



Foraging microhabitat preferences of invertivorous fishes within tropical macroalgal meadows: identification of canopy specialists

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Abstract Invertivorous fishes are key middle-order consumers that connect energy flows across different trophic levels. However, the potential for distinct functional roles to exist within this trophic guild has not been satisfactorily explored to date, meaning that current assessments of ecosystem resilience are likely to over-estimate the level of functional redundancy within a given invertivorous fish assembly. Our study examined the foraging behaviour and microhabitat preferences of invertivorous fish communities within the productive canopy macroalgal meadows of Ningaloo Marine Park, Western Australia. Our aim was to identify foraging specialisations that could yield distinct functional roles for species belonging to the guild. We found that invertivorous fishes at this location were chiefly represented by species belonging to the Labridae, Lethrinidae and Mullidae families. Individual species demonstrated strong preferences for foraging within specific microhabitat types, suggesting that the guild can be grouped into three categories of foraging specialists: ‘canopy forager’, ‘generalist’ and ‘abiotic forager’. Our results highlight subtle niche partitioning of foraging microhabitats within the trophic guild of invertivorous fishes associated with tropical macroalgal meadows. Moreover, this partitioning is consistent across

seasons, despite significant fluctuations in canopy structure and biomass. The resulting refinement of foraging specialisations allows us to identify the functional roles of invertivorous fishes and afford greater protection to individual species that might otherwise be considered functionally redundant. Our results will help to inform knowledge of the functional impact of particular species and their ecological specialisations and improve our understanding of trophic flows in marine food webs for appropriate management and conservation.

Keywords Invertivore · Canopy forager · Abiotic forager · Canopy-forming macroalgae · Ecosystem resilience · Functional complementarity

Introduction

In marine ecosystems, invertivorous fishes (i.e. species that primarily feed on invertebrates) can represent one of the dominant feeding guilds (Longo et al. 2019; Parravicini et al. 2020). For example, nearly 70% of fish species on the Great Barrier Reef, Australia, have been classified as feeding predominantly on invertebrates (Randall et al. 1997; Kramer et al. 2015; Froese and Pauly 2021). The overall guild of invertivorous fishes comprises a diverse range of families, many of which are commonly fished (Sumner et al. 2002; Fulton et al. 2020; Froese and Pauly 2021). Invertivorous fishes have been shown to connect energy flows between primary producers and higher-order consumers, as they are predators that feed on invertebrates supported by primary production, but are themselves also the target prey of mesopredatory piscivores and apex predators (Edgar and Aoki 1993; Newcombe and Taylor 2010; Ashworth et al. 2014; Bergström et al. 2016; Froese and Pauly 2021). The trophic

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links facilitated by invertivorous fishes therefore underpin fundamental processes of marine ecosystem functioning that can influence global recreational and commercial fishery stocks (Lewis and Anderson 2012; Fulton et al. 2020; Froese and Pauly 2021).

The identification of essential habitats used by fishes is a critical step in the process of ecosystem-based fishery management of commercially and recreationally important species (Beck et al. 2001; Thrush and Dayton 2010; Wilson et al. 2017). Foraging behaviour is a key aspect of habitat use by fishes and can be documented as preferences relating to particular microhabitat types (Krajewski and Floeter 2011; Fulton et al. 2016; Kramer et al. 2016). For example, strong dependency on preferred microhabitats can lead to dramatic changes in the temporal and spatial dynamics of fish populations or communities following shifts in the availability of those preferred microhabitats. Local extinction of some coral reef fish species can occur when the corals they exclusively prey on are no longer available (Westmacott et al. 2000; Pratchett et al. 2018), and carnivorous fishes can also be vulnerable to the loss of preferred foraging microhabitats (Munday 2004; Wilson et al. 2008a; Wenger et al. 2018). In addition to that, documenting species' microhabitat specialisations is fundamental to defining their 'ecosystem function' in terms of positioning along the feeding niche resource axis (MacArthur 1958; Hutchinson 1959). The monitoring and management of marine ecosystems is increasingly based around the protection of critical functional groups (Green and Bellwood 2009; Graham et al. 2013; Villéger et al. 2017), where a species' ecosystem function is defined based on its ecological traits (Bellwood et al. 2019). This approach has led to the recognition that members of particular trophic groupings are not ecological equivalents. For example, on coral reefs, the group of fishes previously defined collectively under the trophic status of 'herbivore' has now been carved up into many different ecosystem functions, based on factors such as mode of feeding ('scrapers' versus 'excavators' (Bellwood and Choat 1990), 'grazers' versus 'browsers' (Choat et al. 2002; Fox and Bellwood 2008; Green and Bellwood 2009; Hoey and Bellwood 2009) and 'croppers' (Green and Bellwood 2009) or on microhabitat preferences ('crevice feeders' versus 'open matrix feeders' (Fox and Bellwood 2013; Brandl and Bellwood 2014), 'leaf-biters' versus 'thallus biters' (Streit et al. 2015). This process of trophic group refinement into functional groupings can help to provide a more accurate assessment of ecosystem resilience, by identifying species that perform unique ecosystem functions and yielding a more conservative estimate of the level of functional redundancy associated with the biodiversity present within a particular community structure (Cheal et al. 2010, 2012; Rasher et al. 2013).

Within tropical seascapes, invertivorous fishes have the potential to exploit heterogeneous microhabitats to feed on

epifaunal and infaunal invertebrates (Kwak et al. 2015; van Lier et al. 2018; Sambrook et al. 2019). Although strong microhabitat preferences of tropical invertivorous fishes driven by specific dietary targets have previously been documented (Lukoschek and McCormick 2001; Wilson et al. 2008b; Wenger et al. 2018), most studies to date on the microhabitat utilisation of these invertivorous fishes either have focused on well-studied habitats, such as coral reefs, or have looked only at the microhabitat preferences of a single species of invertivore (Layton and Fulton 2014; Brandl et al. 2015; Kramer et al. 2016; Wenger et al. 2018). Current knowledge of how the *overall* collective trophic grouping of invertivorous fish species demonstrate niche partitioning of their foraging microhabitats in non-reef habitats is limited. Theory would predict, however, that within the overall invertivore assemblage, individual species exploit different portions of the habitat space, exhibiting niche partitioning at a finer scale (Floeter et al. 2007; Berkström et al. 2012; Asher et al. 2017; Brandl et al. 2020). Knowledge of these microhabitat specialisations is therefore an important first step in defining the ecosystem function of species within the invertivore trophic guild.

