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Epifaunal community structure within southern New Zealand kelp forests

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ABSTRACT: Epifaunal communities associated with macroalgal forests are a key link in coastal food webs, yet they are relatively poorly understood in terms of diversity, structure and regional variability. We quantified the biomass, density and richness of epifauna on the 7 most dominant seaweed species from 2 regions of southern New Zealand, i.e. East Otago and Stewart Island. We analysed the epifaunal community structure associated with each macroalgal species and estimated the average biomass of epifauna supported per m^2 of substrate at the shallow (2 m) and deep (10 m) extent of each reef. Significant differences in epifaunal biomass, density and richness were evident between macroalgal species in both regions, and epifaunal community structure differed significantly between regions on 2 of the 4 macroalgal species that were shared. Epifaunal biomass ranged between 5.1 and 186.8 g wet weight m^{-2} and corresponded to 0.01 to 0.08% of the macroalgal biomass. Epifaunal biomass and density were not always linked to the morphological complexity of the host macroalgal species, and some of the highest values were found on species considered morphologically simple, such as the fucoid *Xiphophora gladiata* and laminarian kelp *Ecklonia radiata*. Greater macroalgal biomass at shallow depths did not always result in greater epifaunal biomass when compared to deeper depths, indicating that macroalgal community structure plays a significant role in controlling epifaunal biomass. Significant regional and host-specific factors likely influence epifaunal communities, and these should be considered when estimating secondary productivity and the effects of habitat change.

KEY WORDS: Kelp forest · Epifauna · Community structure · Macroalgae · Secondary productivity

INTRODUCTION

Macroalgae contribute significantly to the base of coastal temperate food webs and provide habitat for higher trophic level species (Duggins et al. 1989, Borum & Sand-Jensen 1996, Gattuso et al. 2006, Miller et al. 2011, Raven & Hurd 2012). Mobile epifaunal communities (MECs) that rely directly on macroalgae for these services contribute significantly to secondary productivity and play an extremely important role in the structure of temperate coastal food webs (Taylor 1998a, Newcombe & Taylor 2010). MECs also provide numerous ecosystem functions and are a fundamental link in the trophic chain, as they facilitate the flow of carbon from lower trophic organisms to upper level consumers (Taylor 1998a, Cowles et al. 2009). These communities are estimated to account for ~80% of the flow of energy and materials through rocky reef ecosystems (Taylor 1998a, Schwarz et al. 2006, Morrison et al. 2009).

The functional diversity of MECs is indicative of the number of roles they play within an ecosystem (Taylor 1998a, Cowles et al. 2009). Communities usually comprise a taxonomically diverse range of spe-

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cies that represent multiple trophic levels (Taylor & Cole 1994), including species from many phyla such as Annelida, Arthropoda and Mollusca (Taylor & Cole 1994, Taylor 1998a, Schwarz et al. 2006, Morrison et al. 2009, Cowles et al. 2009). Filter feeders (Caine 1978, Taylor & Cole 1994), detrital consumers (Zimmerman et al. 1979, Taylor & Cole 1994), direct and indirect grazers (Duffy 1990, Taylor & Cole 1994) and predators (Roland 1978, Taylor & Cole 1994) all fill separate niches in the ecosystem provided by macroalgae. These organisms provide an important link by supplying macroalgal derived carbon to higher trophic level consumers (Taylor & Cole 1994, Taylor 1998a). Other services provided by MECs include the active removal/consumption of fouling epiphytes that may otherwise overgrow and outcompete the host (Duffy 1990, Dudley 1992, Stachowicz & Whitlatch 2005), and the provision of nitrogen by both sessile (Hepburn & Hurd 2005) and mobile (Taylor & Rees 1998) epifaunal species.

The composition of MECs varies considerably depending on the host species (Taylor & Cole 1994, Cowles et al. 2009, Torres et al. 2015), each providing differing values in terms of nutrition (Hooper & Davenport 2006) and refuge (Bolam & Fernandes 2002, Christie et al. 2007, Zamzow et al. 2010). There is consensus that macroalgal species with greater morphological complexity offer greater refuge and host a more abundant and diverse MEC (Taylor & Cole 1994, Hooper & Davenport 2006, Veiga et al. 2014, Torres et al. 2015, Suárez-Jiménez et al. 2017). Taylor & Cole (1994) reported up to 2000 individual epifaunal organisms per 100 g of algal tissue on morphologically complex species such as *Carpophyllum plumosum* and *Cystophora retroflexa* in northern New Zealand. Some studies have also suggested that while morphological complexity is important, the quantity and persistence of available habitat is also a good predictor of MEC structure (Torres et al. 2015). Torres et al. (2015) noted that perennial species such as kelps and fucoids harbour more stable assemblages compared to ephemeral annual species because their longevity allows multiple generations of epifauna to flourish on 1 host. Furthermore, over long periods, factors such as competition and predation shape the MEC, allowing for niche segregation (Torres et al. 2015).

A small number of studies from New Zealand have documented MECs associated with macroalgal species or communities (Taylor & Cole 1994, Taylor 1997, 1998a, Hepburn 2005, Schwarz et al. 2006, Cowles et al. 2009, Newcombe & Taylor 2010, Suárez-Jiménez et al. 2017). Even fewer studies exist regarding quantitative metrics of epifauna at a scale larger than an individual macroalga (Taylor 1998a, Cowles et al. 2009), and, to our knowledge, none exists comparing epifaunal assemblages between regions within New Zealand. This information is important in order to understand variability of MECs across New Zealand and how macroalgal community structure influences MEC composition, and to gain localised estimates of secondary productivity from specific coastal reef systems. All of this information culminates in the ability to better understand coastal ecosystem functioning, detect the effects of anthropogenic disturbances and more accurately estimate higher trophic level productivity including that of important fisheries.

