

Factors influencing distribution and habitat associations in an endemic group of temperate Western Australian reef fishes over a latitudinal gradient

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ABSTRACT: Similarities and differences in the density, distribution and habitat associations of 3 species from the pomacentrid genus *Parma* (*Parma mccullochi*, *P. occidentalis*, *P. victoriae*) were identified across 2000 km of temperate coastline in Western Australia. For *P. mccullochi*, fine-scale habitat associations were also assessed using the position of individual fish as observation points. A fourth species, the endemic *P. bicolor*, was rarely encountered. Satellite-derived sea-surface temperature was a good predictor of the distribution of the 3 commonly encountered species over the survey area. *P. occidentalis* were northerly distributed in warmer waters, *P. victoriae* were southerly distributed in cooler waters, while *P. mccullochi* were cosmopolitan over the survey area, with the highest densities recorded towards the centre of the study area. These findings suggest that eco-physiological theory may be applicable to describing the distribution of these, and similar, species. Similar habitat associations were observed for the 3 commonly encountered species and, in the case of *P. mccullochi*, at a range of spatial scales. All species were associated with vertical or overhanging rock walls and avoided areas of continuous algal canopy. *P. occidentalis* and *P. mccullochi* were associated with turfing and understory algal forms. As the species use similar habitats, we suggest that where their distributions overlap they will experience niche overlap and resource competition. While each species may occupy different fundamental niches defined by different sea-surface temperature requirements, further study may reveal that competition for resources between these species leads to competitive displacement on both local and geographical scales.

KEY WORDS: Pomacentridae · *Parma* · Biogeography · Distribution patterns · Stereo-DOV · Stereo-video

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INTRODUCTION

Large-bodied territorial damselfish species are an abundant and prominent part of the fish assemblage on rocky reefs in temperate Australian waters. This group is dominated by the genus *Parma*. The genus is made up of 10 species, and is confined to Australasian waters (Allen 1987). Damselfish species from the genus *Parma* are territorial and herbivorous (Moran & Sale 1977, Jones 1999). In tropical systems

the role of damselfish as agents of biological disturbance is well documented (Hixon & Brostoff 1983, Lewis 1997, Ceccarelli et al. 2001, Hata & Kato 2004, Ceccarelli et al. 2005). Many tropical damselfishes use and defend algae within their territories as a food resource (Ceccarelli et al. 2001). The composition of these food resources is variable, from small monocultural algal farms, to large species-rich assemblages (Montgomery 1980, Hixon & Brostoff 1983, 1996, Hata & Kato 2002). While research to assess the role

of *Parma* in maintaining food resources, and thus habitat heterogeneity in temperate Australasia is continuing, previous studies have shown only limited effects of herbivory by territorial *Parma* on the algal assemblage (Jones & Andrew 1990, Jones 1992). However, substantial small-scale effects of *P. victoricae* and *P. mccullochi* in the maintenance of spawning sites consisting of short algal turf have been reported (Jones & Andrew 1990, Saunders et al. 2013).