One of the most common and productive non-reef habitats within tropical seascapes is macroalgal meadows, comprised of canopy-forming macroalgae (Tano et al. 2016; Fulton et al. 2020). These macroalgal meadows can extend over significant portions of shallow tropical marine habitats (estimated between 16 and 46% of some shallow coastal areas, Fulton et al. 2019), forming complex habitat structures and contributing a large amount of areal primary production. This primary production supports communities of epifaunal invertebrates, which, in turn, provide nutrition for invertivorous fishes (Edgar and Aoki 1993; Wenger et al. 2018). Recent studies have highlighted the fact that these macroalgal meadows and their associated epifaunal communities are important foraging grounds for invertivorous fishes (Chaves et al. 2013; Chen et al. 2020). Macroalgal meadows can, however, exhibit strong temporal shifts in canopy size (in terms of either overall biomass or the length of macroalgal thalli). In tropical regions, one of the typical temporal canopy shifts is canopy growth in summer and detachment in winter (Leite and Turra 2003; Wong and Phang 2004; Lefevre and Bellwood 2010; Fulton et al. 2014). Seasonal fluctuations in macroalgal canopy size therefore influence the availability of habitat, impacting the abundance and availability of associated epifaunal invertebrate communities (Taylor 1998; Leite and Turra 2003; Ba-Akdah et al. 2016), and the invertivorous fishes that prey on epifauna (Edgar and Aoki 1993; Fulton et al. 2019; Froese and Pauly 2021). However, we lack a basic understanding of the microhabitat preferences of macroalgal-associated invertivorous fishes while foraging within macroalgal meadows, and how such foraging microhabitat preferences of individual invertivorous species

might respond to seasonal fluctuations in canopy size that are likely to affect the availability of epifaunal prey. This hinders our ability to understand spatial niche partitioning within this trophic group and the potential for within-group functional complementarity versus redundancy. The aims of this study were therefore: (1) to document the foraging microhabitat preferences of the dominant invertivorous fish species within macroalgal meadows of the world heritage Ningaloo Marine Park, Western Australia, and determine the potential for functional complementarity based on the microhabitat resource axis within this trophic group and (2) to examine how these microhabitat preferences respond to seasonal shifts in macroalgal canopy structure (summer to winter).

Methods

Study region

This study was conducted within the Maud Recreation Region of Ningaloo Marine Park near Coral Bay, situated in the north-west of Western Australia (Fig. 1). As Australia's largest fringing coral reef (~290 km long), shallow waters (3–5 m depth) in this area are dominated by canopy-forming fucoids chiefly belonging to the genus *Sargassum*. These canopies form extensive macroalgal meadow patches covering over 300 km², which exhibit strong seasonal fluctuations in macroalgal biomass (Kobryn et al. 2013; Fulton et al. 2014; van Lier et al. 2018; Chen et al. 2020). A total of

eight *Sargassum* meadow patches (size: 28,893 ± 11,627 m²) were surveyed during late austral summer (February–March) 2018 to confirm the presence of invertivorous fishes and determine habitat composition (Fig. 1). Only four of these *Sargassum* meadow patches were reinvestigated during the austral winter (August–September) 2018 due to the dramatic seasonal decline of *Sargassum* canopy biomass (Fig. 1).

Habitat composition of macroalgal meadows

Habitat composition of each *Sargassum* meadow patch in summer and winter was documented via underwater visual censuses conducted by divers on SCUBA, following Lim et al. (2016). At each meadow patch, we haphazardly deployed six replicate 10-m transect tapes and recorded the distance along each transect (to the nearest 5 cm) occupied by three distinct habitat categories: (1) canopy macroalgae (leathery macrophytes with the canopy height can reach around 10–50 cm, and up to 1–2 m, e.g. *Sargassum*, *Sargassopsis*), (2) understory macroalgae (foliose macrophytes without canopies, occupying the floor of meadows, e.g. *Lobophora*, *Dictyota*, *Padina*) and (3) abiotic components (e.g. pavement, sand, dead coral, rubble). Converting these distances to a proportion of the 10-m transect length gave us a percentage composition of the three habitat types within each meadow.

Foraging microhabitat preferences of invertivorous fishes

The use of individual foraging microhabitats by species of invertivorous fishes was recorded using underwater visual observations by divers on SCUBA. At each meadow patch during summer and winter, at least three instantaneous focal surveys were conducted (following Fulton et al. 2001) over 8 days in summer and 5 days in winter. In brief, a single diver swam a random, non-overlapping path starting from the centre of each meadow patch out to the patch edge. Surveys commenced 5 min after the diver had reached the patch centre to allow for fish to acclimate to diver presence. For each invertivorous fish observed to show direct foraging behaviour (following Wenger et al. 2018), we recorded the species identity, total length (TL, to the nearest cm), foraging behaviour (searching/feeding) and microhabitat location (e.g. canopy macroalgae). Within these focal observations of direct foraging behaviour, 'searching' was strictly defined as the fish having its head inclined towards the particular microhabitat but without touching, while 'feeding' was defined by its mouth being in contact with the microhabitat. Subsequently, 'searching' and 'feeding' in each season were pooled together for further analysis. To avoid problems associated with inferences based on low sample sizes/sites, during summer, only invertivorous species represented by