In this study, we quantified the biomass, richness and density of epifaunal organisms on the 7 most dominant macroalgal species from 2 regions of southern New Zealand (East Otago and Stewart Island). Data were then extrapolated to provide estimates of epifaunal biomass per m^2 of substrate based on the macroalgal community present at the shallow and deep extent of 3 replicate reef systems in each region. The 2 regions have been shown to differ significantly in their macroalgal community structure, with greater biomass production occurring in the Stewart Island region, most likely as a result of increased light availability (Desmond et al. 2015). We predicted that epifaunal biomass, richness and density would be similar on macroalgal species that were found in both regions when standardised by wet weight of the host, but would differ between macroalgal species within each region due to morphological and physiological differences among host species (see Taylor & Cole 1994, Gestoso et al. 2010). We also predicted that macroalgal standing biomass would show a strong positive correlation with epifaunal biomass and, as a result, the East Otago region would support less epifaunal biomass per m^2 of substrate when extrapolated to the reef scale, particularly at the deepest extent of the reef where the disparity in macroalgal biomass is greater.

MATERIALS AND METHODS

Study sites

This study was conducted in the East Otago and Stewart Island regions of southeast New Zealand (Fig. 1). Three replicate sites were selected in each region; each site had a northeast aspect and was protected from the prevailing southwest swell. The substrate of each reef was a combination of bedrock and

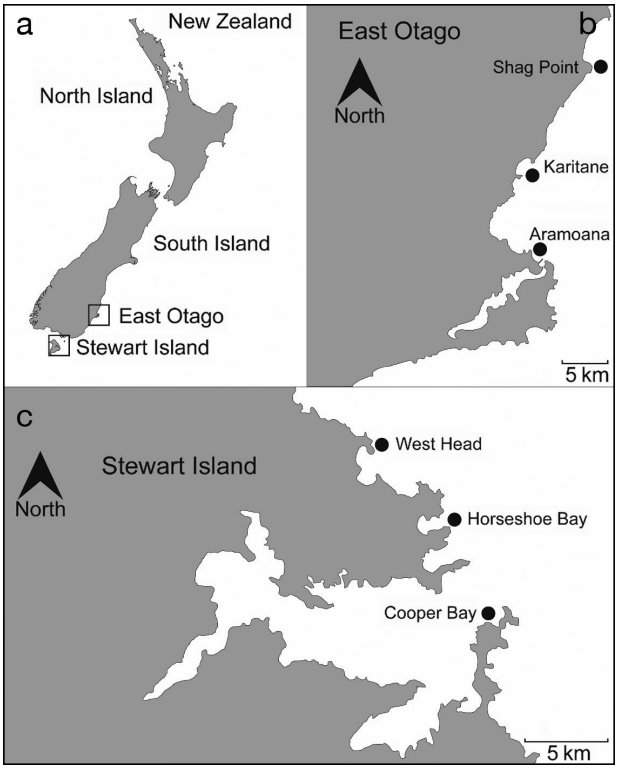

Fig. 1. (a) Study sites in New Zealand; (b) 3 sites were within the East Otago region and (c) 3 sites were within the Stewart Island region

boulders which sloped gently down to a maximum depth of ~10 m before reaching sand. *Macrocystis pyrifera* formed the algal canopy at each site, and the mean annual sea temperature at 2 and 10 m was similar between regions (Desmond et al. 2015). The presence of both *M. pyrifera* and *Durvillaea antarctica* indicates that all sites receive similar moderate wave exposure (Hepburn et al. 2007, Stephens & Hepburn 2014).

Macroalgal species collection

The macroalgal community structure at each site was initially surveyed using SCUBA during summer 2012 to determine the dominant species in each region. At each site, a 30 m transect was laid at the deep (10 m) and shallow (2 m) extent of the reef. Six random 1 m^2 quadrats were placed along the transect line. Randomisation was achieved through computerised random number generation. All fleshy macroalgae within each quadrat (excluding *M. pyrifera* due to its large size) were removed at the holdfast, placed in a catch bag and returned to the laboratory for taxonomic identification and weighing. A total of 28 species were found from the 3 sites in East Otago and 35 from the 3 sites in Stewart Island. The 7 most dominant species in terms of biomass contribution to the community were selected from each region. In each region, the combined biomass of the 7 species (or a combination thereof) comprised >60% of the community biomass at both depth strata. These species were: *Ecklonia radiata* (Laminariales), *Carpophyllum flexuosum, Landsburgia quercifolia* and *Xiphophora gladiata* (all Fucales) in both regions; *Marginariella boryana* (Fucales), *Undaria pinnatifida* (Laminariales) and *Rhodymenia wilsonis* (Rhodymeniales) in East Otago; and *Marginariella urvilliana, Cystophora platylobium* (both Fucales) and *Spatoglossum chapmanii* (Dictyotales) in Stewart Island.

