

Turf-forming algal assemblages on temperate reefs are strongly influenced by the territorial herbivorous fish *Parma mccullochi* (Pomacentridae)

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ABSTRACT: Species belonging to the family Pomacentridae play a key role in altering algal assemblages in tropical systems, but our understanding about this family's role in temperate systems is limited. We examine the role of the abundant and territorial pomacentrid *Parma mccullochi* as an herbivore in temperate waters of southwestern Australia. Through dietary analyses, we showed that this species consumed predominantly red foliose and filamentous algae that were positively selected based on electivity indices. The species composition of macroalgae differed significantly between inside and outside *P. mccullochi* territories, with commonly ingested algae such as *Hypnea* spp. characterising the territory assemblages, while brown algae such as kelp *Ecklonia radiata*, and other foliose or coralline red algae characterised reef area outside the territories. Total algal biomass was significantly lower, while species richness was higher, inside compared to outside territories. In contrast, a caging experiment inside *P. mccullochi* territories showed that species composition, species richness and biomass of recruiting algae did not differ significantly in treatments where damselfishes were excluded or able to forage. A visual census indicated that *P. mccullochi* territories covered nearly 40% of the reef in the study region. We conclude that, while other biological or physical processes are likely to create the patches within kelp canopies where *P. mccullochi* territories are established, the species appears to have a strong and extensive influence in maintaining lower standing crop and higher diversity in turf-forming algal assemblages in this temperate region. Understanding the role of herbivores in temperate regions is becoming increasingly important due to the effects of climate change through the shifting ranges of tropical species into temperate systems.

KEY WORDS: Herbivory · Pomacentridae · Algal composition · Recruitment · Diet

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INTRODUCTION

Herbivory is one of the major forces controlling the evolution, distribution and abundance of plants in marine and terrestrial ecosystems (Huntly 1991). It therefore has the potential to have direct and indirect effects on the availability of resources to other organisms by changing the community structure, diversity (Ceccarelli et al. 2001, Hata & Kato 2004) and physical state of the environment (Jones et al. 1997). The

diversity of herbivorous fish species and associated rates of herbivory can have an extensive effect on reef-algae assemblages in tropical reef systems (Andrew & Jones 1990, Ceccarelli et al. 2001, Ceccarelli 2007, Doropoulos et al. 2013). In comparison, the diversity of herbivorous fish species is considered to be relatively low in temperate ecosystems (Tolentino-Pablico et al. 2008), where large invertebrates, such as sea urchins (Foster & Schiel 2010) and gastropods (Connell & Vanderklift 2007) are gener-

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ally considered to be key consumers of macroalgae. Indeed, the diversity, abundance and grazing rates of herbivorous fishes has been regarded as low in temperate regions due to temperature-limited digestive processes (e.g. Floeter et al. 2005, Bates et al. 2013), but this conclusion is highly contentious (Clements et al. 2009). Herbivorous species can be highly abundant in some temperate regions (e.g. Jones 1992, Kingsford 2002, MacArthur & Hyndes 2007, Vergés et al. 2009), and there is growing evidence that they can have an impact on the algal assemblages (Andrew & Jones 1990, Vergés et al. 2009). Those species shown to graze on macroalgae on temperate reefs tend to graze on canopy-forming species, such as *Odax pululus* on *Ecklonia radiata* (Taylor & Schiel 2010) and *Sarpa salpa* on *Cystoseira* spp. (Vergés et al. 2009), thereby altering canopy structure.

The Pomacentridae is one of the most representative families of herbivorous fishes inhabiting both tropical and temperate reefs (Allen 1991, Aguilar-Medrano et al. 2011), although not all the species are herbivores (Ceccarelli 2007). Most species are tropical (Aguilar-Medrano et al. 2011), with some displaying aggressive and territorial behaviour, protecting algal food sources and shelter in their territories (Low 1971). Since pomacentrid territories can cover >50% of reef substrata (Ceccarelli 2007), pomacentrids can play an important role in shaping tropical reef algal communities (Ceccarelli et al. 2001) by (1) directly feeding on algae; (2) weeding and farming activities; and (3) competitively excluding other herbivorous fishes. For example, through removing undesirable algae and chasing other fishes from their territories, *Stegastes nigricans* maintains territories dominated by the red filamentous alga *Polysiphonia* sp. (Hoey & Bellwood 2010). Fewer pomacentrid species occur in temperate reefs (Aguilar-Medrano et al. 2011), but some, particularly *Parma* spp., are very abundant and display aggressive territorial behaviour (Moran & Sale 1977, Choat 1982), and algae form a major part of their diets (Moran & Sale 1977, Buckle & Booth 2009). Thus, although Jones (1992) concluded that *Parma microlepis* plays a only minor role in maintaining algal community structure in southeastern Australia, other species may play a greater role in that process.