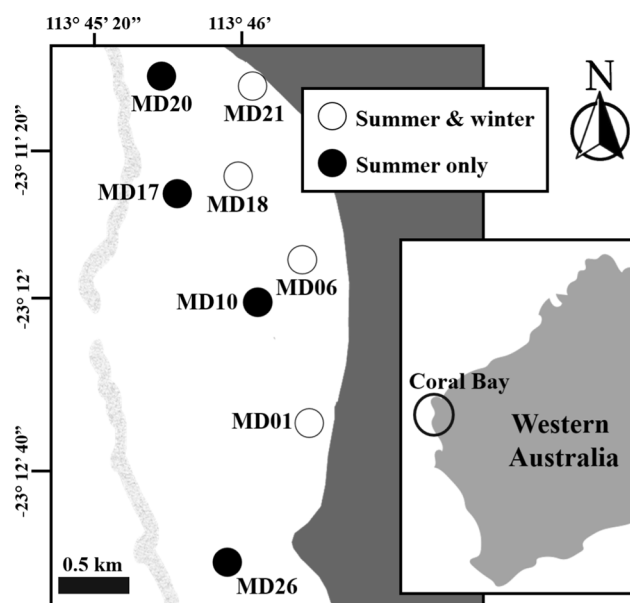


Fig. 1 Map of study region and surveyed *Sargassum* meadow patches within Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, Western Australia

more than ten individuals per meadow patch and present on at least three meadow patches were included in subsequent analyses. During winter, we adjusted this rule to species represented by more than ten individuals per meadow patch and present on at least two of the four meadow patches surveyed. Foraging microhabitat preferences of each invertivorous fish species were determined using the electivity index formula of Vanderploeg and Scavia (1979):

$$E_i^* = [W_i - (1/n)] / [W_i + (1/n)], \quad (1)$$

where E_i^* is the electivity for microhabitat category i , n is the number of microhabitat categories and W_i is the selective coefficient for microhabitat category i calculated as:

$$W_i = (r_i/p_i) / \left(\sum_i r_i/p_i \right), \quad (2)$$

where r_i is the proportional use of the microhabitat category i and p_i is the proportional availability of the microhabitat category i . Values of electivity indices (E_i^*) range from -1 to 1 , with indication of avoidance (negative value), neutrality ($E_i^* = 0$) and preference (positive value) for a particular microhabitat. Electivity index of each species was averaged across patches within a given season to determine the patterns of season-specific foraging microhabitat associations of individual invertivorous fishes in the Maud Recreation Region of Ningaloo Marine Park.

Results

Invertivorous fish communities

Based on 3207 individual foraging behaviour recorded (2538 in summer and 669 in winter, Supplemental Table S1), we observed a total of 36 invertivorous fish species foraging within macroalgal meadows in the summer (34 species) and winter (24 species). Of these 36 species, 12 species in summer and 5 in winter (Table 1) met our criterion for the analysis of foraging microhabitat preferences (Table 2). The majority of invertivorous fishes for whom we recorded foraging abundance (the number of individuals exhibiting foraging behaviour) belonged to the family Labridae (71% in summer, 75% in winter), followed by Lethrinidae (17% in summer, 10% in winter) and Mullidae (11% in summer, 15% in winter). The 12 most abundant species were as follows: (1) Labridae: *Anampses geographicus*, *Cheilio inermis*, *Coris caudimacula*, *Halichoeres nebulosus*, *Pseudojuloides elongatus*, *Stethojulis bandanensis*, *Stethojulis interrupta* and *Thalassoma lunare*; (2) Lethrinidae: *Lethrinus atkinsoni* and *Lethrinus nebulosus*; and (3) Mullidae: *Parupeneus barberinoides*

Table 1 Invertivorous fish species observed foraging within macroalgal meadows in the Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, Western Australia. Species with a sufficient number of cases (see text) to calculate foraging microhabitat preferences during each season are in bold

Family	Species	Number in summer	Number in winter
Balistidae	<i>Rhinecanthus aculeatus</i>	4	
Carangidae	<i>Gnathanodon speciosus</i>	2	
Labridae	<i>Anampses caeruleopunctatus</i>	1	1
	<i>Anampses geographicus</i>	135	56
	<i>Bodianus bilunulatus</i>	1	
	<i>Cheilinus bimaculatus</i>	1	
	<i>Cheilinus chlorourus</i>	2	1
	<i>Cheilinus trilobatus</i>	6	
	<i>Cheilio inermis</i>	221	93
	<i>Choerodon rubescens</i>	1	
	<i>Coris auricularis</i>	2	2
	<i>Coris aygula</i>	7	
	<i>Coris caudimacula</i>	360	90
	<i>Epibulus insidiator</i>	1	
	<i>Halichoeres nebulosus</i>	165	67
	<i>Hemigymmus melapterus</i>	1	
	<i>Hologymnosus annulatus</i>	2	
	<i>Macropharyngodon ornatus</i>	10	2
	<i>Pseudojuloides elongatus</i>	160	15
<i>Pteragogus enneacanthus</i>	30	3	
<i>Pteragogus flagellifera</i>	38	2	
<i>Stethojulis bandanensis</i>	127	21	
<i>Stethojulis interrupta</i>	182	33	
<i>Stethojulis strigiventer</i>		3	
<i>Thalassoma lunare</i>	264	87	
<i>Thalassoma lutescens</i>	67	15	
<i>Xenajulis margaritaceus</i>	30	10	
Lethrinidae	<i>Lethrinus atkinsoni</i>	216	16
	<i>Lethrinus nebulosus</i>	181	20
	<i>Lethrinus variegatus</i>	37	29
Mullidae	<i>Parupeneus barberinoides</i>	110	13
	<i>Parupeneus indicus</i>	10	6
	<i>Parupeneus spilurus</i>	160	83
	<i>Upeneus australiae</i>		1
	<i>Upeneus tragula</i>	1	
Nemipteridae	<i>Scolopsis bilineata</i>	3	

and *Parupeneus spilurus* (Table 1). The number of species and/or the total number of foraging individuals of each species declined in winter, which changed the community composition (in terms of foraging abundance) at each meadow patch (Table 2).