Five replicate adult individuals of each species, over a range of sizes, were subsequently collected from across the 3 sites within each region. These were collected between the depth range of 2 and 10 m in order to capture any variation in epifaunal community associated with depth. Where possible, at least 1 individual of each species was collected at each site depending on its presence. The method of collection involved enclosing each macroalgal individual inside a large plastic bag (120 × 65 cm; 100 microns thick) down to the holdfast. The bag was then sealed above the holdfast using a drawstring cord and the individual removed from the reef (Taylor & Cole 1994). Each bag had a 100 µm mesh opening at the top which allowed water to exit the bag but retained all epifauna greater than the mesh size. All samples were transported in a cooler bin to the laboratory (approximately 1 h travel by boat) and processed immediately.

Epifaunal collection and taxonomic identification

In order to detach epifaunal species, each macroalgal individual was submerged and vigorously washed in 5 l of fresh water. This process was performed twice to achieve maximum removal of epifauna (Taylor & Cole 1994). After the second wash, macroalgae were blotted dry and weighed to determine the wet weight of each individual. The 10 l of fresh water containing epifaunal species from each macroalgal individual was passed through a stacked sieve setup with 2 mesh sizes, 1 mm and 100 µm. Both containers and the collection bag were then rinsed twice through the same sieves to remove any remaining epifauna (Taylor & Cole 1994). Epifauna contained in the sieves were transferred to 70 ml

plastic specimen jars, weighed to determine total biomass, and then ~50 ml of Shandon Glyo-Fixx preservative (Thermo Scientific™) was added to preserve each sample. Partitioning into the size classes of >1 mm and >100 µm was performed to make the taxonomic identification process easier.

Epifaunal identification was conducted on only 3 of the 5 replicate samples due to the time-intensive nature of the identification process. Where possible, 1 sample was chosen from each site; however, if a macroalgal species was not present at a particular site then a randomly selected sample from 1 of the other 2 sites was chosen as the third. Identification was performed on the whole sample using a dissecting microscope. All epifaunal organisms were identified and counted for each replicate. To assess epifaunal richness, classification was performed to the lowest possible taxonomic level. If an organism could not be identified to the species level but was distinctly different from others, it was assigned a number. For multivariate analysis, a broader approach was taken whereby all taxa were grouped by order, with the exception of 'Unidentified Gastropoda' and 'Unidentified Bivalvia' which were 2 groups that could not be resolved any further. This information was used for analysis of community structure where it was important to know the major organism groups and would provide insight into their likely role in the ecosystem. A total of 26 groups were assigned, which encompassed the 119 unique taxa.

Statistical analysis

Epifaunal biomass and density (number of individual organisms) data were all standardised to 100 g wet weight (WW) of macroalgal tissue based on Taylor & Cole (1994). One-way analysis of variance (ANOVA) was used to test for differences in mean epifaunal biomass, density and richness between species within regions. Suárez Jiménez (2017) demonstrated little variation in epifaunal metrics on the same algal species between sites within the Otago region; therefore, no test for site differences within region was undertaken. Pairwise comparisons between means were made using Tukey's honestly significant difference (HSD) post hoc test. To estimate average epifaunal biomass per m^2 of reef at 2 and 10 m depths, the macroalgal biomass of each of the 7 species within the 6 replicate quadrats at each site was multiplied by the region-specific epifaunal biomass that corresponded to that species. In all cases, data met the assumptions of an ANOVA comparison, i.e. normality (Shapiro-Wilk test) and equal variance (Levene median test). Student's *t*-tests were used to test for differences in mean epifaunal biomass, density and richness on macroalgal species shared between regions. For all tests, significance was set at the 5% level (α = 0.05). All univariate analyses were performed using the R statistical software package (V.3.0.1, R Development Core Team 2013). No formal statistical test was carried out on the extrapolated estimates of epifaunal biomass at the reef scale, due to inadequate replication at the site and depth level.

A Bray-Curtis dissimilarity matrix was created based on standardised, square-root transformed, epifaunal density data for each macroalgal species (n = 3). Principal coordinates analysis (PCO) based on Bray-Curtis dissimilarity was conducted to visualise relationships in epifaunal community structure between macroalgal species and regions. Similarity percentages (SIMPER) analysis was performed to quantify the contribution of each group to the dissimilarity between regions. Permutational multivariate ANOVA (PERMANOVA) and pairwise tests based on Bray-Curtis dissimilarity were used to test for differences in epifaunal community structure between macroalgal species and regions using 9999 permutations. Monte Carlo (MC) p values were used due to the low number of unique permutations and the small sample size. Significance was set at the 5% level (α= 0.05). All multivariate analyses were performed using PRIMER (PERMANOVA + for PRIMER, PRIMER-E).

RESULTS

A total of 119 individual epifaunal taxa were identified from the 42 macroalgal samples. When reduced to the order level for multivariate analysis, a total of 26 groups were represented, 24 of which were found at East Otago and 22 at Stewart Island. At the lowest taxonomic classification the 3 most dominant taxa in both East Otago and Stewart Island were Harpacticoida, Gastropoda and Amphipoda. Eatonielliadae, Ischyroceridae and Stegocephalidae were also highly prevalent at East Otago, while Ostracoda, Gammaridae and Serpulidae were abundant at Stewart Island. At East Otago, 12 groups were only found on 1 particular macroalgal species; these were *Ecklonia radiata* (5 groups), *Marginariella boryana* (4), *Undaria pinnatifida* (2) and *Xiphophora gladiata* (1). At Stewart Island, 8 epifaunal groups were found on only 1 particular macroalgal species; these were *E. radiata* (3 groups), *X. gladiata* (3), *Carpophyllum flexuosum* (1) and *Landsburgia quercifolia* (1). Actiniaria were

only found on *E. radiata* in both regions, while Tanaidacea were only found on *U. pinnatifida* at East Otago and on *X. gladiata* at Stewart Island.