Parma mccullochi is an abundant pomacentrid that displays strong territorial behaviour (Saunders 2011) in southwestern Australia, where the diversity of reef algae is high (Bolton 1996). This species tends to inhabit gaps within the canopy-forming kelp on reefs (Thomson et al. 2012). In this study, we investigated if the territorial, herbivorous pomacentrid *Parma mccullochi* influences the assemblage structure and

diversity of macroalgae in gaps within kelp habitats in temperate reefs. To achieve our aim, our specific objectives were to (1) determine the dietary composition and feeding selectivity of *P. mccullochi*; (2) compare the algal assemblages inside and outside *P. mccullochi* territories and determine whether the feeding activity of the species affect the algal composition and recruitment of algae on temperate reefs; and (3) determine the proportion of reef occupied by *P. mccullochi* territories. Based on our results, we discuss the possible mechanisms by which the fish influence algal assemblages, and more broadly, the implications of these results in our understanding of herbivory in temperate marine systems.

MATERIALS AND METHODS

Study area

This study was undertaken in Marmion Marine Park (31° 50' S, 115° 42' E) in temperate southwestern Australia, where subtidal habitats primarily comprise sandy patches, seagrass and kelp-dominated (particularly *Ecklonia radiata*) limestone reefs (Wernberg et al. 2003). Study sites were randomly chosen to represent the reef habitats where *Parma mccullochi* is abundant.

Diet of *P. mccullochi*

Juvenile (<20 cm total length [TL], n = 5) and adult (>20 cm TL, n = 5) *P. mccullochi* were collected by hand-spear at each of 4 sites located 3 to 10 km apart on 2 sampling occasions in April and September 2012. Juvenile and adult fish were examined separately as other pomacentrids have been shown to undergo ontogenetic dietary changes (Letourneur et al. 1997). All fish were collected between 10:00 and 14:00 h, as pilot studies indicated that gut fullness would be greatest and dietary items least digested during this time. Once captured, each fish was placed in an ice slurry until its total length (to 1 mm) and weight (to 0.1 g) were measured and the stomach was removed, weighed (to 0.1 g) and frozen. Once thawed, the contents of each stomach were evenly spread over a grid and a dissecting microscope was used to identify the species of algae at each of 100 systematically placed points on the grid (Buckle & Booth 2009). The percentage contribution of each taxon to the total of each sample was then calculated.

Algal assemblage within and outside *P. mccullochi* territories

The boundaries of 8 randomly selected *P. mccullochi* territories at each of 4 study sites (as described above) were determined by observing the movements of each fish for 15 min (Altmann 1974, Saunders et al. 2013) prior to sampling. At each site, a knife and scraper were used to collect all algae from within a 25 × 25 cm quadrat that was randomly placed on similar habitat inside and outside each of the 8 territories. Observations and sampling were carried out between the 16th and 25th of February 2012. Samples were stored on ice in the field and frozen until they were thawed and rinsed to remove sediment, and then separated into taxa and oven dried at 80°C for 48 h. The dried tissue of each taxon were then weighed to 0.001 g.

Impact of *P. mccullochi* feeding on algal recruitment

At each of 3 of the 4 sites, 12 roughened 25 × 25 cm PVC tiles (Smale et al. 2011) were fixed with pegs to the reef inside 12 randomly chosen *P. mccullochi* territories for 4 mo (January to May), a time period considered suitable to examine the recruitment of algae on reefs (Doropoulos et al. 2013). The degree of wave exposure precluded deploying tiles at the fourth site. At each site, 4 tiles were caged to prevent feeding by *P. mccullochi*, while 4 were uncaged and 4 were partially caged (i.e. with 2 open sides) to act as cage controls. The cages were 27.5 × 27.5 cm at the base, 40 cm high and covered with 5 cm mesh. The tiles and cages were inspected and maintained every 10 d (Smale et al. 2011) for the duration of the experiment. After being retrieved from the field, each tile was rinsed to remove sediment and a high-resolution image was taken for reference. The algae were scraped from each tile, separated into taxa and oven dried at 80°C for 48 h. The dried tissue of each taxon was then weighed to 0.001 g.

Proportion of reef occupied by *P. mccullochi* territories

The abundance of adult (i.e. >20 cm TL) *P. mccullochi* was recorded at 12 reef sites in Marmion Marine Park, including the 4 used for the prior parts of this study. Sites were separated between 1 and 10 km over a total area of 50 km². At each site, fish were

counted during a 20 min unidirectional swim along a haphazardly placed 10 m wide belt transect (Meyer & Holland 2005). The linear distance covered by the counter on each transect was recorded and used to determine the number of fish m⁻². This survey was carried out on 3 occasions over 12 mo from August 2012. The proportion of each sampling transect that was occupied by *P. mccullochi* territories was estimated by multiplying the number of fish on the transect by the average area of a *P. mccullochi* territory (9 m²) estimated by Saunders (2011) and expressed as a proportion of the total area of the belt transect.

Data analysis

Dietary composition was tested between adult and juvenile stages (2 levels; fixed factor), time of the year (2 levels; random factor), and sites (4 levels; random factor) nested in adult and juvenile stages. The composition, total biomass and species richness of algae on the reefs were tested inside and outside *P. mccullochi* territories (2 levels, fixed factor), with sites nested in territory (4 levels, random factor). Similarly, the composition, total biomass and species richness of algae on the settlement tiles were tested among treatments (3 levels; fixed factor), with sites nested in treatment (4 levels, random factor). All analyses were undertaken using the PERMANOVA+ add-on package for PRIMER v. 6 (Anderson et al. 2008).

