobile predators and percent cover of *Dictyopteris*, *Dictyota* and *Lobophora*) provided the best explanation for variations in *X. margaritaceus* density across macroalgal sites (Fig. 3, Table S4). In particular, higher densities of *X. margaritaceus* were associated with taller macroalgal canopies and higher densities of strong competitors (Fig. 3B), with marginal tests indicating that these 2 predictors explained the highest amounts (15 and 11%, respectively) of the summer variation in *X. margaritaceus* density across sites.

Seasonal comparisons for a subset of 21 sites revealed significant interactions between site and season for *X. margaritaceus* abundance and macroalgal habitat structure and composition (Table 1). The mean density ( $\pm$  SE) of *X. margaritaceus* displayed an overall decline of 40% from summer ( $0.83 \pm 0.22$  fish  $20 \text{ m}^{-2}$ ) to winter ( $0.50 \pm 0.14$ ). However, this was not consistent across all sites (Table 1). Although there were general declines in macroalgal habitat structure and composition in terms of canopy height ( $19.9 \pm 0.9$  to  $12.0 \pm 1.3$  cm), canopy density ( $5.1 \pm 0.3$  to  $3.2 \pm 0.3$  holdfasts

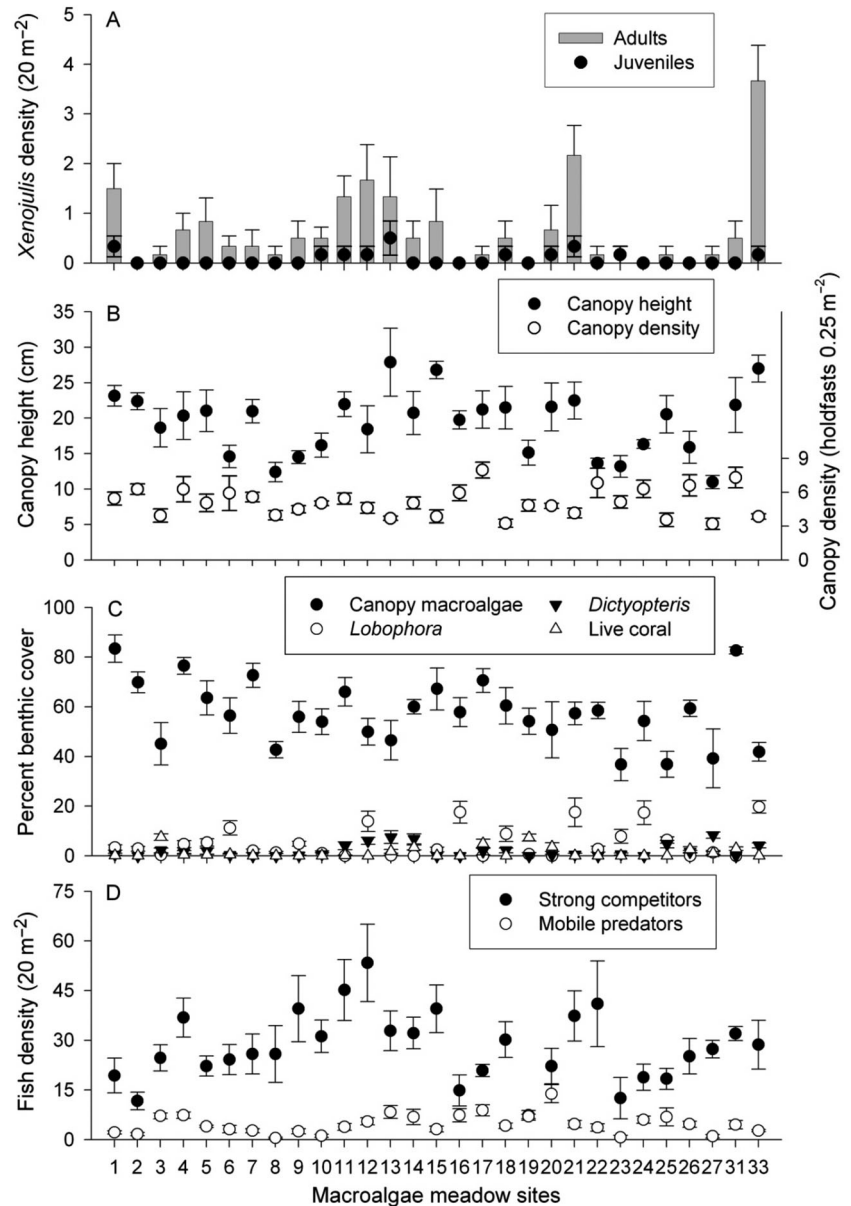