MEC metrics

Average epifaunal biomass, density and richness differed significantly among macroalgal species in the East Otago region (Fig. 2a,c,e, Table 1). Biomass ranged between 2.04 g (*U. pinnatifida*) and 9.33 g (*X. gladiata*) 100 g^{-1} WW tissue (Fig. 2a). *U. pinnatifida* hosted approximately a quarter of the epifaunal biomass that the species *L. quercifolia* (Tukey's HSD, p = 0.045), *X. gladiata* (Tukey's HSD, p = 0.017) and *Rhodymenia wilsonis* (Tukey's HSD, p = 0.049) supported (Fig. 2a). It must be noted that *U. pinnatifida* was the only non-native species sampled, and the only non-native in this region. *C. flexuosum* hosted relatively low biomass, but the highest density of organisms, 519 individuals 100 g^{-1} WW tissue (Fig. 2c). The opposite was true for *L. quercifolia*,

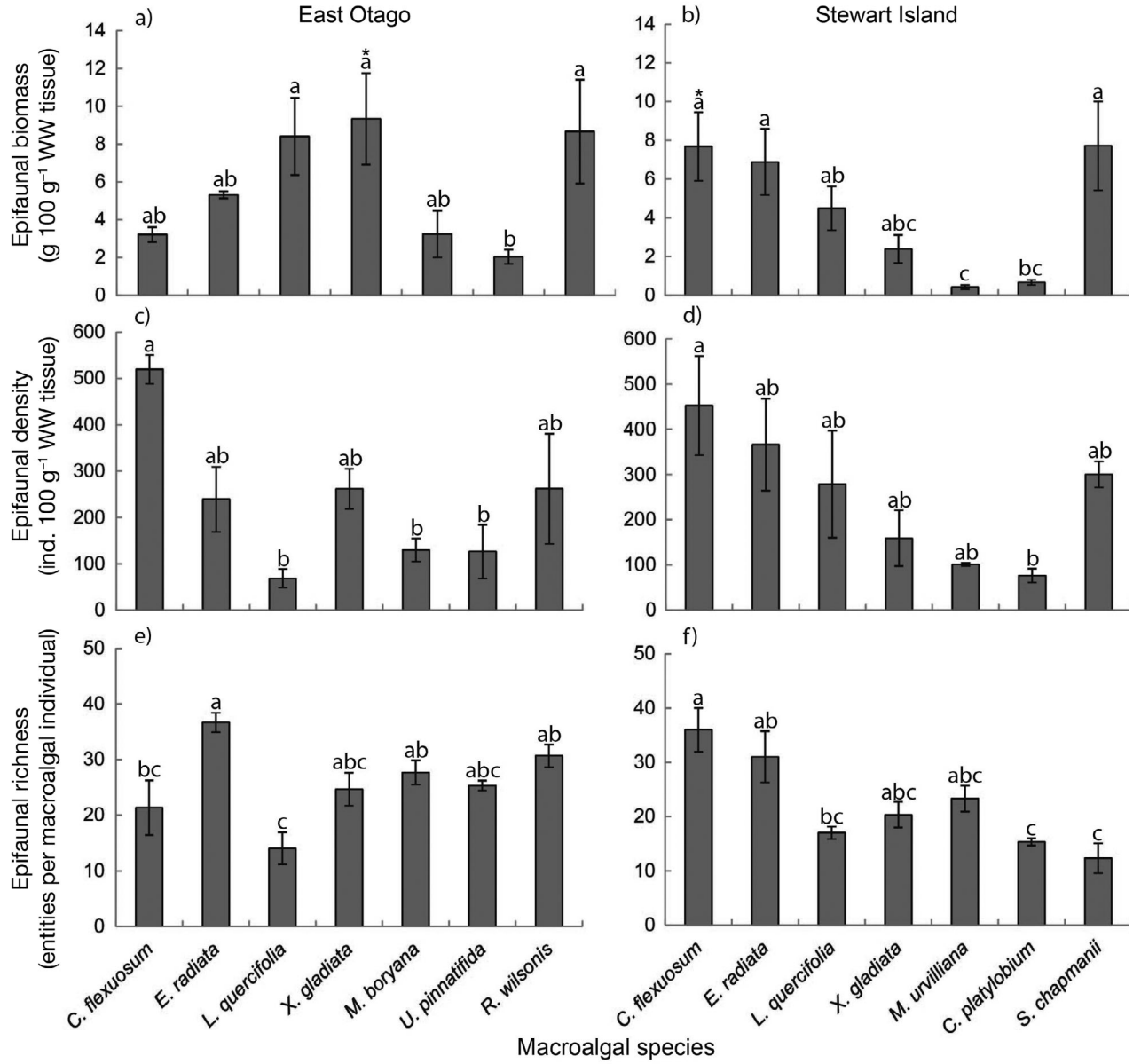

Fig. 2. Epifaunal biomass (n = 5), density (n = 3) and richness (n = 3) on macroalgal species from the (a,c,e) East Otago and (b,d,f) Stewart Island regions. Values represent means (±SE). Significant differences between species within a region are indicated by different letter combinations above bars (Tukey's HSD), and significant differences between regions are indicated by * (α = 0.05). Full species names are given in the 'Results'