The geographical distribution of species is influenced by their physiological tolerance along environmental gradients such as water temperature (Pörtner et al. 2010, Langlois et al. 2012), as well as oceanographic and recruitment processes. However, on smaller scales the distribution of site-associated species such as territorial damselfish may be more heavily influenced by discrete local habitat variables (Galaiduk et al. 2013), such as the reef topography, the algal community, or disturbance events. Individual damselfish species can exhibit strong habitat preferences within their latitudinal range (Kingsford 1999, Galaiduk et al. 2013). The habitat associations of territorial damselfish are likely to relate to their dietary needs, their requirement for shelter and for a suitable substrate on which to lay eggs (Tzioumis & Kingsford 1995). The requirement for shelter and suitable substrate upon which to lay eggs should lead to an association with complex reef environments. Indeed, *P. mccullochi* have previously been shown to be more abundant on high-relief reefs than low-relief reefs (Harman et al. 2003), and *P. microlepis*, a species endemic to New South Wales, were more abundant when shelter sites of 30 cm or greater height were available (Moran & Sale 1977). As a result of this need for shelter, substrate upon which to spawn, and their dietary requirements, another limiting factor in the distribution of temperate damselfish species is likely to be macroalgal cover. Many damselfish species are herbivorous, preferring to consume filamentous red algae (see review by Ceccarelli et al. 2001). Elsewhere in Australasia *Parma* have been shown to be associated with small filamentous and foliose algal patches on reefs (Moran & Sale 1977, Norman & Jones 1984, Jones 1992, Shepherd et al. 2008, Buckle & Booth 2009), or sea urchin barrens habitat (Anderson & Millar 2004, Galaiduk et al. 2013). However, in temperate Western Australia reefs are dominated by canopy-forming algae (Wernberg et al. 2003, Toohy et al. 2007, Smale et al. 2010). Algal canopies physically restrict feeding access to more palatable understory algae, and affect the species composition and biomass of the associated under-

storey algae (Kennelly 1987b, Kendrick et al. 1999, Wernberg et al. 2005). As a result, temperate damselfish may avoid reef dominated by algal canopy. As examples, the abundance of *P. mccullochi* on low-relief limestone reefs was higher when the canopy-forming algae *Ecklonia radiata* and *Sargassum* spp. were not abundant (Harman et al. 2003). Western Australian *Parma* species might respond in a similar fashion to their congeners elsewhere in Australasia by inhabiting patches in the canopy caused by physical disturbance or other processes. An integrated sampling program that measures the abundance patterns of *Parma* and considers both continuous environmental variables and discrete habitat variables together may allow us to identify habitat associations, and limiting resources for *Parma*.

Langlois et al. (2012) proposed the notion that the south-western Australian coastal waters are an old, climatically buffered, infertile seascape (OCBIS), the marine equivalent of the terrestrial area of old, climatically buffered, infertile landscapes (OCBILs) in south-western Australia described by Hopper (2009). Langlois et al. (2012) suggested that the OCBIS of south-western Australia provided a simple model system in which to test predictive models. They modelled the distributions of 20 abundant fish species over the south-west of Australia, however did not investigate the abundance distributions of *Parma*. The ranges of the 4 species of *Parma* present in Western Australia have been described previously (Allen & Hoese 1975, Hutchins 1994, 2001), and the abundances across their range have been estimated using a rapid census technique. Previous studies, though, have been limited through the use of qualitative abundance estimates or presence-absence recording. As such, the density of populations of species of *Parma* and their habitat associations on Western Australian reefs remain relatively unknown. To begin to evaluate the ecological function of *Parma* in temperate Australia, it is important to investigate the patterns in distribution and density of the temperate damselfish genus *Parma*, with emphasis on their relationship to habitat, at a range of spatial scales. In this study broad-scale geographical patterns in the density of each species along a water temperature gradient from mid/south-western to south-eastern Western Australia were investigated. *P. mccullochi* was anticipated to be the most abundant and widely distributed species (Hutchins 1994, 2001), so fine-scale habitat correlations were investigated in the area where this species was most abundant.

This study aimed to identify similarities and differences in the habitat associations of each species of

Parma across the biogeographic scale of temperate Western Australia. Using the most abundant of the study species, *P. mccullochi*, the habitat associations of each recorded fish were assessed at a single location. In addressing these aims we:

1. Describe the distribution and density of *Parma* species on shallow rocky reefs in temperate Western Australia.

2. Quantify the correlations between discrete abiotic and biotic habitat variables and sea-surface temperature (as a proxy for water temperature) with geographical patterns in densities of *Parma* spp.

3. Perform fine-scale analyses to determine whether the habitat associations of individual *P. mccullochi* are random or whether the fish 'select' for specific habitats.