Fig. 2. Fish abundance and habitat composition across macroalgal meadow sites at Ningaloo during summer, in terms of (A) density of *Xenojulis margaritaceus* juveniles and adults, (B) height and density of canopy-forming macroalgae, (C) percent cover of benthic organisms and (D) density of fishes that may be strong competitors and predators of *X. margaritaceus* (see Table S2 in the Supplement at [www.int-res.com/articles/suppl/m590p187\\_supp.pdf](http://www.int-res.com/articles/suppl/m590p187_supp.pdf)). All errors are standard errors of the mean ( $n = 6$  site $^{-1}$ ). Sites 28–30 and 32 were coral-dominated sites (Fig. 1) where no *X. margaritaceus* were recorded

$0.25 \text{ m}^{-2}$ ) and canopy cover ( $57.8 \pm 2.9$  to  $26.3 \pm 3.9\%$ ) from summer to winter, these were inconsistent among sites. Seasonal change in *X. margaritaceus* density was significantly correlated to the extent of seasonal canopy height variation among sites (Fig. 4), but not any other habitat or predator/competitor variable.

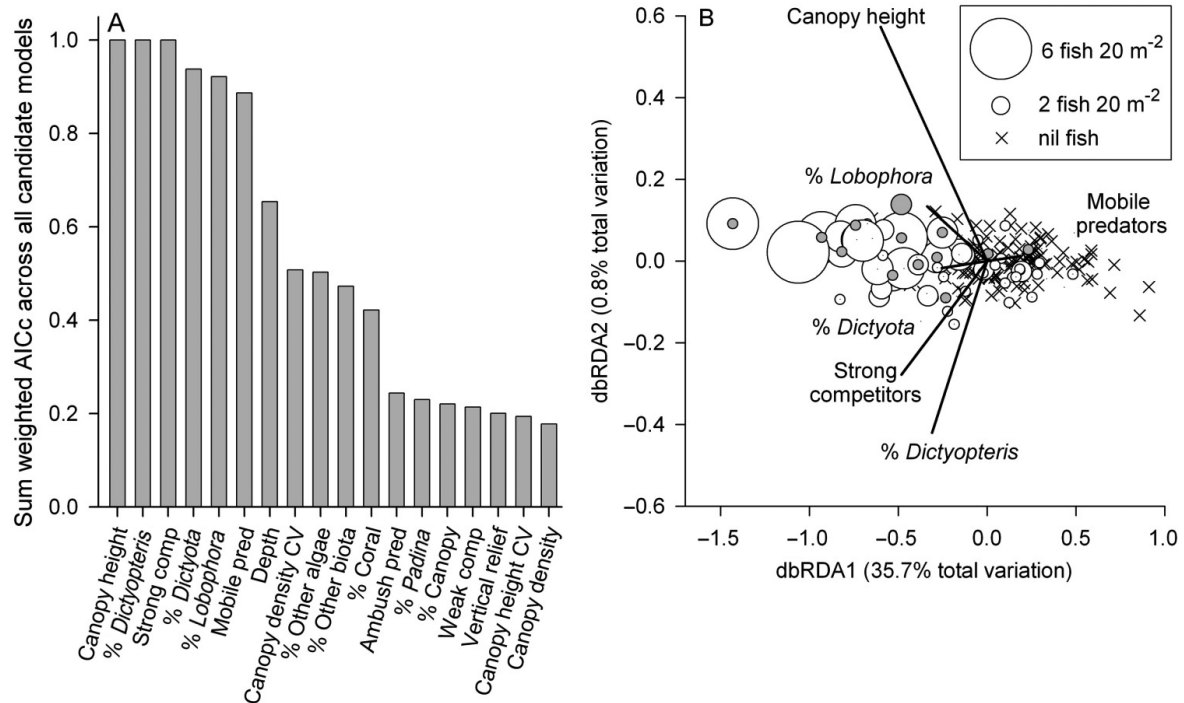


Fig. 3. Summary of (A) summed model weights for all predictor variables and (B) distance-based redundancy analysis (dbRDA) ordination of the most parsimonious model explaining variation in *Xenojulis margaritaceus* juvenile (grey) and adult (white) densities (indicated by bubble sizes) across 29 macroalgal sites at Ningaloo during summer. Correlations between the ordination structure and the best model predictors of macroalgae canopy height, % cover of *Lobophora*, *Dictyota* and *Dictyopteris*, and strong competitors and mobile predators are indicated as vector overlays