Dietary composition and algal composition data, based on the percentage contribution of each taxon, were subject to multivariate analyses. A Bray-Curtis similarity matrix was constructed using square-root transformed data, which were tested for homogeneity using a sphericity test (Mauckly test). Analyses were based on 9999 permutations. Dissimilarity among samples was visually represented by constructing nMDS plots using PRIMER v.6. The algal species likely to be driving the differences in algal composition across treatments (either territories or cages) were determined by their correlations (Spearman correlation coefficient set at $r > 0.6$) with the canonical axes of the nMDS.

For univariate analyses (biomass and species richness of algae on reefs and tiles), we used Euclidean distance-based linear models with significance tests by permutation using the PERMANOVA+ add-on package for PRIMER v.6 (Anderson et al. 2008). Estimates of sums of squares using Euclidean distance measures are equivalent to parametric ANOVA, but without the assumption of normality due to the use of

permutations (Anderson et al. 2008). Data were tested for homogeneity using a sphericity test (Mauckly test), and in the case of biomass data, log-transformation was required to achieve homogeneity of variance.

Feeding selectivity measures were based on comparing the mean overall percentage contribution of algal taxa to the diet of *P. mccullochi* collected in April to the mean overall percentage contribution of algal taxa in their territories in the same period. We used Ivlev's electivity index (E_i) (Ivlev 1961) due to its simplicity and its suitability for dietary studies (Jones & Norman 1986). $E_i = (r_i - p_i) / (r_i + p_i)$, where r_i is the percentage of the i^{th} algal species in the diet and p_i is the percentage of the same i^{th} species in the field. E_i values range from -1 (lowest selectivity) to 1 (maximum selectivity), with a value of zero indicating random feeding (Ivlev 1961).

RESULTS

Diet of *P. mccullochi*

Twenty-two algal taxa were identified in *Parma mccullochi* stomachs (Table 1), all of which were $\geq 80\%$ full and typically contained a high proportion of undigested items. A variety of red (Rhodophyta), green (Chlorophyta) and brown (Eterorkontophyta) algae were consumed, with red algae forming the most important dietary items in terms of frequency of occurrence and volume (Table 1).

PERMANOVA showed that there was no significant difference (at $p = 0.05$) between the dietary compositions of juvenile and adult *P. mccullochi* ($p = 0.6253$), but there was a significant difference among sites ($p = 0.0001$) and between months ($p = 0.0023$) as well as a significant interaction between site and month ($p = 0.0001$; Table 2). In April (Fig. 1A), *Dasyclonium* spp., *Brongniartella* sp. and *Hypnea* spp. were the species that characterised the diet of *P. mccullochi* collected at Sites 1 and 2, while *Hypnea* spp. and *Ulva lactuca* characterised the diets of fish at Sites 3 and 4. During August (Fig. 1B), *Brongniartella* spp. characterised the diets of fish at Sites 1

Table 1. Frequency of occurrence (%F), percentage volume in the guts (%V Gut) and inside the territories (%V Terr), and Ivlev's Electivity index (E_i) of dietary items in the stomachs of juvenile and adult *Parma mccullochi*. Data have been pooled from 2 sampling occasions (April and August 2012), 4 sites, and 40 juveniles and 40 adults

Species	%F	%V Gut	%V Terr	E_i
Rhodophyta	76.355	87.94	25.12	
Foliose	22.69	23.93	8.59	
<i>Dictyomenia sonderi</i>	17.1	1.00	7.23	-0.76
<i>Dictyomenia tridens</i>	6.95	1.64	0.52	0.47
<i>Heterodoxia</i> sp.	19.9	2.05	0.36	0.69
<i>Rhodimonia sonderi</i>	30.7	1.32	0.47	0.45
Unidentified	38.8	17.92	0	0
Corticated	30.705	23.79	13.11	
<i>Asparagopsis</i> sp.	13.05	0.89	2.96	-0.54
<i>Botrocladia</i> sp.	6.7	0.23	3.09	-0.87
<i>Champia</i> spp.	47.4	2.74	0.11	0.92
<i>Hypnea</i> spp.	92	18.96	3.89	0.65
<i>Pterocladia lucida</i>	9.3	0.40	2.80	-0.75
<i>Pterocladia rectangularis</i>	15.8	0.58	0.26	0.38
Filamentous	22.96	40.23	3.41	
<i>Ceramium</i> spp.	41.25	13.79	0.01	1.00
<i>Brongniartella</i> sp.	27.15	18.16	2.54	0.75
<i>Dasyclonium</i> spp.	8.25	6.10	0.42	0.86
<i>Polysiphonia</i> sp.	11.95	0.52	0.37	0.15
<i>Erythrimenia minuta</i>	26.2	1.66	0.08	0.91
Heterokontophyta	59.335	6.71	2.91	
Foliose	25.685	4.43	2.33	
<i>Dictyata dichotomia</i>	14.65	0.75	0.48	0.19
<i>Dictyopteris</i> spp.	53.2	3.38	0.71	0.65
<i>Sargassum</i> spp.	9.2	0.29	1.15	-0.60
Filamentous	33.65	2.29	0.58	
<i>Hinksia</i> spp.	33.65	2.29	0.58	0.57
Chlorophyta	78.7	5.30	0.032	
Foliose	41	3.79	0.01	
<i>Ulva</i> spp.	41	3.79	0.01	1.00
Filamentous	37.7	1.52	0.31	
<i>Cladophora</i> sp.	37.7	1.52	0.31	0.64
Seagrasses	5.1	0.05	0	
<i>Amphibolis</i> spp.	5.1	0.05	0	1.00

and 2 while *Ceramium* spp. and red foliose algae dominated diets at Sites 3 and 4.