MATERIALS AND METHODS

Survey design

This survey targeted shallow complex rocky reefs of between 4 and 12 m depth, along Western Australia's warm temperate coastline. Surveys were performed between November of 2005 and June of 2006. A nested hierarchical survey design was used, with 7 geographical regions (Fig. 1). Within each region 4 locations were chosen and within these 4 locations 4 different reef sites were selected. Twelve replicate 25 by 5 m belt transects were carried out at each reef site. Distance between samples varied on a hierarchical spatial scale, with regions being separated by thousands of kilometres to tens of kilometres, locations within regions being separated by tens of kilometres to kilometres, reef sites within locations being separated by kilometres to hundreds of metres and transects within reef sites being separated by at least 10 m. Geographical regions and locations within regions were positioned along a temperature gradient following the coastline of south-western Australia (Fig. 1). This design resulted in a total of 7 regions, 28 locations, 112 reef sites and 1344 transects, and spanned almost 7° of latitude and 10° of longitude, or approximately 2000 km of coastline.

Survey method

Diver-operated stereo-video, as originally described in Harvey & Shortis (1995), was used to swim transects of 5 by 25 m (sample area: 125 m²), with a 10 m spacing between transects. All surveys were

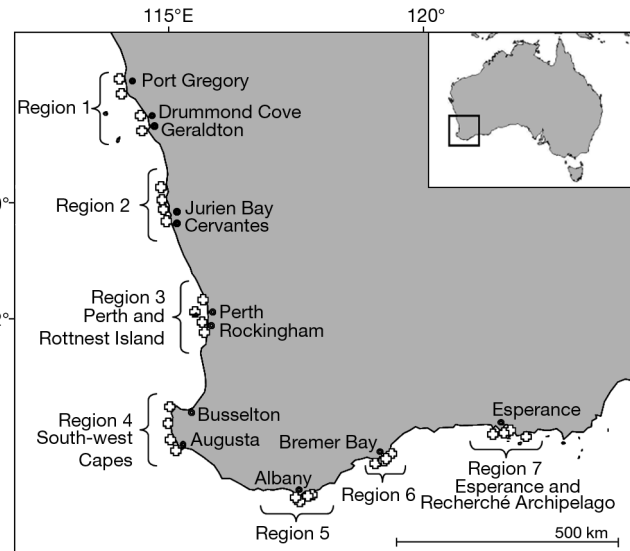


Fig. 1. Survey design illustrating the 7 geographical regions surveyed. Within each region 4 locations are illustrated. Regions from north to south and west to east (locations in parentheses)—1: Port Gregory to Geraldton (Port Gregory North, Port Gregory South, Drummond Cove and Geraldton); 2: Jurien Bay (Leeman, Green Head, Jurien Bay and Cervantes); 3: Perth and Rottnest Island (Marmion Lagoon, Rottnest Island, Carnac Island and Shoalwater Islands Marine Park); 4: South-West Capes (Geographe Bay, Cape Freycinet, Hamelin Bay and Flinders Bay); 5: Albany (Cosy Corner, Albany, Two Peoples Bay West and Two Peoples Bay East); 6: Bremer Bay (Dillon Bay, Point Henry, Back Beach Bommie and Peppermint Beach); 7: Esperance and inshore islands of the Recherche Archipelago (Observatory Island, Cull and Black Islands, Thomas and Woody Islands and Cape Le Grand)

recorded in visibility of 7 m or greater. A 25 m transect length was selected due to the patchy nature of the complex reefs targeted by this survey. By selecting a short transect length, each transect could be completed within the target habitat type. Transects were swum by teams of 2 SCUBA divers. The first diver swam the stereo-video system, while the second measured the transect length. The 2 divers were separated by a 10 m rope. The rope allowed communication between the divers, meaning that only 1 diver was present at the cameras, and so reduced the effects of diver presence on the fish assemblages that were captured on the video. The effects of SCUBA diver presence on recorded fish abundance can be variable and species specific, possibly attracting or repelling fish (see Watson & Harvey 2007). Each transect was as linear as possible within the target habitat, and the 10 m distance between transects was measured using the 10 m rope between divers. The stereo-video system allows accurate and precise measurements of the length of fish, as well as the