Table 1. Results of 1-way ANOVAs comparing mobile epifauna community (MEC) biomass, density and richness between macroalgal species within East Otago and Stewart Island. All differences were significant at α = 0.05

Region	df	*F*	p
Biomass			
East Otago	6, 28	4.1	0.004
Stewart Island	6, 28	9.6	<0.001
Density			
East Otago	6, 14	5.8	0.003
Stewart Island	6, 14	3.3	0.029
Richness			
East Otago	6, 14	6.6	0.001
Stewart Island	6, 14	8.7	<0.001

which hosted relatively high biomass but supported only 68 individuals 100 g^{-1} WW tissue (Fig. 2c). *C. flexuosum* hosted 2- to 7-fold greater density of epifauna compared to *E. radiata, L. quercifolia* (Tukey's HSD, p = 0.002), *M. boryana* (Tukey's HSD, p = 0.007), and *U. pinnatifida* (Tukey's HSD, p = 0.006), with this difference being statistically significant for the latter 3 species (Fig. 2c). The richness of epifaunal organisms ranged between 14 (*L. quercifolia*) and 36 (*E. radiata*) taxa ind.$^{-1}$. *L. quercifolia* supported significantly less richness than *E. radiata* (Tukey's HSD, p = 0.001), *M. boryana* (Tukey's HSD, p = 0.044) and *R. wilsonis* (Tukey's HSD, p = 0.011) (Fig. 2e).

Average epifaunal biomass, density and richness also differed significantly among macroalgal species in the Stewart Island region (Fig. 2b,d,f, Table 1), ranging between 0.43 g (*Marginariella urvilliana*) and 7.72 g (*Spatoglossum chapmanii*) 100 g^{-1} WW tissue (Fig. 2b). *C. flexuosum*, *E. radiata* and *S. chapmanii* supported 10- to 18-fold more epifaunal biomass than *M. urvilliana* and *C. platylobium* (Fig. 2b, Tukey's HSD, p < 0.05 for all comparisons). *L. quercifolia* also supported significantly greater biomass than *M. urvilliana* (Fig. 2b, Tukey's HSD, p = 0.024). Epifaunal density ranged from 76 (*C. platylobium*) to 452 (*C. flexuosum*) individuals 100 g^{-1} WW tissue (Fig. 2d). Only *C. flexuosum* and *C. platylobium* showed a significant difference from one another (Fig. 2d, Tukey's HSD, p = 0.046). The richness of epifaunal organisms ranged between 12 (*S. chapmanii*) and 36 (*C. flexuosum*) taxa ind.$^{-1}$ (Fig. 2f). *C. flexuosum* individuals supported 1–3 times greater richness than *L. quercifolia* (Tukey's HSD, p = 0.013), *C. platylobium* (Tukey's HSD, p = 0.006) and *S. chapmanii* (Tukey's HSD, p = 0.003), while *E. radiata* supported twice the richness of *C. platylobium* (Tukey's HSD, p = 0.046) and *S. chapmanii* (Tukey's HSD, p = 0.024) (Fig. 2f).

No consistent trend in epifaunal biomass existed between regions (Fig. 2a,b). Biomass on *C. flexuosum* was significantly greater in Stewart Island (Fig. 2a,b, Table 2). *X. gladiata* supported 4 times more biomass in East Otago compared to Stewart Island, and *L. quercifolia* twice as much, although the latter difference was not statistically significant (Fig. 2a,b, Table 2). No significant difference in epifaunal density or richness occurred between any of the 4 shared species (Fig. 2c–f, Table 2).

MEC structure

Regional differences in MEC structure were shown by separation in multivariate space (Fig. 3). Numerous groups were responsible for this general separation but some played a more influential role at the regional scale than others (see Table 4). Gammaridae, Amphipoda and Harpacticoida were more abundant on Stewart Island macroalgae (Table S1 in the Supplement at www.int-res.com/articles/suppl/m596p071_supp.xlsx), while macroalgae from East Otago hosted a greater density of Gastropoda, Limnoriidae, Ischyroceridae, Jaeropsidae, Eatoniellidae and Spirillinida (Table S2 in the Supplement). Among the macroalgal species shared between regions, both *C. flexuosum* and *E. radiata* hosted a significantly different epifaunal community, while *L. quercifolia* and *X. gladiata* did not (Fig. 3, Table 3). Differences in the epifaunal community on *C. flexuosum* were driven

Table 2. Results of Student's *t*-tests comparing mobile epifauna community (MEC) biomass, density and richness on macroalgal species shared between regions. Significant differences are in **bold**; significance was set at the 5% level (α = 0.05)

Species	df	*t*	p
Biomass			
Carpophyllum flexuosum	7	−3.793	**0.007**
Ecklonia radiata	8	−0.915	0.387
Landsburgia quercifolia	8	1.674	0.133
Xiphophora gladiata	8	3.511	**0.008**
Density			
C. flexuosum	4	0.585	0.589
E. radiata	4	−1.026	0.362
L. quercifolia	4	−1.751	0.155
X. gladiata	4	1.362	0.245
Richness			
C. flexuosum	4	−2.049	0.109
E. radiata	4	0.965	0.389
L. quercifolia	4	0.667	0.541
X. gladiata	4	0.585	0.589