Ivlev's electivity index indicated that *P. mccullochi* exhibited a high positive selectivity for red filamentous algae, such as *Ceramium* spp., *Brongniartella* sp. and *Dasyclonium* spp. (Table 1). Other positively selected taxa that contributed notably to overall dietary volume were *Hypnea* spp. *Dictyopteris* spp. and *Ulva* spp. Conversely, red foliose and corticated algae, such as *Dictyomenia sonderi*, *Botrocladia* sp., and *Pterocladia lucida*, showed a high negative selectivity. The high electivity index value for *Amphibolis* spp. (Table 1) was due to this seagrass species not being recorded in the assemblage of the fish territories, but being present in small volumes in the guts of fish.

Table 2. Results of a nested PERMANOVA testing life stage (L: fixed factor, juveniles or adults) and temporal differences in the diet of *Parma mccullochi*. Mixed design with sites (S: random factor, 4 levels) nested in treatments (fixed factor, 2 levels), and time of the year month) (M: fixed factor, 2 levels). Fish were collected in April and August 2012, data were square root transformed. Significant ($p < 0.05$) values are in **bold**

	df	MS	Pseudo- <i>F</i>	p (perm)	perms
L	1	4913.5	0.55	0.6253	1667
M	1	33 726	8.80	0.0023	9946
S(L)	6	9084.8	7.83	0.0001	9880
L × M	1	4681.7	1.22	0.3139	9954
S(L) × M	6	3863.3	3.33	0.0001	9826
Residual	59	1160.5			

Algal assemblages inside and outside *P. mccullochi* territories

PERMANOVA showed that the species composition of macroalgae differed significantly between inside and outside the territories of *P. mccullochi* ($p = 0.0103$) and also among the 4 sites ($p = 0.0022$; Table 3). The difference between inside and outside the territories was supported by samples associated with inside or outside the territories forming clusters on the nMDS plot (Fig. 2). Algal assemblages inside the territories were characterised by *Hypnea* spp. and *Dasyclonium* spp., while those outside the territories were characterised by the brown algae *Ecklonia radiata*, *Sargassum* spp. and the foliose red alga *Rhodimenia sonderi*. Mean biomass of *Hypnea* spp. and *Dasyclonium* spp. was higher inside (0.601–0.892 g) compared to outside the territories (0.063–0.022 g). In contrast, mean biomass of *Ecklonia radiata* and *Sargassum* spp. were higher outside (10.391–51.556 g) compared to inside (0.271–3.316 g) the territories. Species richness was higher inside than outside the territories ($p = 0.0114$, Fig. 3A), and there was no significant difference among sites ($p = 0.4325$, Table 3). In comparison, total algal biomass

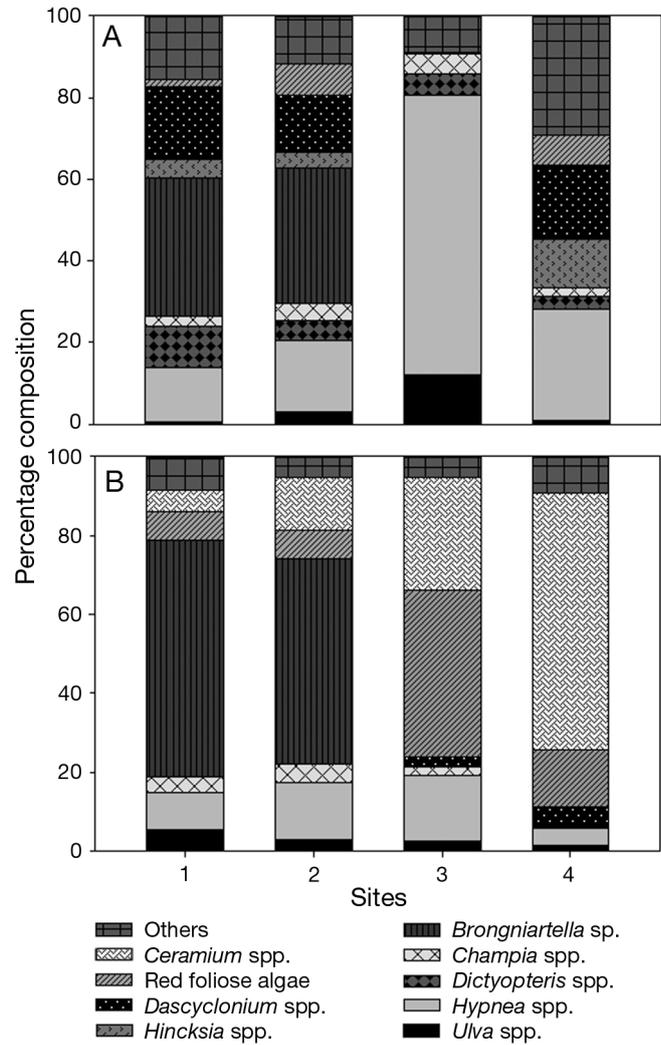


Fig. 1. Percentage contribution of the various algal taxa to the diet of *Parma mccullochi* collected in (A) April and (B) August 2012, within each of 4 sites

inside the territories was significantly lower than outside the territories ($p = 0.0126$, Fig. 3B), and there was no significant difference among sites within treatment ($p = 0.5123$, Table 3).