range and angle of a fish from the camera system (Harvey & Shortis 1998, Harvey et al. 2001). This allowed us to exclude fish that were outside the transect area. The video recording created a permanent record of each transect, which allowed ex situ habitat analysis. The benefits of using this type of system for measuring fish densities and lengths have been discussed elsewhere (Harvey et al. 2001, 2002, 2004, Watson et al. 2005, Langlois et al. 2010).

The stereo-video system used in this survey consisted of 2 Sony TRV 900 digital video cameras in underwater housings. The cameras and housings were securely mounted 70 cm apart onto a base bar and inwardly converged at an angle of 8°. A synchronisation diode was positioned on a fixed bar 1 m in front of the cameras where it was within the field of view of both cameras. This diode allowed the synchronisation of the stereo images, so that accurate range and angle measurements could be obtained. The cameras were calibrated using the software package Vision Measurement System (Robson et al. 2006) before and after each field trip. This allowed us to calculate consistently accurate length and range measurements by accounting for any changes in the position of the cameras during transportation or use.

Image processing

The video from the left and right cameras for each transect was captured onto a PC as an audio video interlaced (.avi) file. The software package Vision Measurement System (VMS; Robson et al. 2006) was used to measure the fork length of each fish, and also the 3-dimensional positions of fish relative to the camera system. These 3-dimensional positions were used to exclude fish that were further than 7 m from the camera system (7 m was the minimum usable visibility), or >2.5 m from the centre of the transect line. This allowed standardisation of the field of view used to the minimum visibility (Harvey et al. 2004) and control of the transect area to 125 m². Fish that were within the sample area, yet were visible in only 1 camera as they were hidden by benthos or rugose substrate, could not be measured, but were still counted and included in the density data.

Broad-scale habitat quantification

Habitat analysis was undertaken from the video footage using a visual basic program in Microsoft Excel. This program was modified from that pre-

sented by Holmes (2005). Five estimates of habitat were made for each 25 m transect. The video file was split into 5 equal non-overlapping sections, and a frame from each section was selected for analysis haphazardly, but at a point where the field of view encompassed a wide view of the habitat. Therefore, the categorisation of the habitat was done on a horizontal image, with a depth of field of approximately 5 m. Rather than to quantify percentage cover absolutely as is possible with downward facing images with a consistent scale, we chose to categorise each observation into percentage cover or reef height/slope bins, or by recording the presence/absence of difficult to classify habitat variables. This approach was chosen to reduce any bias associated with the horizontally facing image.

At each observation point the reef height and slope were estimated from the field of view and assigned categorical values. The reef or outcrop height was ranked from 1 to 4 according to the following categories: (1) platform reef, (2) small outcrops (boulders or outcrops <1 m in height), (3) large outcrops (boulders or outcrops >1 m but <3 m) and (4) massive outcrops (outcrops >3 m in height). Slope was estimated and assigned to 1 of the following categories: (1) <30° (gentle slope), (2) 30–70° (steep slope), (3) 70–110° (vertical wall), (4) >110° (overhanging wall) and (5) overhead overhanging reef or cave. Benthic biota cover was estimated at each observation point for the following variables: sessile invertebrates, *Ecklonia radiata* (kelp) canopy, non-*Ecklonia* canopy-forming algae (fucal species) and understory algae, which included fucal, foliose and turfing algae where a canopy was not present. These were assigned a rank from 0 to 6 according to the following estimated percentage cover categories: (0) nil, (1) <1%, (2) 1–10%, (3) 10–25%, (4) 25–50%, (5) 50–75% and (6) >75% cover. The category understory algae was further divided into 3 groups: foliose algae, turf algae and seagrass, the presence or absence of each of these 3 groups at each observation point was recorded. For geographical analysis these categorical observations were averaged to give measures of mean habitat at the reef site level (60 measurements, 1500 m⁻²).