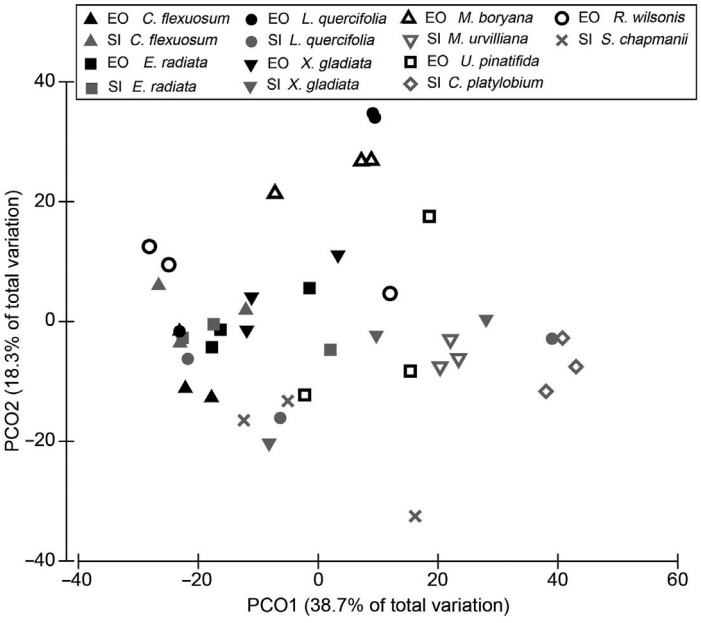

Fig. 3. Principal coordinates analysis based on the square-root transformed density of epifaunal groups at the order taxonomic classification, in East Otago (EO, black) and Stewart Island (SI, grey). Symbols correspond to the 10 macroalgal species examined. Full species names are given in the 'Results'

primarily by a 3.6 times greater density of 'Unidentified Gastropoda' at East Otago which contributed to 51.7% of the total dissimilarity between regions (Table 4). Also of notable importance was a greater density of Harpacticoida at Stewart Island (15.4% of dissimilarity, Table 4). On *E. radiata* the difference between regions was driven by twice as many Amphipoda at Stewart Island (25.6%, Table 4), a comparatively low density of Myodocopida at East Otago (20%, Table 4) and a greater abundance of Harpacticoida at East Otago (19.6%, Table 4).

Table 3. Permutational multivariate ANOVA, main and pairwise tests for differences in mobile epifauna community (MEC) structure for shared macroalgal species between regions. Unrestricted permutation (9999 times) was carried out on the raw data. Significant interactions are in **bold**; significance was set at the 5% level (α = 0.05). Monte Carlo (MC) p values were used due to the low number of unique permutations and the small sample size

Factor	Main test			
	df	MS	Pseudo-*F*	p(MC)
Species by region	13	2229.7	3.99	**<0.001**
Shared species			Pairwise tests *t*	p(MC)
Carpophyllum flexuosum			2.7	**0.028**
Ecklonia radiata			1.75	**0.033**
Landsburgia quercifolia			1.37	0.267
Xiphophora gladiata			2.24	0.056

Estimated epifaunal biomass per m^2

All sites showed greater macroalgal biomass at 2 compared to 10 m depth (Fig. 4a). Shag Point and Karitāne both had relatively low macroalgal biomass at both depths when compared to the other 4 sites (Fig. 4a). When epifaunal biomass was estimated based on the biomass of macroalgae per m^2 of substrate, it was found that at 2 m, epifaunal biomass ranged between 47 g (Karitāne) and 67 g WW m^{-2} (Cooper Bay) (Fig. 4b). At 10 m, this range was greater, 13 g (Karitāne) and 186 g WW m^{-2} (Horseshoe Bay), with Horseshoe Bay supporting the greatest epifaunal biomass of all sites (Fig. 4b). Horseshoe Bay and West Head were the only sites where epifaunal biomass was greater at 10 m than at 2 m even though macroalgal biomass was greater at 2 m (Figs. 4a,b). The proportion of epifaunal biomass to macroalgal biomass at 2 m was greater at Shag Point and Karitāne when compared to Aramoana, Horseshoe Bay and West Head (Fig. 4c).

DISCUSSION

Macroalgal community structure controls MECs

Macroalgal community structure is the driving factor that controls MECs, with both the type of host species present and its abundance being key determining attributes. However, the degree to which these 2 features of community structure influence MECs remains unclear and should be the focus of future work. Within both of our study regions, significant differences in MEC biomass, density and richness were observed between macroalgal species. In general, epifaunal density was greater on macroalgae with a more complex morphology, a finding that is consistent across studies in New Zealand and other countries (Taylor & Cole 1994, Viejo 1999, Parker et al. 2001, Buschbaum et al. 2006, Hooper & Davenport 2006, Gestoso et al. 2010, Suárez-Jiménez et al. 2017). Morphologically complex species such as *Carpophyllum flexuosum*, *Rhodymenia wilsonis* and *Spatoglossum chapmanii* all hosted high epifaunal density, while morphologically simple species such as *Marginariella* spp., *Undaria pinnatifida* and *Cystophora platylobium* hosted relatively lower density. There were exceptions, however. For example *Xiphophora gladiata*, which is con-

Table 4. Similarity percentages (SIMPER) analysis of invertebrate groups and their contribution to the dissimilarity in mobile epifauna community (MEC) structure of shared macroalgal species between East Otago and Stewart Island. Average % dissimilarity is the overall dissimilarity in MEC between regions. % contribution to dissimilarity shows the contribution of each group to the overall dissimilarity between macroalgae from each region. Only groups that accounted for more than 10% of overall dissimilarity are shown. Epifaunal density is given per 100 g (wet weight) of algal tissue