### Seasonal microhabitat use

*X. margaritaceus* exhibited distinct microhabitat preferences within macroalgal meadows that appeared to shift in tendency and variance across the 2 seasons. During summer, the majority of *X. margaritaceus* individuals ( $n = 435$  total across all sites) were observed using canopy macroalgae (predominantly *Sargassum*), with relatively few occupying understorey macroalgae (mostly *Lobophora* and *Dictyopteris*) or abiotic components of the substratum (Fig. 5A). Electivity indices for the summer observations supported these findings to reveal a strong preference by *X. margaritaceus* for canopy macroalgae during summer, and either avoidance (negative electivity) or neutrality (zero electivity) towards understorey macroalgae and abiotic components of the substratum (Fig. 5B). During winter, the quality of canopy macroalgae decreased at the focal sites (typically down to bare stipes). Accordingly, the proportion of *X. margaritaceus* individuals ( $n = 320$  total) observed using canopy macroalgae decreased during winter, and with a consistently low use of the abiotic components of the substratum in both summer and winter, the proportional occupation of under-

storey macroalgae by *X. margaritaceus* tripled in winter (Fig. 5A). Electivity indices, which take into account shifts in microhabitat availability, revealed that *X. margaritaceus* displayed increased variance in their electivity, with a slightly stronger preference for understorey macroalgae during winter (although still neutral when considering the among-site errors), and neutral preference for canopy macroalgae and understorey *Dictyota* (Fig. 5B).

### Trophic resource use

Availability of macroalgal epifaunal prey, in terms of volumetric density of the 9 prey functional groups, differed significantly among macroalgal hosts (ANOSIM global  $R = 0.481$ ,  $p < 0.01$ ), primarily due to the EAM displaying markedly lower epifaunal densities than the other macroalgal categories (Fig. 6A). Overall volumetric densities were quite variable within each genus of macroalgal host (Fig. 6A). The most diverse and abundant epifauna were found on individuals of the canopy-forming *Sargassum*, where epifaunal abundance tended to increase linearly with *Sargassum* volume, particularly micro-Crustacea ( $r =$

Table 1. Summary of PERMANOVAs comparing the density of *Xenajulis margaritaceus* juveniles and adults, their putative competitors (see Table S2 in the Supplement at [www.int-res.com/articles/suppl/m590p187\\_supp.pdf](http://www.int-res.com/articles/suppl/m590p187_supp.pdf)), putative predators (Table S2) and macroalgal habitat structure and composition among 21 meadow sites at Ningaloo across the 2 seasons of summer and winter

Source	df	SS	MS	Pseudo-F	p
<b><i>X. margaritaceus</i></b>					
Site	20	29.15	1.46	6.33	<0.001
Season	1	2.29	2.29	3.40	0.06
Site × Season	20	13.49	0.67	2.93	<0.001
Residual	210	48.35	0.23		
Total	251	93.29			
<b>Putative competitors</b>					
Site	20	45.58	2.28	7.01	<0.001
Season	1	34.01	34.01	29.50	<0.001
Site × Season	20	23.06	1.15	3.55	<0.001
Residual	210	68.26	0.33		
Total	251	170.92			
<b>Putative predators</b>					
Site	20	47.04	2.35	5.97	<0.001
Season	1	40.37	40.37	20.09	<0.001
Site × Season	20	40.19	2.01	5.10	<0.001
Residual	210	82.71	0.39		
Total	251	210.30			
<b>Habitat structure and composition</b>					
Site	20	1367	68.37	11.66	<0.001
Season	1	263	262.69	8.05	<0.001
Site × Season	20	652	32.62	5.56	<0.001
Residual	210	1231	5.86		
Total	251	3514			