Table 2 Foraging abundance and community composition (%) of the 12 valid invertivorous fish species within each macroalgal meadow patch in the Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, Western Australia, during summer and winter

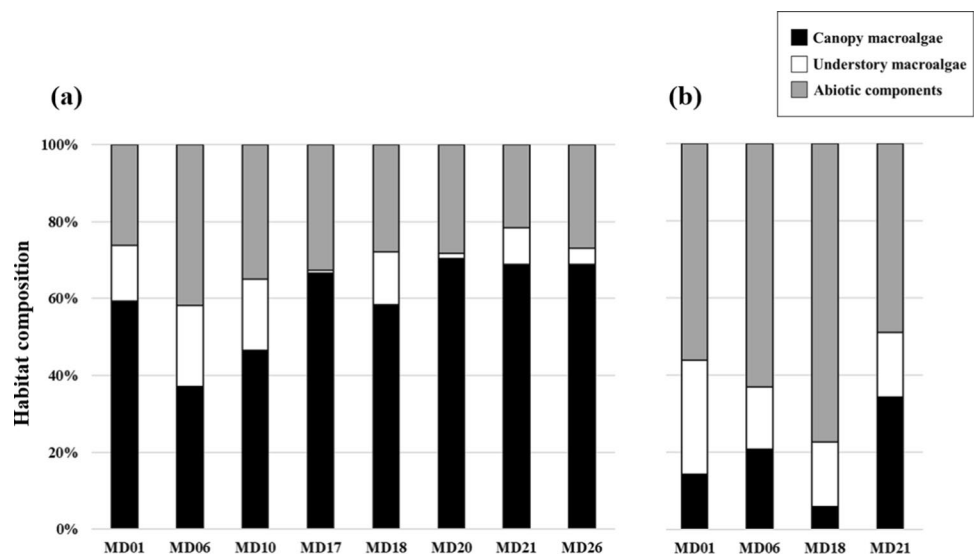
Species	MD01	MD06	MD10	MD17	MD18	MD20	MD21	MD26
<i>(a) Summer</i>								
<i>Anampses geographicus</i>	12 (3%)	15 (4%)	4 (2%)	19 (8%)	18 (7%)	24 (9%)	16 (6%)	27 (11%)
<i>Cheilio inermis</i>	30 (9%)	36 (9%)	32 (13%)	23 (9%)	14 (6%)	27 (10%)	44 (17%)	15 (6%)
<i>Coris caudimacula</i>	54 (16%)	63 (16%)	53 (21%)	31 (12%)	45 (18%)	42 (15%)	35 (13%)	37 (15%)
<i>Halichoeres nebulosus</i>	20 (6%)	31 (8%)	12 (5%)	17 (7%)	15 (6%)	31 (11%)	20 (8%)	19 (8%)
<i>Lethrinus atkinsoni</i>	39 (11%)	41 (10%)	31 (12%)	22 (9%)	23 (9%)	13 (5%)	27 (10%)	20 (8%)
<i>Lethrinus nebulosus</i>	40 (12%)	27 (7%)	22 (9%)	20 (8%)	23 (9%)	14 (5%)	19 (7%)	16 (6%)
<i>Parupeneus barberinoides</i>	24 (7%)	44 (11%)	13 (5%)	8 (3%)	6 (2%)	0 (0%)	14 (5%)	0 (0%)
<i>Parupeneus spilurus</i>	29 (8%)	19 (5%)	24 (10%)	20 (8%)	21 (9%)	8 (3%)	18 (7%)	21 (8%)
<i>Pseudojuloides elongatus</i>	22 (6%)	32 (8%)	18 (7%)	12 (5%)	17 (7%)	13 (5%)	22 (8%)	24 (10%)
<i>Stethojulis bandanensis</i>	10 (3%)	26 (7%)	14 (6%)	21 (8%)	18 (7%)	16 (6%)	11 (4%)	11 (4%)
<i>Stethojulis interrupta</i>	22 (6%)	33 (8%)	12 (5%)	19 (8%)	15 (6%)	35 (13%)	19 (7%)	27 (11%)
<i>Thalassoma lunare</i>	44 (13%)	28 (7%)	15 (6%)	39 (16%)	32 (13%)	52 (19%)	20 (8%)	34 (14%)
Species	MD01	MD06	MD18	MD21				
<i>(b) Winter</i>								
<i>Cheilio inermis</i>	13 (13%)	25 (27%)	19 (17%)	36 (30%)				
<i>Coris caudimacula</i>	15 (15%)	21 (23%)	23 (20%)	31 (26%)				
<i>Halichoeres nebulosus</i>	4 (4%)	15 (16%)	19 (17%)	29 (24%)				
<i>Parupeneus spilurus</i>	13 (13%)	29 (31%)	28 (25%)	23 (19%)				
<i>Thalassoma lunare</i>	58 (56%)	3 (3%)	25 (22%)	1 (1%)				

Habitat availability and microhabitat use

Habitat composition in each meadow patch showed that canopy macroalgae was the dominant microhabitat in summer (Fig. 2a). In winter, patches shifted to be dominated by the abiotic component due to the dramatic seasonal decline in *Sargassum* canopy biomass (Fig. 2b). Invertivorous fishes used distinct microhabitats while foraging (Figs. 3, 4). During the summer, five invertivorous

fishes (*Anampses geographicus*, *Cheilio inermis*, *Coris caudimacula*, *Pseudojuloides elongatus* and *Thalassoma lunare*) were observed foraging primarily within the canopy macroalgae compared with the understory macroalgae or abiotic components (Fig. 3a–e). The proportional use of canopy macroalgae was higher than its availability for these species, suggesting a strong foraging microhabitat preference for canopy macroalgae. The opposite pattern, which suggested a strong microhabitat preference for

Fig. 2 Habitat composition of each macroalgal meadow patch during **a** summer and **b** winter in 2018