As this survey encompassed both the warm and cold extremes of range for different *Parma* species, mean water temperature throughout the year was used instead of winter temperature. Sea-surface temperature (SST) data derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument was obtained from ocean color web (oceancolor.gsfc.nasa.gov). A Level 3 product, an-

nual mean SST, was obtained for 2 adjacent 9 km pixels at each location. The mean of these 2 pixels was calculated for each of 5 yr (2002 to 2006 inclusive). These were then averaged across the 5 yr to give a 5 yr mean SST for each location. The 5 yr mean SST was used as it represented the historical record of water temperatures on a scale that was thought to be relevant to long-lived, site-associated species such as those of the genus *Parma*.

Fine-scale habitat quantification

Parma mccullochi have been reported as the most abundant and widely spread of the *Parma* species in Western Australia (Hutchins 1994, 2001), so they were selected for habitat analysis on a finer scale. This analysis was carried out using data from 1 location in Region 3 (Marmion Lagoon, Perth), because densities of this species were found to be highest there. Rather than averaging habitat observations to the site level, the data from each of the 5 individual habitat observation points on each transect were used. These were compared to similar observation points made where each *P. mccullochi* was encountered. These observations were made from a single video frame, at a point in time when the fish was measured. The habitat visible in the entire field of view in that frame was characterised following the procedure described above.

Statistical analysis

Geographical patterns in density and range

Total numbers of fish per reef site (1500 m²) for each *Parma* species at each of the 7 geographical regions were calculated and represented graphically. Univariate ANOVA analyses were performed using MINITAB Release 13 on square-root-transformed densities of each species, using a 3-factor (region, location and site) hierarchical nested model. Region was a fixed factor with 7 levels. The factor location had 4 levels and was nested within region. The factor reef site also had 4 levels and was nested within location. A square-root transformation was applied as this resulted in the data most closely fitting a normal distribution as tested using Anderson-Darling normality tests.

The distribution patterns for each species of *Parma* were plotted against SST. Following the method outlined in Langlois et al. (2012), quantile regression

spline models (Koenker & Bassett 1978) were used to fit 95th percentile splines of the density of each species to mean SST (after Anderson 2008). Models were fitted using the function `rq()` (part of the 'quantreg' package; Koenker 2010) combined with the function `bs()` in the 'splines' package in the R computer programming language (R Core Team 2012). The appropriate degree of the polynomial for each spline was determined from a set of models having a polynomial of degree 1, 2, 3, or 4 using the corrected Akaike's information selection criteria (AICc). The quantile regression sandwich formula and Hall–Sheather's bandwidth rule were used to estimate goodness-of-fit and calculate p-values for each polynomial degree to assess the polynomial degree that was selected using the AICc (after Cade et al. 2005).

Geographical relationship of density to SST and habitat

In order to elucidate the role of environmental variables in determining the distribution and community structure of the 3 *Parma* species over the survey area, a distance-based linear model (DistLM) was calculated using the PERMANOVA+ (Anderson et al. 2008) package in PRIMER 6 (Clarke & Gorley 2006). This analysis selects the environmental variables that best explain the variation in the density of the 3 *Parma* species over the entire survey area. A resemblance matrix of the densities per reef site (1500 m²) of each of the 3 *Parma* species was constructed from square-root-transformed data using the zero-adjusted Bray-Curtis coefficient (Clarke et al. 2006). The Bray-Curtis coefficient was selected as it has the property of independence of joint absences. However, this property results in an undefined value where samples contain no individuals at all. To avoid this difficulty, the zero-adjusted Bray-Curtis includes a dummy species of value 1 in all samples. Habitat predictor variable data were not transformed. Where habitat variables were strongly correlated (more than ±80%), 1 variable was excluded. Sand cover was negatively correlated to reef cover and so was excluded from analysis. Mean SST data were also included in the model. No environmental variables were strongly correlated with SST. DistLM was performed using the best selection procedure and the AICc. AICc was originally proposed by Sugiura (1978) to reduce bias in linear regression models. It has since been shown to also greatly improve model selection with small sample sizes (Hurvich & Tsai 1989, Hurvich et al. 1990). For these reasons it was