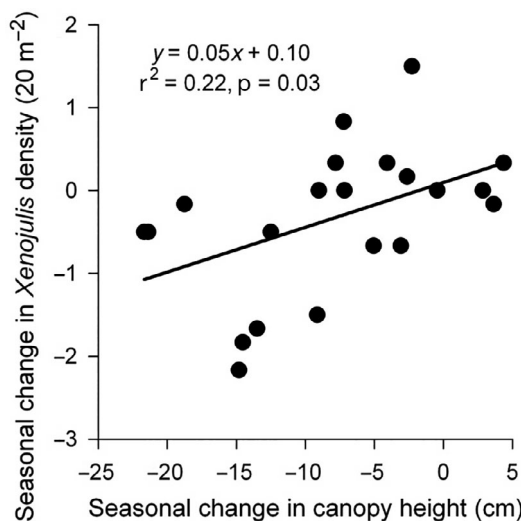


Fig. 4. Least-squares linear relationship between seasonal change (summer to winter) in *Xenajulis margaritaceus* density and macroalgae canopy height across 21 macroalgal sites

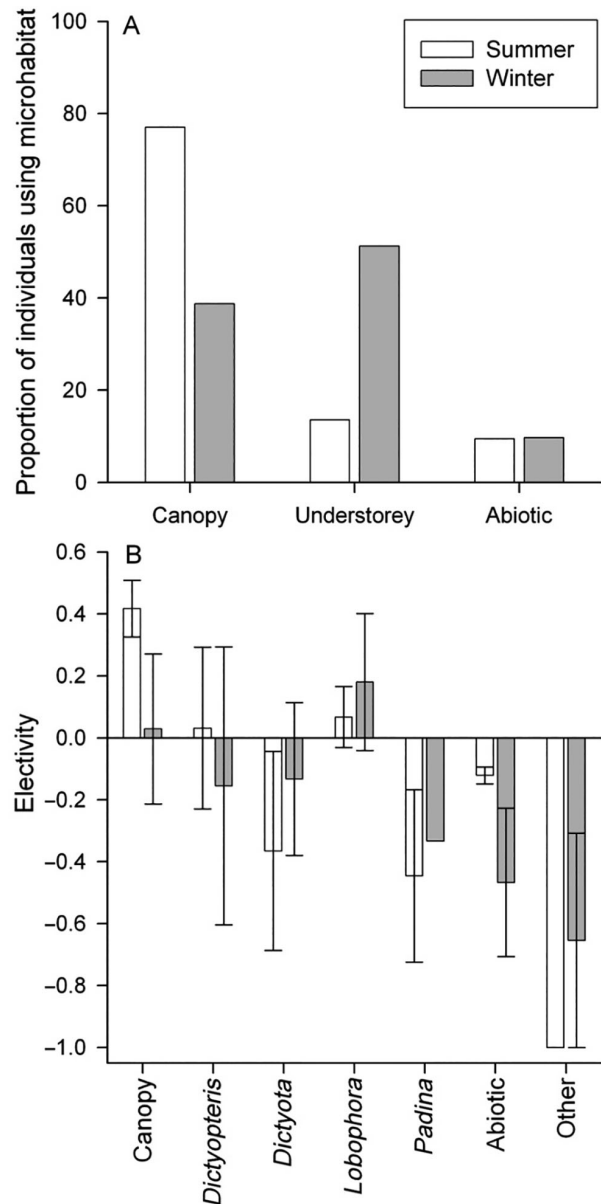


Fig. 5. Seasonal microhabitat use by *Xenajulis margaritaceus* as indicated by (A) proportion of individuals observed using different microhabitat types, and (B) electivity towards these same microhabitats, averaged ( $\pm$ SE) across 3 macroalgal sites. Additional detail for understorey algae is provided in Fig. S1 in the Supplement

0.920,  $p = 0.009$ ) and worms ( $r = 0.948$ ,  $p = 0.016$ ; Fig. 6B). Epifaunal volumetric density on *Lobophora* and *Sargassum* differed significantly among seasons (ANOSIM global  $R = 0.685$ ,  $p < 0.01$ ), but not among the 2 macroalgal genera (ANOSIM global  $R = 0.035$ ,  $p = 0.28$ ), largely due to reductions in the winter density of forams, gastropods and bivalves on both *Sargassum* and *Lobophora*, and the large inter-individual variation within seasons. However, overall