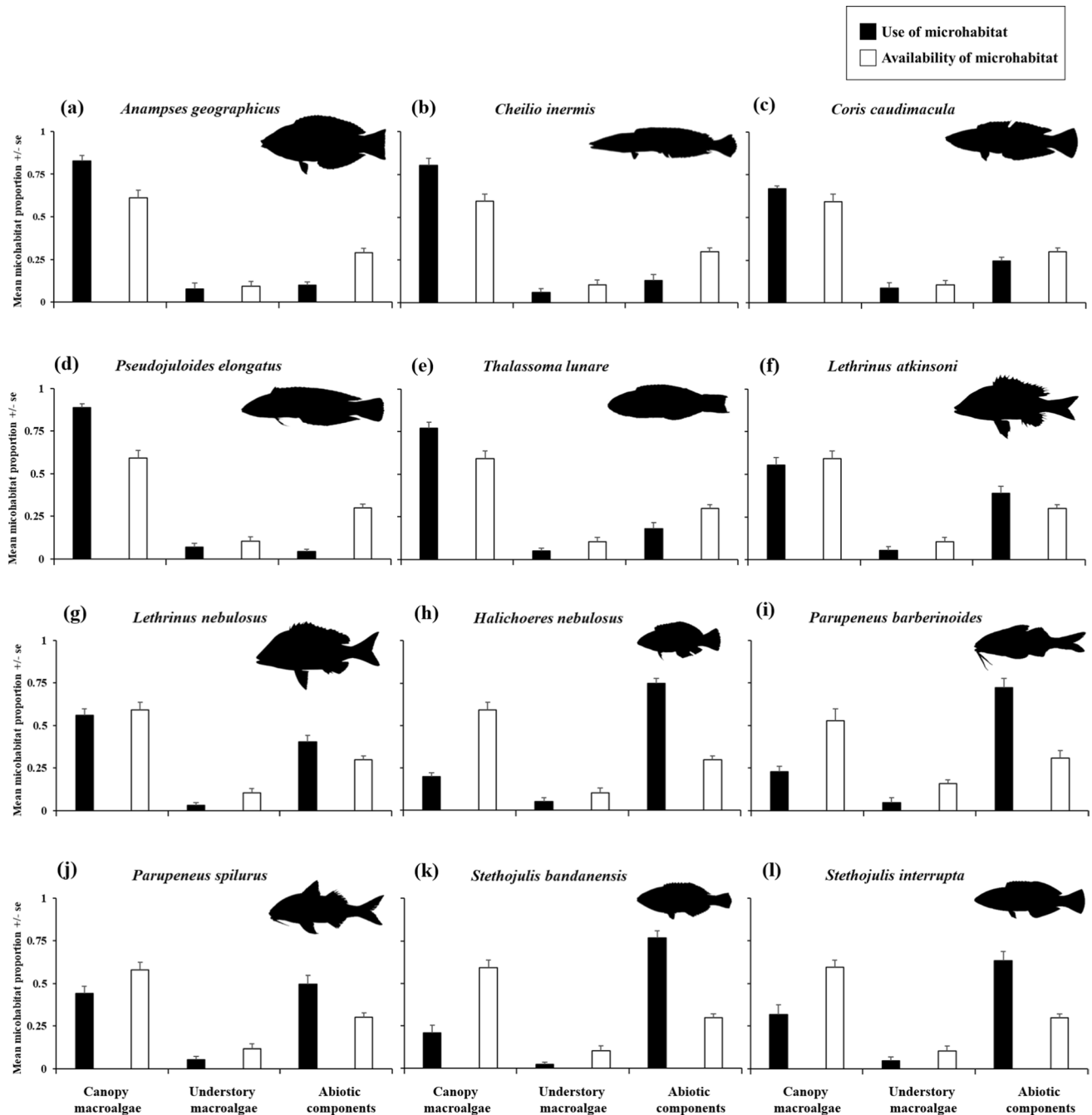


Fig. 3 Foraging microhabitat use by invertivorous fishes in summer, as indicated by the proportional use relative to the proportional availability of three microhabitat categories: **a** *Anampses geographicus*, **b** *Cheilio inermis*, **c** *Coris caudimacula*, **d** *Pseudojuloides elongatus*, **e**

Thalassoma lunare, **f** *Lethrinus atkinsoni*, **g** *Lethrinus nebulosus*, **h** *Halichoeres nebulosus*, **i** *Parupeneus barberinoides*, **j** *Parupeneus spilurus*, **k** *Stethojulis bandanensis* and **l** *Stethojulis interrupta*

abiotic components, was found for *Halichoeres nebulosus*, *Parupeneus barberinoides*, *Parupeneus spilurus*, *Stethojulis bandanensis* and *Stethojulis interrupta* (Fig. 3h–l). Interestingly, these patterns of disproportionately using

certain microhabitats were consistent for the four species (*Cheilio inermis*, *Coris caudimacula*, *Halichoeres nebulosus* and *Parupeneus spilurus*) observed in both seasons, with *Thalassoma lunare* as the only exception (Fig. 4).