Algal species	Average dissimilarity	Epifaunal group	Average density East Otago	Stewart Island	% contribution to dissimilarity
Carpophyllum flexuosum	45.5	Unid. Gastropoda	272	75.5	51.7
		Harpacticoida	93.1	109	15.4
		Amphipoda	84.2	81.55	10.9
Ecklonia radiata	52.6	Amphipoda	44.7	101.12	25.6
		Myodocopida	4.8	59.7	20
		Harpacticoida	105.6	75.6	19.6
		Unid. Gastropoda	42.6	9.6	11.3
		Canalipalpata	0.5	31.5	10.1
Landsburgia quercifolia	75.7	Harpacticoida	28.1	106.1	34.2
		Amphipoda	23.9	82	22.2
		Unid. Gastropoda	95.6	8.6	19.5
Xiphophora gladiata	60.9	Harpacticoida	125.6	63.4	34.1
		Isopoda	38.6	2.2	21.8
		Amphipoda	48	26.2	16.1

sidered morphologically simple (Taylor & Cole 1994, Suárez-Jiménez et al. 2017), hosted relatively high epifaunal density and biomass at East Otago. The same was true for *Ecklonia radiata*, which is also deemed morphologically simple (Taylor & Cole 1994, Taylor 1998a), but in both regions supported relatively high epifaunal density and biomass. Although it is possible that morphological complexity may differ between regions, or between this and other studies, the large disparities in epifaunal metrics observed indicates that morphology is not the only factor that controls epifaunal communities. It follows that morphology alone cannot be used as the sole indicator of a host's potential to support epifaunal communities, and additional characteristics such as epiphytic growth, nutritional value, palatability and chemical defences likely play a large role (Levin et al. 2002) and should be the focus of future research.

Due to differences in MEC metrics among macroalgal species, differences in the proportion of epifaunal biomass to macroalgal biomass were observed between sites when scaled to the community level. This likely resulted from a relative increased presence or absence of key macroalgal host species. For example, due to the high contribution of the invasive species *U. pinnatifida* at shallow depths at Aramoana, the proportion of epifaunal biomass to macroalgal biomass was less than at other sites at East Otago, whereas at Shag Point and Karitāne, the proportion of epifaunal biomass to macroalgal biomass was the highest out of all sites as a result of a high contribution of *X. gladiata*. Similarly, at deep depths at Horseshoe Bay and West Head, an increased presence of *E. radiata* resulted in greater epifaunal biomass than observed at the other 4 sites, and even greater epifaunal biomass than was found at shallow depths at these 2 sites. An understanding of species-specific contributions to secondary productivity is necessary if we are to comprehend how the trend of global macroalgal loss (Steneck et al. 2002, Gorman & Connell 2009, Strain et al. 2014) and spread of invasive species (Casas et al. 2004, Veiga et al. 2014) will influence higher trophic levels and ecosystem functions (Graham 2004, Ling 2008, Waycott et al. 2009). Mounting evidence suggests that effects are highly variable across geographical regions and depend on the type of change that occurs in community composition (Casas et al. 2004, Wernberg et al. 2004, Dijkstra et al. 2017).

Although the 7 macroalgal species from each region made up the vast majority of community biomass at each site in the present study, the presence of other macroalgae and their potential influence on MECs must be acknowledged. A total of 28 macroalgal species were observed in the East Otago region and 35 in the Stewart Island region. Relatively high levels of host-specific associations were observed, and it is therefore likely that the true richness of epifauna was greatly underestimated at a reef scale by not sampling all macroalgae (Parker et al. 2001). Based on the difference in macroalgal richness between regions, the true difference in regional epifaunal richness may not be as exaggerated as suggested by this study, and epifaunal diversity is likely to be positively correlated to macroalgal diversity (Parker et al. 2001). Future work should focus on assessing how relatively rare macroalgal species influence reef-wide epifaunal communities. Additionally, more resolution regarding the effects of depth on epifaunal communities would help improve the accuracy of reef-wide epifaunal biomass estimates; this would involve replicate samples to be collected at certain depth strata, which was unachievable in this study due to the time-intensive nature of the work.