Table 3. Results of a nested PERMANOVA testing the differences in terms of algal species composition, algal species richness and total biomass of algae inside and outside *Parma mccullochi* territories. Nested design with sites (random factor, 4 levels) nested in treatments (fixed factor, 2 levels). Species richness and algal composition data were square root transformed, and biomass data were $\log(x+1)$ transformed. Significant ($p < 0.05$) values are in **bold**

	df	— Species composition —			— Species richness —			— Total biomass —		
		MS	Pseudo- <i>F</i>	p	MS	Pseudo- <i>F</i>	p	MS	Pseudo- <i>F</i>	p
Treatments	1	33892	7.72	0.0103	3228.3	36.83	0.0114	3382.3	18.16	0.0126
Sites (Treat)	6	4397.2	1.60	0.0022	87.654	1.02	0.4325	186.18	208.4	0.5123
Residual	54	2742.8			86.187			208.4		

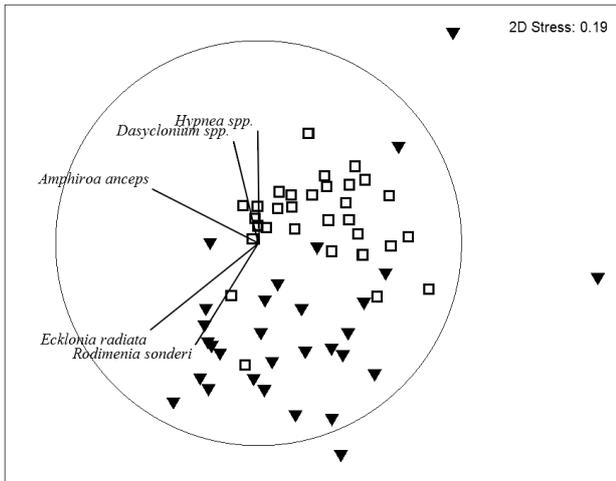


Fig. 2. Non-metric multidimensional scaling (nMDS) plot based on a Bray-Curtis similarity matrix representing the algal composition inside (squares) and outside (triangles) the territories of *Parma mccullochi*. Vectors represent the species characterizing the algal composition of the samples (Spearman correlation = 0.5). Data were square root transformed

Impact of the feeding activity of *P. mccullochi* on the algal recruitment

Species richness and total algal biomass of algal recruits on tiles did not differ among treatments (Fig. 4), but did differ among sites ($p < 0.05$, Table 4). Species of algae with the greatest biomass were *Dictyopterus* spp. (mean biomass = 0.206 g) and *Ceramium* spp. (mean biomass = 0.580 g). In contrast, *Ecklonia radiata* was completely absent. In terms of species composition of algae on tiles, there was no significant treatment effect ($p = 0.8377$, Fig. 5), but there was a site effect within treatment ($p = 0.0001$, Table 4). This was highlighted by a general separation of samples from Sites 1, 2 and 3 (data not shown).

Density of *P. mccullochi* and the percentage of reef occupied by their territories

The mean density (\pm SE) of adult *P. mccullochi* over the 12 sites and 3 sampling times was 42.1 ± 16.8 fish

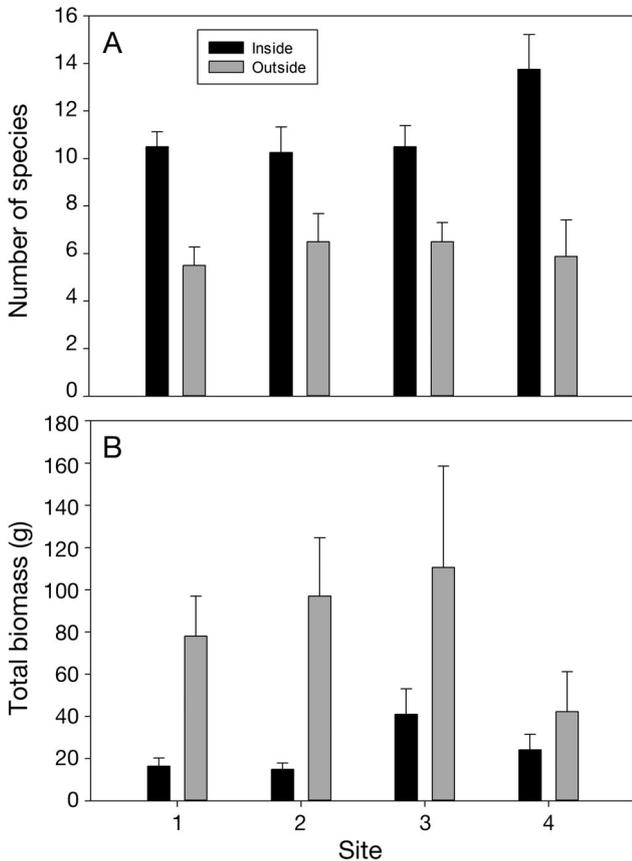


Fig. 3. Mean +SE (A) species richness and (B) total biomass of algae inside and outside the territories of *Parma mccullochi* at 4 sites