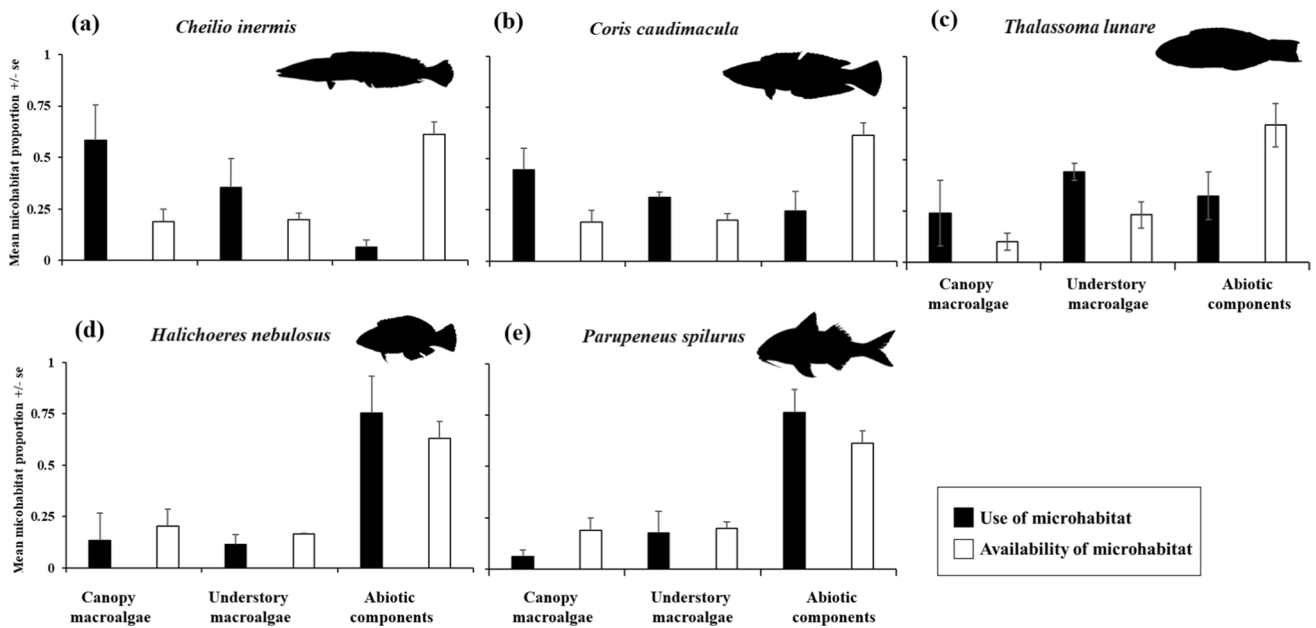


Fig. 4 Foraging microhabitat use by invertivorous fishes in winter, as indicated by the proportional use relative to the proportional availability of three microhabitat categories: **a** *Cheilio inermis*, **b** *Coris*

caudimacula, **c** *Thalassoma lunare*, **d** *Halichoeres nebulosus* and **e** *Parupeneus spilurus*

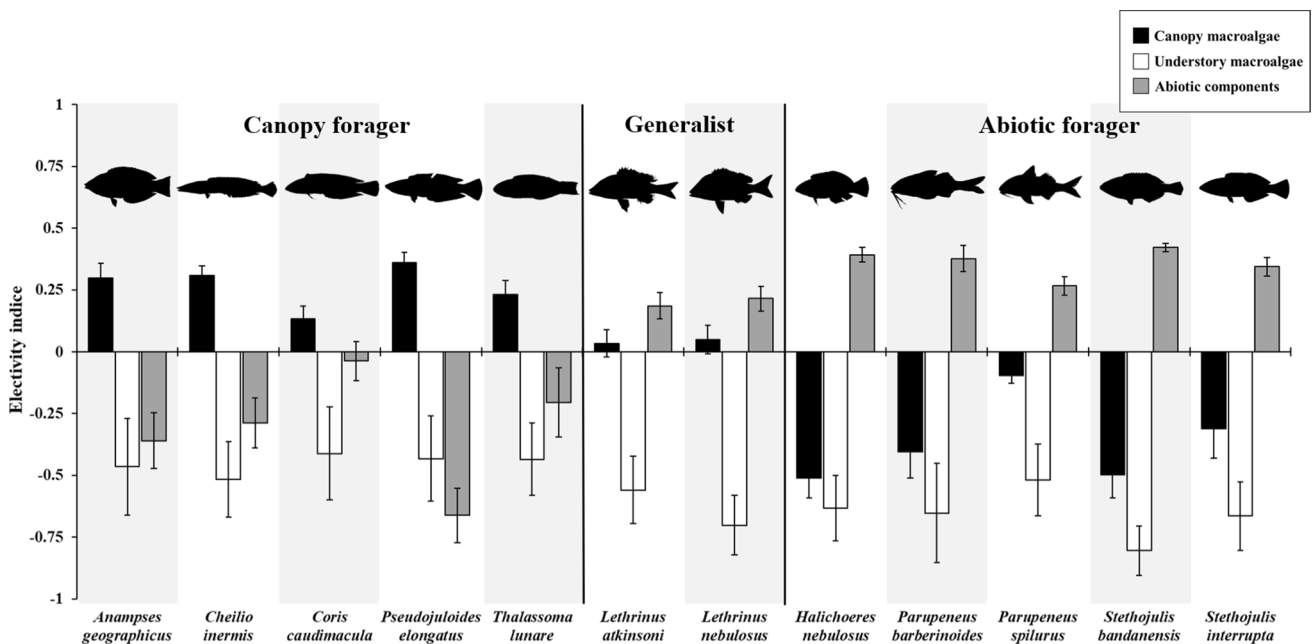


Fig. 5 Foraging preferences of common invertivorous fishes for three microhabitat categories (canopy macroalgae, understory macroalgae and abiotic components) averaged (\pm standard error) across eight meadow patches within Maud Recreation Zone of Ningaloo Marine