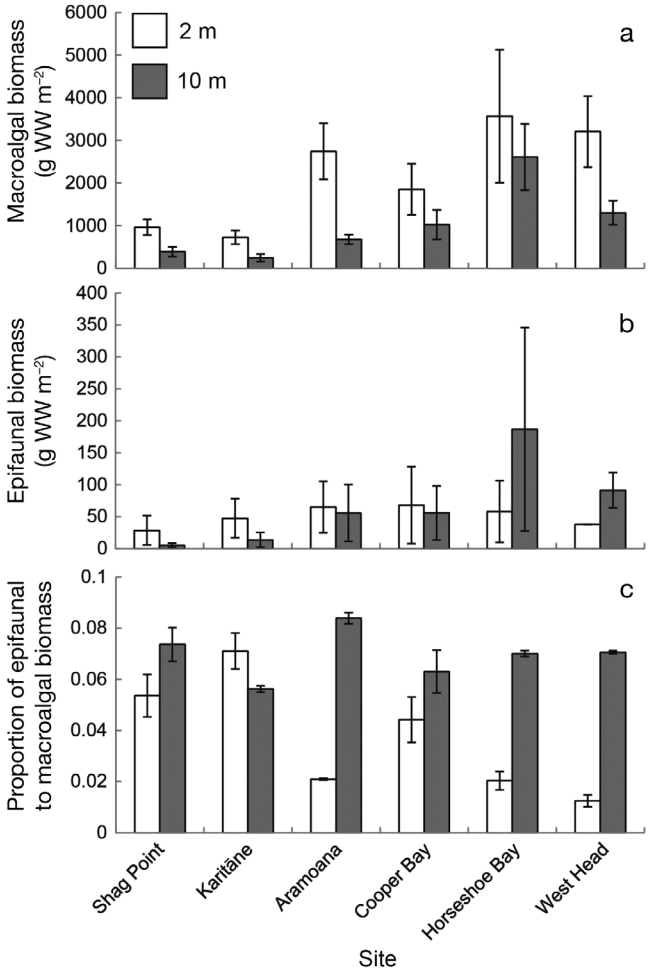

Fig. 4. (a) Macroalgal biomass, (b) estimated reef scale epifaunal biomass and (c) proportion of epifaunal biomass to macroalgal biomass at each of the 6 study sites at 2 m (white bars) and 10 m depth (grey bars). Values represent means (±SE)

Drivers of regional MEC variability

Highly abundant epifaunal groups tended to be the main drivers of difference in MEC structure at the regional scale. Although the dominant groups were generally similar between regions, their relative density differed. At Stewart Island, Harpacticoida were more abundant and evenly distributed across macroalgal species, as were Gammaridae and the cumulative Amphipoda group (i.e. the group containing multiple taxa that could not be identified to a lower taxonomic level). At East Otago, particularly high densities of Gastropoda, Limnoriidae and Ischyroceridae were observed. The reasons for differences in group density are difficult to disentangle but are most likely the result of a combination of factors such as competitive interactions (Taylor 1997, Cacabelos et al. 2010), host morphology (Taylor & Cole 1994, Taylor 1998a, Parker et al. 2001) and predation by reef fishes (Russell 1983, Taylor 1998a) that are more abundant at Stewart Island (Desmond 2016). Although wave exposure was estimated to be similar between sites based on the structure of the macroalgal community, future work should focus on determining the role it plays in influencing MEC structure (Norderhaug & Christie 2011). Another influential factor that may differ between regions is the presence of epiphytic algae, a key food source for epifauna (Edgar & Aoki 1993), but a factor that was not measured in this study. Due to likely differences in sediment loading and light availability between these 2 regions (Desmond et al. 2015), the availability of epiphytic algae, which is typically negatively correlated with increased sediment and decreased light (Edgar 1991, Schwarz et al. 2006), may also differ between regions and influence MEC dynamics (Johnson & Scheibling 1987). However, it was noted that epiphyte presence was visibly absent or extremely low in both regions (M. Desmond pers. obs.).

The East Otago region was observed to support greater epifaunal richness in terms of total number of taxa found, as well as more regional and macroalgal specific epifaunal associations. Among the 15 groups that were only found at East Otago, no clear common characteristic was present among the groups that would suggest adaptation to particular environmental conditions. All of the 15 groups were relatively rare, both in density (typically less than 1 ind. per 100 g WW tissue) and in distribution (10 were found on only 1 or 2 macroalgal species). The same was true of the 4 unique groups found at Stewart Island. This suggests that regional differences in MEC structure may relate more to connectivity and dispersal (Cowen & Sponaugle 2009) than to region-specific adaptation. Nikula et al. (2013) demonstrated that long-distance dispersal of species via passive rafting on kelp *Durvillaea antarctica* results in significant connectivity between islands in New Zealand's southern waters. However, the Southland Current, which flows northward from the bottom of Stewart Island up the east coast of the South Island (Heath 1981, 1985, Chiswell 1996, Chiswell & Rickard 2011), may play a role in limiting southward dispersal and could account for the greater number of epifaunal taxa present in East Otago.

The estimation of site-specific productivity, at multiple trophic levels, is necessary in order to understand energy transfer at a scale appropriate for the management of habitat and fisheries. When MEC metrics from this study were compared to those of the same macroalgal species elsewhere in New Zealand

(Taylor 1994, 1998b, Taylor & Cole 1994, Schwarz et al. 2006), southern macroalgal individuals were shown to support relatively high epifaunal densities and similar richness. Suárez-Jiménez et al. (2017), who conducted the only other study to quantify MEC metrics for southern New Zealand, reported similar MEC density values to those of this study. Suárez-Jiménez et al. (2017) also showed that, while epifaunal density and diversity remained relatively stable across sites and season at East Otago, the epifaunal community assemblage differed among macroalgal species. Therefore, estimates of secondary productivity should not be generalised across regions, even if the same or similar macroalgal species are present.

Conclusions

This study demonstrates that both macroalgal community structure and biomass play a key role in controlling mobile epifaunal communities within rocky reef ecosystems of southern New Zealand. It also highlights the fact that some macroalgal species may contribute disproportionately to secondary biomass and that predicting species contribution cannot be based solely on host morphological complexity. Finally, the true epifaunal richness in each region was likely underestimated by only sampling the 7 most dominant species, and also by the level of taxonomic resolution of the epifauna currently possible. Further work should focus on determining the role of additional species in supporting MECs as well as on how macroalgal diversity influences epifaunal diversity and community function. This information is particularly relevant as the global trend of macroalgal loss increases and there is a need to understand what such loss may mean for higher trophic level communities, including associated fisheries.

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