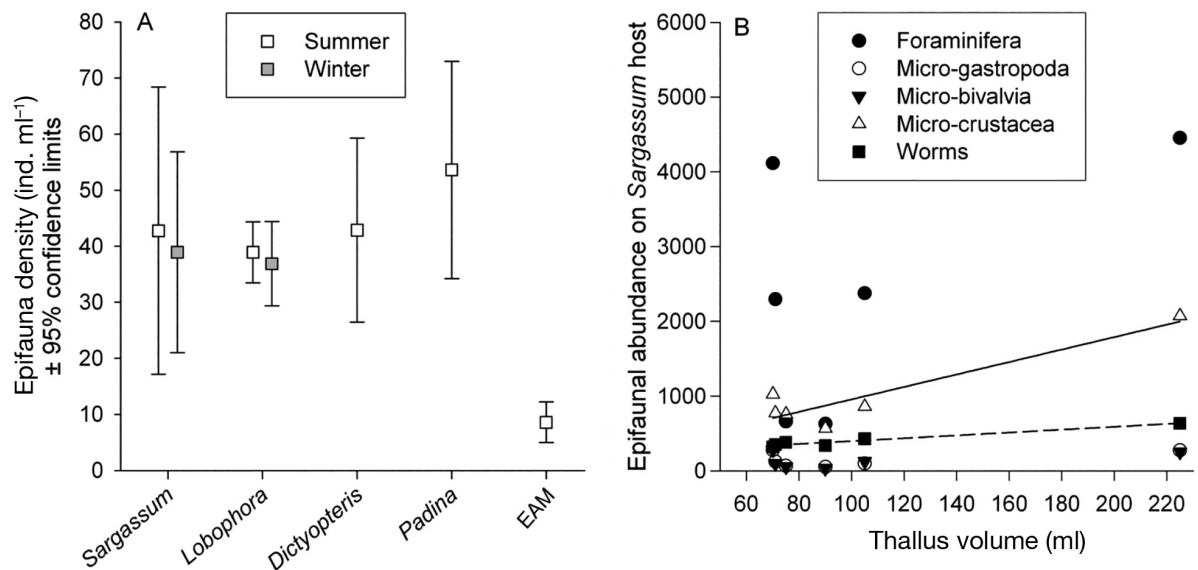


Fig. 6. (A) Mean volumetric density of epifauna on 4 macroalgae hosts and within the epilithic algal matrix (EAM) during summer, with seasonal comparisons for the canopy-forming *Sargassum* and understory *Lobophora*. (B) Epifaunal prey availability versus volume of the *Sargassum* host macroalgae, with the significant relationships for micro-Crustacea (solid line) and worms (dashed line) indicated

epifaunal abundance (rather than density) did shift dramatically among these 2 macroalgal hosts: an average reduction of 80% in the canopy volume of *Sargassum* from summer to winter ( $106 \pm 24$  to  $22 \pm 5$  ml) was linked to a major (~83%) drop in total epifauna abundance ( $4210 \pm 980$  to  $690 \pm 120$ , respectively); *Lobophora* had the reverse trend, with canopy volume ( $21 \pm 3$  to  $28 \pm 4$  ml) and overall epifaunal abundance ( $815 \pm 126$  to  $976 \pm 108$ , respectively) increasing during winter. By far the most abundant epifauna on these 2 macroalgal genera were Foraminifera (mostly brown, cf. *Amphistegina*), which represented up to 68% of all fauna in a given sample in summer (mean = 53%). Other common fauna included harpacticoid copepods (15%), tanaids (8%), polychaetes (5%), gammarid amphipods (3%), micro-gastropods (3%), micro-bivalves (3%), nematodes (2%) and isopods (2%; Fig. 7).