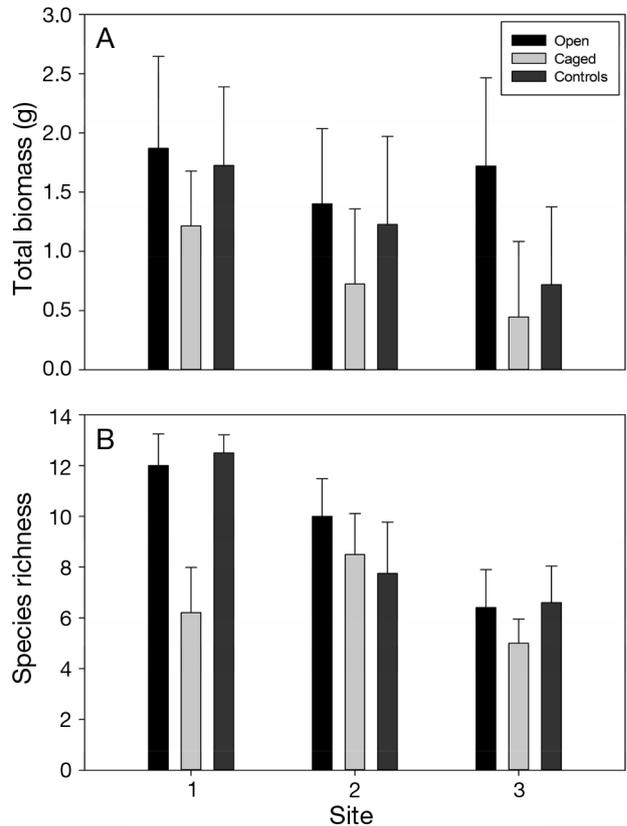


Fig. 4. Mean +SE (A) total biomass and (B) species richness of recruiting algae on tiles within caged, uncaged (open) and control treatments at 3 sites, examining the effect of *Parma mccullochi* feeding activity on recruiting algae

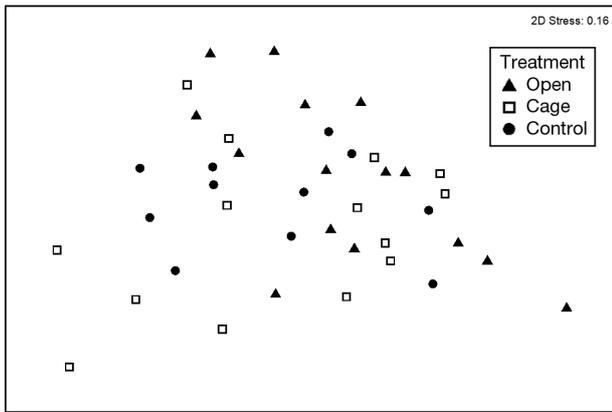


Fig. 5. nMDS plot based on a S17 Bray-Curtis similarity matrix representing the species composition of algal recruits on PVC tiles, highlighting the differences among the caged, uncaged (open) and control treatments. Data were square root transformed

1000 m⁻² and ranged from 34.5 ± 13.1 to 51.7 ± 10.2 fish 1000 m⁻². Based on adult *P. mccullochi* each using an average of about 9 m² of reef as territory (Saunders 2011), the total area used by this species accounted for 39% (388.3 ± 135.6 m² 1000 m⁻²) of the total area surveyed and ranged between 31 and 46% of the reef surface.

DISCUSSION

This study has shown that the algal assemblages inside the territories of the herbivorous *Parma mccullochi* were distinctly different from areas outside their territories. Compared to areas outside of territories, assemblages sampled inside territories contained about 1.5 to 2.0 times more algal species, 0.2 to 0.6 times the algal biomass, and a different algal species composition. It is unlikely that grazing by *P. mccullochi* created the observed open patches in the canopy-forming kelp, but the results suggest that *P.*

mccullochi at least maintain lower algal biomass and different algal diversity in their territories through selective feeding on particular red macroalgae. Furthermore, based on our density estimates and known territorial size (Saunders 2011), *P. mccullochi* territories could make up almost 40% of the reef area. This suggests that the feeding activities of *P. mccullochi* has widespread influence on algal assemblages in this temperate region; likely similar to its tropical counterparts, which are considered to exert considerable influence on shaping benthic communities in those systems (Jones et al. 2006, Barneche et al. 2009). Thus, our study supports the growing evidence that herbivory by fishes can be a significant process in temperate reef systems (Andrew & Jones 1990, Verges et al. 2009, Taylor & Schiel 2010). While these earlier studies suggest that species such as the odacine *Odax pullus* and the sparid *Sarpa salpa* feed on canopy-forming species of brown algae, our study suggests that the consumption of red algae by *P. mccullochi* maintains different red algal assemblages over extensive areas.