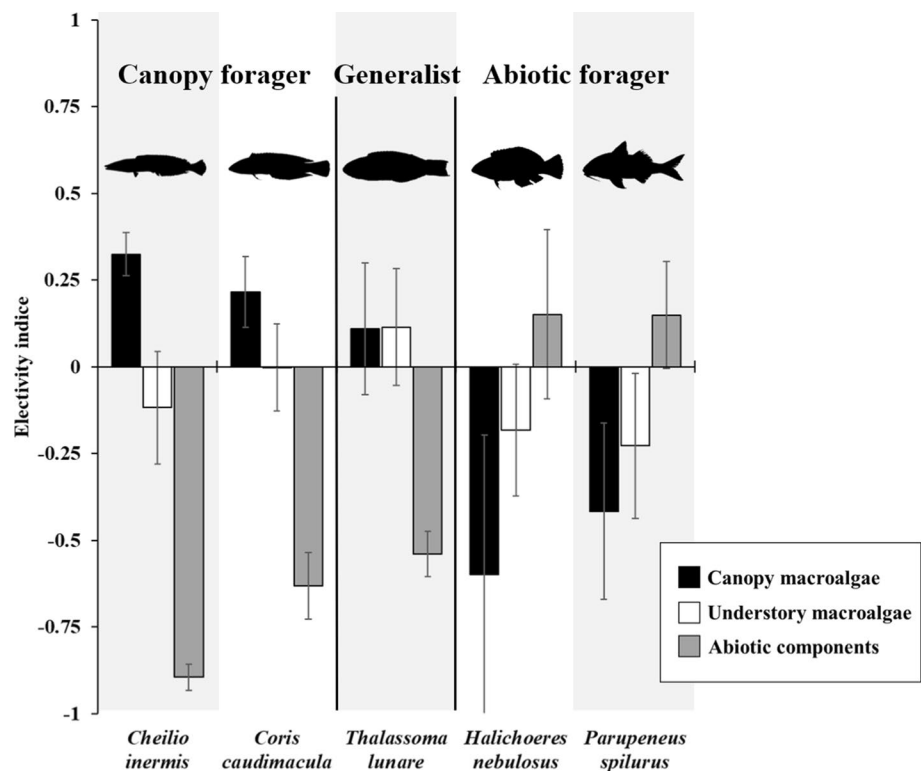
Park near Coral Bay, during summer season 2018. Values of 0 indicate neutrality, while positive and negative values indicate preference and avoidance, respectively

Foraging microhabitat preferences of invertivorous fishes

Electivity indices revealed that invertivorous fishes foraging within macroalgal meadows can be chiefly grouped into

three categories of foraging specialisations: ‘canopy forager’, ‘generalist’ and ‘abiotic forager’ (Figs. 5, 6). ‘Canopy foragers’ (i.e. those fish that search for prey and feed within macroalgal canopies) were overwhelmingly represented by Labridae, specifically the species *Anampses geographicus*,

Fig. 6 Foraging preferences of common invertivorous fishes for three microhabitat categories (canopy macroalgae, understory macroalgae and abiotic components) averaged (\pm standard error) across four meadow patches within Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, during winter season 2018. Values of 0 indicate neutrality, while positive and negative values indicate preference and avoidance, respectively



Cheilio inermis, *Coris caudimacula*, *Pseudojuloides elongatus* and *Thalassoma lunare* in summer (Fig. 5) and *Cheilio inermis* and *Coris caudimacula* in winter (Fig. 6). Notably, this positive preference for canopy macroalgae was consistent across seasons, even in winter when there was significantly lower availability of macroalgal canopy (Figs. 5, 6). The only exception was *Thalassoma lunare*, which showed foraging preferences for both canopy and understory macroalgae in winter, indicating a shift from canopy forager to being a generalist when canopy macroalgae were less available (Fig. 6). Species belonging to the family Mullidae (*Parupeneus barberinoides* and *Parupeneus spilurus* in summer; *Parupeneus spilurus* in winter) as well as the labrid species (*Halichoeres nebulosus*, *Stethojulis bandanensis* and *Stethojulis interrupta* in summer; *Halichoeres nebulosus* in winter) were found to be ‘abiotic foragers’ (fish that search for prey and feed on pavement, sand, dead coral, rubble) (Figs. 5, 6). Finally, during summer, species belonging to the family Lethrinidae (*Lethrinus atkinsoni* and *Lethrinus nebulosus*) were found to be ‘generalists’, showing a positive electivity for foraging within both canopy macroalgae and on abiotic substrates (Fig. 5). However, none of these lethrinid generalist species were observed in sufficient number during the winter surveys. Interestingly, almost all the fish species (excluding *Thalassoma lunare* in winter) in this study showed a strong tendency to avoid foraging within understory macroalgae, despite its high availability within the macroalgal patches (Figs. 5, 6).

Discussion

This study presents the seasonal foraging abundance and foraging microhabitat utilisation of invertivorous fish communities within tropical macroalgal meadows of Coral Bay, Ningaloo Marine Park, Western Australia. The family Labridae were the most abundant invertivorous taxa that foraged within the macroalgal meadows, making up over 70% of our foraging observations, followed by the families Mullidae and Lethrinidae. Our study revealed that fishes categorised as ‘invertivores’ have distinct foraging microhabitat preferences in canopy-forming macroalgal meadows and that individual species have different functional impacts within these systems. The invertivorous fish communities in this study can be divided into three categories of foraging specialists: ‘canopy forager’, ‘abiotic forager’ and ‘generalist’, based on their microhabitat preferences, highlighting a previously unappreciated aspect of functional complementarity within this particular trophic group. Surprisingly, almost all the invertivorous fish species avoided understory macroalgae while foraging, and this pattern was consistent between summer and winter, even though understory macroalgae are proportionally more available in winter.

Invertivorous fishes categorised as ‘canopy foragers’ in both summer and winter were from the family Labridae, whereas ‘generalists’ were from the family Lethrinidae in summer and a single labrid species in winter. The ‘abiotic foragers’ were from the families Labridae and Mullidae,

with the mullids exclusively recorded under this category, suggesting that the division of the microhabitat niche axis is likely to be based on sharing similar morphological traits. For example, for labrids that are canopy foragers, their characteristically pointed snout and protruding canine teeth make it possible to flip the macroalgal blades to expose hidden epifaunal prey (Choat and Bellwood 1998; Froese and Pauly 2021), whereas labrids, which are considered to have good swimming abilities (higher fin aspect ratio to body size), are more capable of escaping from potential predators that use canopies as ambush sites (Fulton et al. 2001; Willis and Anderson 2003; Hoey and Bellwood 2011). However, the potential relationships between morphological traits and behavioural specialisation need to be further investigated, as morphology traits such as fin aspect ratio and body size, are not necessarily related to taxonomy.