The majority of *X. margaritaceus* gut contents were dominated by AOM (mean  $\pm$  SE =  $40 \pm 2\%$ ) and micro-Crustacea ( $20 \pm 6\%$ ), followed by sediment, macroalgal fragments, micro-Gastropoda and worms (Fig. 7). Behavioural observations confirmed that the majority of foraging behaviour by *X. margaritaceus* was directed

towards macroalgae (91% of 143 feeding and searching observations across summer and winter), with only 9% of individuals searching or feeding upon the abiotic (pavement, sand, rubble) components that covered on average 25–60% (summer to winter, respectively) of the substratum within the macroalgal meadows. During summer, the majority of foraging

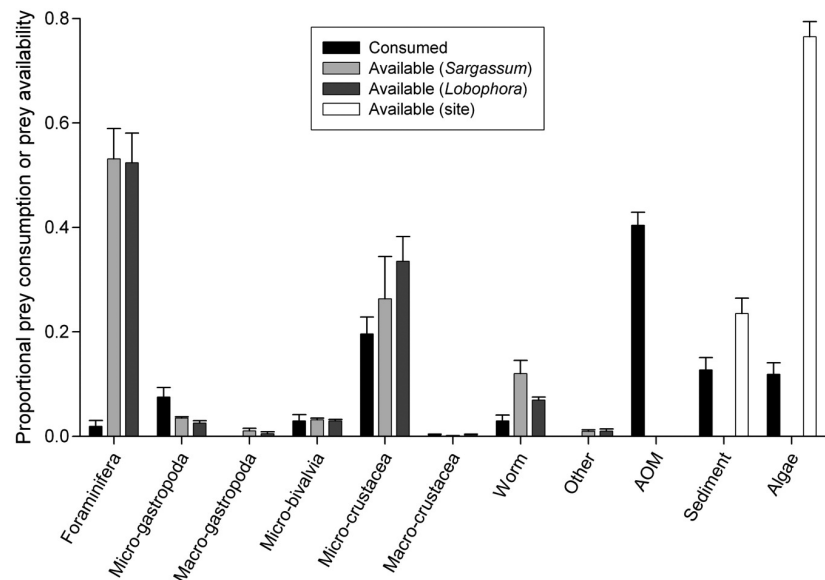


Fig. 7. Mean ( $\pm$ SE) proportion of epifaunal prey categories consumed by *Xenopus margaritaceus*, alongside the summer availability of these same prey categories on *Sargassum* and *Lobophora* macroalgae hosts, or within the same macroalgal site (sediment, macroalgae) as indicated by line transects. No estimate of environmental availability could be obtained for amorphous organic matter (AOM)

behaviour by *X. margaritaceus* was directed towards *Sargassum* (74 % of observations); the top microhabitats for foraging behaviour in winter were both *Lobophora* (33 %) and *Sargassum* (30 %). Comparison of *X. margaritaceus* diet with the abundance of prey on *Sargassum* and *Lobophora* (canopy-forming and understory macroalgae most frequently used by *X. margaritaceus*) suggests that *X. margaritaceus* appear to be consuming micro-Crustacea and micro-Bivalvia at roughly the same proportion as they are available on the macroalgal hosts, and micro-Gastropoda at higher proportions than available (Fig. 7). Notably, the abundance of some of these epifauna was related to the size of the macroalgal hosts (Fig. 6B). In contrast, *X. margaritaceus* consumed far less macroalgae and sediment than were available within the macroalgal meadow (Fig. 7).

## DISCUSSION

Habitat heterogeneity is a prominent feature of many coastal seascapes, including Ningaloo (Kobryn et al. 2013), where we found clear links between variations in macroalgal habitat and the abundance of a tropical reef fish over space and time. In *Xenojulis margaritaceus*, we found a habitat specialist that exclusively occupied macroalgal meadows as juveniles and adults, and throughout major seasonal changes in canopy habitat structure. Behavioural and gut content analysis also indicated a trophic dependence on macroalgal epifauna. During summer, *X. margaritaceus* preferentially occupied the canopy-forming macroalgae *Sargassum*, the height of which provided a key habitat-based predictor for fish abundance across the seascape, alongside variations in predator and competitor fish abundance. Due to this tendency to specialise towards macroalgal habitats of a certain quality, *X. margaritaceus* displayed significant seasonal declines in abundance according to the extent of macroalgal canopy loss within each meadow during winter. While this seasonal trend was congruent with that found in a herbivorous fish that is also a macroalgal meadow specialist (Lim et al. 2016), the carnivorous *X. margaritaceus* displayed a less severe response to canopy habitat loss. Related to this, the percent cover of understory macroalgae was also a key predictor for *X. margaritaceus* abundance across the seascape, presumably due to their use of this microhabitat type under various macroalgal canopy states. Similar links to understory macroalgae have been reported in other carnivorous reef fishes (e.g. Levin 1994, Taylor

1998, Pérez-Matus et al. 2016), which has often been attributed to the availability of trophic resources in these understory microhabitats. Moreover, *X. margaritaceus* abundance was less strongly correlated to canopy cover and holdfast density, which contrasts with evidence of these metrics being important for other macroalgae-associated fishes (Anderson 1994, Levin & Hay 1996, Wilson et al. 2014). This reinforces that although a range of species may exclusively occupy the same habitat type, different qualities of that habitat may be important for each species.