Although the algal assemblages inside and outside *P. mccullochi* territories differed in biomass and species diversity, it should be noted that the initial difference in the algal assemblages inside and outside their territories may relate to the fish establishing territories in areas altered by other biological or physical processes, such as the dislodgement of kelp during storm events (Thomson et al. 2012). While areas outside the territories are likely to be influenced by other biological or physical processes, we argue that grazing by *P. mccullochi* in its territories is likely to be a major factor further altering or maintaining the algal assemblages in those patches, through grazing predominantly on particular red algal species.

In tropical systems, pomacentrids are considered to have an impact on algal assemblages via 3 different, but not mutually exclusive, mechanisms: (1) directly feeding on algae; (2) weeding and farming activities;

Table 4. Results of a nested PERMANOVA testing the effect of *Parma mccullochi* feeding activity on recruiting algae and the differences in the composition of recruiting algae on tiles among treatments (caged, uncaged and controls) and sites. Nested design with sites (random factor, 4 levels) nested in treatments (fixed factor, 3 levels). Species richness data were square root transformed, and biomass data were log transformed. Significant (p < 0.05) values are in **bold**

	df	— Species composition —			— Species richness —			— Total biomass —		
		MS	Pseudo-F	p	MS	Pseudo-F	p	MS	Pseudo-F	p
Treatments	2	1937.1	0.52	0.8377	1.091	1.35	0.3475	0.6336	3.51	0.0742
Sites (Treat)	6	3873.8	4.08	0.0001	0.8299	2.47	0.045	0.1848	2.42	0.0473
Residual	31	950.01			0.3352			7.6665		

and/or (3) excluding other competitive herbivorous fishes (Brawley & Adey 1977, Hata & Kato 2004, Hoey & Bellwood 2010, Saunders 2011). Our results suggest that *P. mccullochi* could influence algal assemblages through the first and possibly the second mechanism, but not the third. The lower biomass of algae inside *P. mccullochi* territories suggests that this species can alter or maintain the algal community through higher levels of grazing than in those areas outside the territories. This is supported by Saunders et al. (2013), who showed that this damselfish species alters algal assemblages in its nests during the breeding season, presumably through intensive cropping of foliose and filamentous algae. Observations by those authors suggest that farming activities were not a mechanism for altering algal assemblages. Since our study was carried out in autumn, well after nesting activities which occur from late spring to summer, we have shown that *P. mccullochi* influences algal assemblages more broadly in their territories, which average ca. 9 m² (Saunders 2011). In comparison to this temperate species, the tropical territorial damselfishes *Plectroglyphidodon lacrymatus* and *S. nigricans* promote the growth of preferred algae inside their territories through farming activities and territorial behaviour (Hata & Kato 2004, Jones et al. 2006). However, *Eupomacentrus planifrons*, another tropical territorial damselfish, has an impact on the algal composition of the reef by excluding other herbivorous fish from their territories, where they maintain a higher algal biomass and biodiversity, while the algae on flat reef outside the territories are heavily grazed by other herbivorous species (Brawley & Adey 1977). Selective feeding and farming are foraging mechanisms considered to promote the growth of the preferred algae inside territories (Klumpp et al. 1987, Jones 1992), and the former mechanism is likely to be the driving process for *P. mccullochi*, and possibly other temperate *Parma* species.

The different assemblage composition inside *P. mccullochi* territories is likely to reflect the feeding behaviour and preferences of the species. Firstly, *P. mccullochi* fed almost exclusively on red algae, demonstrating a strict herbivorous diet. This contrasts with some other *Parma* species, including *P. microlepis*, which exhibit a far higher level of omnivory (Moran & Sale 1977, Buckle & Booth 2009). The lack of an influence of *P. microlepis* on temperate algal assemblages (Jones 1992) may therefore reflect a more diffuse grazing pressure on algae within its territories. Secondly, the diet of *P. mccullochi* comprised mostly red foliose and filamentous red algae

such as *Hypnea* spp., *Ceramium* spp. and *Brongniatella* sp., which were also shown to be highly selected food sources based on electivity indices. Similarly, the few other temperate pomacentrids whose diets have been examined forage on foliose red algae. For example, *P. microlepis*, *Parma unifasciata* and *Parma victoriae* consume mostly red foliose algae (Jones & Norman 1986), with the first of these species displaying a preference for red foliose species (Taylor & Steinberg 2005). In support of this, tropical territorial pomacentrids have a highly selective diet, but as discussed above, exhibit farming behaviours (Montgomery 1980, Jones et al. 2006, Ceccarelli 2007). For example, the tropical *S. nigricans* maintains a monoculture of *Polysiphonia* sp. inside its territories, which is also the most abundant food item in its diet (Hata & Kato 2004). In contrast, our study demonstrates higher species richness inside *P. mccullochi* territories, suggesting minimal if any farming behaviour by this species.