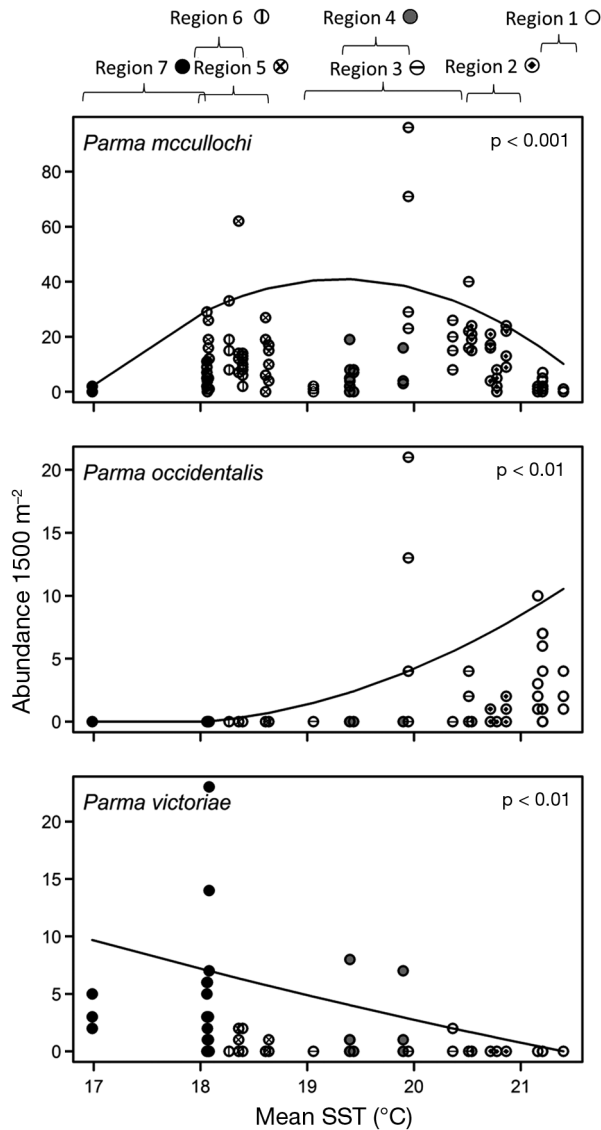


Fig. 2. Abundance (fish 1500 m⁻²) and 95th percentile regression spline models for each *Parma* species and the mean sea-surface temperature (SST) at each location. p-values for the fit of the polynomials are shown

selected for use in our analysis. The variables selected to make up the model were then plotted using distance-based redundancy analysis (dbRDA). Spearman rank correlations of the densities of each *Parma* species to the dbRDA axis were calculated.

Habitat associations of each species

While the analysis above considered the 3 common species together, we also wanted to assess the habitat associations of each species individually. For this analysis DistLM, using the best selection procedure,

and AICc were used to model the distributions of each of the 3 species individually, using the environmental variables described above. Marginal tests were used to identify the environmental variables that explained a significant portion of the variation in the densities of each of these species. For *P. mccullochi* DistLM and marginal tests were performed across all 7 regions, as this species was ubiquitous. For *P. occidentalis* and *P. victoriae* this analysis was carried out only using data from the 1 region where they were most abundant (Regions 1 and 7, respectively). This was to reduce the likelihood of detecting spurious relationships with habitat, as these species were rare in other regions.