Variation in macroalgal canopy height was one of the best predictors of *X. margaritaceus* abundance, which adds to a growing body of evidence for positive relationships between fish abundance and macroalgal canopy extent (Levin & Hay 1996, Ornelas & Coutinho 1998, Lim et al. 2016). In tropical systems, this is significant because canopy-forming macroalgae such as *Sargassum* typically display seasonal fluctuations in biomass and height (Fulton et al. 2014). However, these changes in macroalgal canopy extent are not consistent across all sites, such that a complex mosaic of meadow habitat quality occurs across the seascape (Wilson et al. 2014, Lim et al. 2016, this study). In microhabitat specialists, this heterogeneity in habitat quality across the landscape can manifest in large-scale variations in distribution and abundance, and create localised habitat refugia where populations can persist across seasons and years (Brown et al. 1995, Resetarits 2005, Lim et al. 2016). Indeed, we found that *Sargassum* meadows with the largest reductions in canopy height during winter had the deepest population declines in *X. margaritaceus*. Given that we surveyed all of the available macroalgal meadows within this region, and no individuals were found in coral-dominated habitat, we are left to conclude that the declines in *X. margaritaceus* abundance were due to increased mortality within canopy-denuded meadows. Such mortalities may arise from increased susceptibility to predation, and/or a reduction in macroalgal epifaunal prey resources. To what extent these relationships may arise from shifts in habitat-related reproductive success and/or recruitment of this species remains unknown, and should be a priority for future work. While we have no evidence here of shifts in predation pressure with macroalgal canopy extent, we note that evidence from seagrass beds suggests that macrophyte canopy height may not be a major factor in piscivore prey capture success, and therefore, predator-related fish mortality (Horinouchi 2007, Horinouchi et al. 2013). However, we can look to evidence for a trophic mechanism to discover why

canopy declines may affect the capacity for a macroalgal meadow to sustain *X. margaritaceus* in the face of competition from other micro-carnivorous fishes.

Strong links between patterns of habitat use and preferred dietary resources are well documented for a range of fish species and habitats (e.g. McIvor & Odum 1988, Morton et al. 2008, Pratchett et al. 2004). In our study, a suite of evidence indicated that *X. margaritaceus* predominantly foraged for invertebrate epifaunal prey living on a range of macroalgal genera, particularly *Sargassum* and *Lobophora* (Randall & Adamson 1982, Kuitert 2002). While limited to a single site in our region, our assessment of prey availability found that the type (genus) of macroalgal host was largely irrelevant for epifaunal prey density, but host macroalgal thallus volume was a significant predictor of epifaunal abundance. As a consequence, larger macroalgae tended to house higher overall numbers of epifaunal prey for *X. margaritaceus*, which is congruent with epifaunal assessments of other tropical and temperate macroalgal taxa (Edgar 1983, Tano et al. 2016, Kramer et al. 2017). Accordingly, canopy-forming macroalgal genera had the greatest potential for *X. margaritaceus* to find large amounts of epifaunal prey during peak canopy state in summer, with an individual *Sargassum* housing around 8000 individual epifauna. During winter, however, the total number of epifauna present per *Sargassum* host at Ningaloo decreased by around 80%, which is comparable to estimates from temperate ecosystems that found total micro-invertebrate abundance decreases by an order of magnitude from summer to winter (Edgar 1983). By contrast, biomass of understory algae, such as *Lobophora*, tends to increase and even exceed that of *Sargassum* in winter (Fulton et al. 2014). As such, carnivorous fishes such as *X. margaritaceus* may be just as likely to find their preferred micro-crustacean food in these erect forms of understory macroalgae during winter (Edgar 1983, Edgar & Klumpp 2003, Kramer et al. 2017). This helps explain the seasonal shifts in foraging microhabitat use in *X. margaritaceus*, which afforded some versatility for this carnivorous fish to respond to macroalgal habitat change, which is not available to herbivorous fish dependent on certain palatable macroalgal taxa. Such seasonal switches in resource use can be an effective response to changing habitat quality and quantity (Jedlicka et al. 2006, Dirnwöber & Herler 2007). However, our evidence does suggest that in this species, such resource switching was still limited to a small suite of erect macroalgae to support their dietary needs. Indeed, we note that the sediment-laden EAM in which the macroalgal meadows