Recent studies have compared epifaunal communities between neighbouring habitats across latitudes and seasons and found that epifaunal community structure can vary between habitats across microhabitat and seascapes, with strong seasonal fluctuations in their biomass driven by the availability of microhabitat (Chen et al. 2020, 2021; Fraser et al. 2020). In principle, this allows for assessment of whether differences in community composition between habitats translate either into differences in dietary target or nutritional quality. It is likely that particular dietary targets are more within communities at certain locations, driving specialisations in foraging microhabitat preferences of invertivorous fishes. In our study, we were unfortunately unable to collect specimens for gut content analysis to verify potential dietary targets that might drive the division of the foraging habitat resource axis. However, this represents a profitable future direction of research to test whether the prey selection and dietary targets of invertivorous fish species vary with microhabitat in macroalgal meadows.

Although the taxonomic composition of foraging invertivorous fishes in our survey varied seasonally, four of the five fish species which were observed foraging within the winter meadow patches showed consistent foraging microhabitat preferences in both seasons (Figs. 5, 6). This suggests that the observed microhabitat niche partitioning is likely to be based on real foraging specialisations, rather than just resulting from microhabitat crowding and resource competition in a given season. In our study, the foraging abundance of invertivorous fishes (in terms of individual or species) underwent dramatic declines in winter, associated with the extent of *Sargassum* canopy loss (Fig. 2, Tables 1, 2), indicating that canopy foragers may move to adjacent habitats due to the local absence of preferred microhabitats. Previous studies have shown the periodical migration of fish assemblages within marine macrophytal habitats which undergo systematic and predictable seasonal fluctuations (Green et al. 2009; Wilson et al. 2014; Lim et al. 2016). However, two

canopy foraging labrid species '*Cheilio inermis*' and '*Coris caudimacula*' with large home range (72,000 m and 320 m, respectively, van Lier et al. 2018) continued to forage within the winter meadows, without moving to adjacent coral reefs, suggesting they are stronger habitat specialists than the other canopy foragers. Notably, one of the summer canopy foragers, *Thalassoma lunare*, shifted to being a generalist that utilised both canopy and understory macroalgae in winter, indicating that this species changed its foraging microhabitat preferences in response to fluctuations in the availability of favoured resources. However, this finding requires corroboration as only two of the four surveyed meadow patches in winter were included in our analysis (Supplemental Fig. S1h).

Surprisingly, only two abiotic foraging species '*Halichoeres nebulosus*' and '*Parupeneus spilurus*' were observed in sufficient numbers to measure their foraging preferences in the winter meadow patches despite there being no equivalent reduction in abiotic components compared with canopy macroalgae (so we did not expect to see a significant reduction in the foraging abundance of 'abiotic foragers' and 'generalists'). This suggests that, for such non-canopy foraging species, macroalgal canopies may provide other important functions including nurseries for recruitment, or refuge from predators (Tano et al. 2017; Wilson et al. 2017). Once macroalgal canopies start to dieback, these satellite functions might be lost, meaning that generalists and abiotic foragers are forced to move to adjacent habitats.

Almost all the fish species documented in the current study showed a strong tendency to avoid foraging on understory macroalgae. This accords with previous studies of the foraging behaviour of individual fish species within macroalgal meadows (herbivorous *Leptoscarus vaigiensis*: Lim et al. 2016; invertivorous *Xenojulis margaritaceus*: Wenger et al. 2018). Potential factors that may discourage invertivores from foraging in the understory include: (1) nutritional differences and/or differences in taxonomic structure of epifaunal prey communities between the two microhabitats and (2) differential predation threat in the two microhabitats. Previous studies have suggested that canopy macroalgae are able to harbour a greater biomass of epifaunal invertebrates and/or to provide better quality of shelters than non-canopy species due to their more complex structure (Taylor and Cole 1994; Cacabelos et al. 2010; Carvalho et al. 2018; O'Brien et al. 2018). Hence, the understory macroalgae at Ningaloo Reef may represent a poorer dietary resource for invertivorous fishes. Interestingly, this pattern of avoidance of understory macroalgae was weaker in winter (Figs. 6, Supplemental Fig. S1), suggesting that understory macroalgae are a less undesirable habitat when canopy macroalgae are scarce.

Previous studies have already shown that environmental changes (either seasonal fluctuations or climate anomalies)

can lead to the extensive loss of macroalgal canopy cover and can be replaced by less-complex algal species (Feng et al. 2013; Graba-Landry et al. 2020; Figueiredo et al. 2020; Chen et al. 2021). Given that future disturbance induced by climate change (e.g. extreme weather events, thermal anomalies) will become more frequent and more intense, a reduction in invertivorous fish abundance within canopy macroalgal meadows can be expected. This could dramatically reduce fishery production underpinned by the trophic links facilitated by invertivorous fishes, and an overall decline in trophic interactions by invertivorous fishes across all latitudes due to climate-driven thermal events has been predicted (Inagaki et al. 2020).

The refinement of foraging specialisations of invertivorous fishes based on foraging microhabitat preferences that we have presented here will aid future studies to identify the specific functional roles of invertivorous fishes and how these relate to ecosystem functioning, to yield a more conservative estimate of the level of functional redundancy within the ecosystem. This information will be important for management actions going forward. For example, over-exploitation of species that all fall within the ‘canopy forager’ role is likely to have consequences for top-down control of epifaunal invertebrate communities and cascading effects on primary producers. Moreover, as the foraging microhabitat preferences of invertivorous fish species are unravelled further, particular species may be found to play a unique role in facilitating particular trophic links between organisms. For example, previous studies of invertivorous fishes in the canopy macroalgal meadows of Ningaloo have tended to focus on fishery or recreational targets, especially fishes from the family Lethrinidae (Westera 2003; Wilson et al. 2010, 2014, 2017). However, due to the consistency of their abundance and foraging microhabitat preferences across seasons, canopy foragers such as the labrids are also likely to be vital components of macroalgal meadow ecosystems. As these ecosystems come under pressure from climate change (Smale and Wernberg 2013; Straub et al. 2019; Graba-Landry et al. 2020), the predicted range contractions of canopy macroalgal meadows will impact on associated invertivorous fish communities, especially on canopy specialists. Future research should examine the potential implications of loss of macroalgal meadow habitats for ecosystem dynamics, based on the refinements to functional specialisations of the species presented here.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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