While herbivores can affect algal assemblages through grazing on recruiting algae (Diaz-Pulibo & McCook 2003), there was no apparent effect of *P. mccullochi* on recruiting algae in our experiment. In contrast, tropical pomacentrids can have a large impact on recruiting algae, significantly affecting the algal composition on recruitment tiles (Doropoulos et al. 2013). Similarly, *Odax pullus* (Labridae) has been shown to have an impact on recruiting kelp through its feeding activity in southern New Zealand (Taylor & Schiel 2010). Although we recognise that our experiment was carried out during a restricted time of the year, it was at a time when algal recruitment occurs in the region (Smale et al. 2011, Mohring et al. 2013)

P. mccullochi territories were present in gaps in the canopy of the habitat-forming kelp *E. radiata*. These gaps within kelp canopies are usually created by natural events such as storms (Kennelly 1987), and previous studies have shown that the abundance of territorial pomacentrids increases within these openings, where they establish new territories (Jones 1992, Thomson et al. 2012). Furthermore, Thomson et al. (2012) suggested that *Parma* spp. may play a role in maintaining those gaps once they have been created. Here, we show that juvenile sporophytes of *E. radiata* were present outside but rarely inside *Parma* territories, which may reflect damselfish grazing on *E. radiata* recruits or other biological or physical processes. No kelp was found in the diet of *P. mccullochi*, but this is perhaps not surprising given the low density of kelp recruits during the time of year when sampling occurred (Wernberg & Goldberg 2008).

Since Saunders et al. (2011) showed that *P. mccullochi* only rarely exercises farming activities, such as scraping the reef, tidying, and weeding unwanted algae from their nests, it is plausible that *P. mccullochi* maintains gaps within the kelp canopy through its feeding activities and other mechanisms that need further investigation. However, other processes could equally, but not mutually exclusively, influence the recruitment of kelp in these patches. For example, the growth of turf algae on the reef (Kennelly 1987), and/or wave-induced hydrodynamic forces (Thomson et al. 2012) could limit or alter kelp recruitment. Yet, our recruitment experiment did not support these mechanisms, since kelp recruits were not present on any of the tiles, including those where fish grazing was excluded. The recruitment experiment, which removed the effect of established turf algae, was carried out over the period when recruitment of kelp would be expected, i.e. summer and early autumn (Mohring et al. 2013). However, since the recruitment density of *E. radiata* is patchy (Wernberg 2009) and recruitment of kelp is lower on flat tile surfaces used here compared to those with higher rugosity (Muth 2012), the likelihood of detecting recruits in adequate numbers on the tiles would be low. Thus, while it is possible that *P. mccullochi* could contribute to maintaining gaps in the kelp habitat, other mechanisms could be important in this process, and this would provide a fruitful area for further work.

Unlike other temperate pomacentrids (Buckle & Booth 2009), *P. mccullochi* has an exclusively herbivorous diet, feeding predominantly on foliose and filamentous red algae. Based on our average visual census estimates of 42 fish per 1000 m² and feeding activities within average territorial areas of 9 m² (Saunders 2011), feeding activities of *P. mccullochi* could cover almost 40% of reef habitat in the region. This, combined with its selective feeding, suggests that *P. mccullochi* has the capacity to substantially influence the standing crop and diversity of assemblages of red algae on reefs in the region. Furthermore, this influence is likely to extend along temperate reefs of southwestern Australia due to its wide distribution (Hutchins 2001). Since territorial damselfishes, particularly *Parma* spp., can be highly abundant on temperate reefs in Australia (Saunders 2011, Galaiduk et al. 2013) and elsewhere (Cooper et al. 2009), other *Parma* species could also exhibit a similar impact on reef algal assemblages. In addition to pomacentrids, other families comprising herbivorous fishes such as kyphosids and labrids (particularly *Odax* spp.) are also abundant in temperate regions

(Kingsford 2002, Harman et al. 2003, Hyndes et al. 2003, Salter et al. 2010). In this context, *Odax pullus* has been shown to graze heavily on the kelp *Durvillaea* spp. in New Zealand (Taylor & Schiel 2005), while *Sarpa salpa* grazes on *Cystoseira* spp. in the Mediterranean Sea (Verges et al. 2009), suggesting that they can influence the canopy structure of reefs. Our study suggests that *Parma* spp. also play a role in shaping algal assemblages in temperate systems, but their influence is likely to be limited mainly to the red algal assemblages. This is also likely to be the case for abundant kyphosids in the study region, which feed predominantly on red algae (A. Turco unpubl. data), although the greater mobility of these species (e.g. Pillans et al. 2011) suggests that their impacts on algal assemblages may be less obvious than those of territorial damselfishes. Understanding the role that herbivorous fish species play in temperate reef systems is important, particularly since rising sea temperatures appear to be extending the range of tropical species into temperate waters (known as tropicalisation), such that tropical herbivores are having an impact on some reef systems (Verges et al. 2014). In this context, it is noteworthy that a marine heatwave to the north of the study region in 2011 resulted in a decline of the canopy-forming kelp *E. radiata*, and a subsequent increase in the abundance of some species, including *Parma occidentalis* (Wernberg et al. 2013). With declines in the biomass of canopy-forming species (e.g. *E. radiata*) as a result of tropicalisation, herbivorous fish species such *Parma* spp. may play a greater role in the structuring of algal assemblages and food-web dynamics in temperate reefs.

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