were embedded, and which was often the dominant microhabitat in terms of benthic cover, was not a favoured foraging microhabitat for *X. margaritaceus*. Unlike the diverse and abundant crustacean communities within sediment-free EAM on coral reefs, which are targeted by many reef fishes (Kramer et al. 2014, 2015), sediment-filled EAM provides a relatively poor microhabitat for benthic micro-carnivores to find prey (Bellwood & Fulton 2008).

Collectively, this evidence suggests that meadow carrying capacity may be a key factor in shaping the population dynamics of macroalgae-associated fauna. Primary production by canopy-forming *Sargassum* supports extensive secondary production within their epiphytic fauna (Edgar 1990, Martin-Smith 1994, Edgar & Klumpp 2003), which tend to reach an equilibrium in biomass and productivity due to a primary production resource ceiling (Edgar & Aoki 1993). Given the dynamic nature of canopy-forming *Sargassum*, changes in thallus volume translate to major changes in this resource ceiling available to herbivores (including both epiphytic fauna and fishes), which then flows through to the production of epifaunal prey biomass for higher-order consumers like carnivorous fishes (Edgar & Aoki 1993, Taylor 1998, Koenigs et al. 2015). Through this trophic pathway, there is strong potential for bottom-up effects within macroalgal habitats to be driving the population dynamics of a suite of both herbivorous and carnivorous macroalgae-associated fishes (Christie et al. 2009, Koenigs et al. 2015, Merkle et al. 2016). Attempts to quantify how variation in macroalgal primary production may affect the productivity of middle and upper level consumers are rare (Edgar & Aoki 1993, Taylor 1998), yet they highlight the potential consequences of losing canopy-forming macroalgal habitats in coastal ecosystems (Koenigs et al. 2015).

In identifying the key role of habitat-forming macroalgae in coastal ecosystems, we find real concern in the threat of climate anomalies for the future of macroalgae-dependent fauna and ecosystem processes (Wernberg et al. 2016). In tropical *Sargassum*, studies from around the world have shown that the timing and extent of canopy growth and decay are closely linked to seasonal and inter-annual variations in sea surface temperature (Glenn et al. 1990, Ateweberhan et al. 2005, Fulton et al. 2014). And while macroalgal growth is seen as a threat to biodiversity on coral reefs, these macroalgal meadows do naturally occur along tropical and temperature coastlines as a complementary part of the seascape, where they support macroalgae-dependent species of commercial value and conservation concern (Aburto-

Oropeza et al. 2007, Eggertsen et al. 2017, Wilson et al. 2017). Our study joins these examples in the literature to emphasise that tropical fishes can be specialised towards non-coral habitat types as well as coral (Rossier & Kulbicki 2000). Indeed, we now know that both carnivorous and herbivorous fishes can depend on macroalgal habitats for food and shelter to the extent that major changes in abundance occur in response to macroalgal canopy habitat loss (Wilson et al. 2014, 2017, Lim et al. 2016). Given the risk posed by shifting trends in average and extreme sea surface temperatures, storms and other disturbances (McClanahan 2002, Hwang et al. 2004, Wernberg et al. 2016), we need to assess the consequences for macroalgal habitat quality, tropical biodiversity and key ecosystem services like fishery replenishment. For now, we suggest that macroalgal meadows be considered a key habitat type in holistic examinations of their role and influence across seascapes (Rossier & Kulbicki 2000, Berkström et al. 2012), and that both macroalgal and coral habitats be given equal priority for spatial conservation and management. In doing so, we recommend using a suite of macroalgal canopy metrics as measures of habitat quality for monitoring and predicting changes in macroalgae-associated biodiversity and ecosystem processes.

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