Fine-scale habitat associations

Fine-scale habitat analysis for *P. mccullochi* was performed at 1 location in Region 3 (Marmion Lagoon, Perth). This analysis was designed to determine whether the distribution of *P. mccullochi* along a transect was random or whether the fish were 'selecting' for specific habitats. Observations of habitat were recorded from the point on the video where each *P. mccullochi* was measured. These observations were compared to the available habitat, which was calculated from 5 haphazard observations along each transect, as described previously. The percentage of observations where each category of habitat variable was recorded was plotted for the expected habitat and observed habitat when *P. mccullochi* were present. Chi-squared goodness-of-fit tests were calculated to test a hypothesised difference between expected and observed observations. Categories where the expected values were very low were summed together to allow testing.

RESULTS

Geographical patterns in density and range

Over the entire survey area only 1 *Parma bicolor* individual was recorded, in Region 3 at Rottnest Island. This species has been omitted from analysis due to its extreme rarity. Differences in the densities of the 3 commonly observed *Parma* species per reef site sampled (1500 m²) were observed throughout the survey area (Fig. 2). Significant differences at $\alpha = 0.05$ in densities of all *Parma* species were observed between regions (Table 1). While these were significant for each species, significant results were also

Table 1. Results of a 3-factor fully nested analysis of variance on square-root-transformed densities of 3 *Parma* species across 7 regions. Region is a fixed factor. Significant p-values (at $p < 0.05$) in **bold**

	df	SS	MS	F	p
<i>Parma mccullochi</i>					
Region	6	133.17	22.20	4.45	0.005
Location (Region)	21	104.69	4.99	3.37	<0.001
Reef site (Location [Region])	84	124.27	1.48	4.12	<0.001
Error	1232	442.32	0.36		
Total	1343	804.45			
<i>Parma occidentalis</i>					
Region	6	8.88	1.48	4.633	0.004
Location (Region)	21	6.71	0.32	2.232	0.005
Reef site (Location [Region])	84	12.02	0.14	2.504	<0.001
Error	1232	70.41	0.06		
Total	1343	98.02			
<i>Parma victoriae</i>					
Region	6	16.98	2.83	8.09	<0.001
Location (Region)	21	7.35	0.35	1.68	0.051
Reef site (Location [Region])	84	17.51	0.21	3.70	<0.001
Error	1232	69.34	0.06		
Total	1343	111.18			

returned for locations within regions and reef sites within locations. There is a high degree of variability expressed in the sums of squares at all levels of the ANOVA design. This variability reflects the patchily distributed nature of these 3 species.

P. mccullochi reached a maximum density of 96 individuals 1500 m^{-2} (Fig. 2) at a reef site in Region 3 (Wanneroo Reef, Marmion Lagoon, Perth). *P. occidentalis* also reached its maximum density of 21 individuals 1500 m^{-2} (Fig. 2) at a site in Region 3 (Cow Rocks, Marmion Lagoon, Perth). Away from the Marmion Lagoon *P. occidentalis* was absent from reefs surveyed in Region 3, as a result of which the mean (\pm SE) density per reef (3.3 ± 0.7 , $n = 16$) is highest in Region 1 (Port Gregory to Geraldton), where it was consistently present. *P. victoriae* was found to reach its maximum density of 23 individuals 1500 m^{-2} in Region 7 (Esperance) at Cull Island (Fig. 2).

P. mccullochi showed a unimodal distribution across the geographical range studied here, with high densities at both Regions 3 and 5 (Perth and Albany, respectively; Fig. 2). At both the northern and south-eastern extremes of the survey area, the mean (\pm SE) density of *P. mccullochi* was very low, <2 and <4 individuals on average per 1500 m^2 , respectively (Region 1, 1.6 ± 0.5 , $n = 16$; Region 7, 3.3 ± 0.9 , $n = 16$). The extremes of the survey area are likely to be close to the range limits of *P. mccullochi*. *P. occidentalis* was present only in the 3 northernmost regions (Fig. 2). It reached the highest mean density

(3.3 ± 0.7 , $n = 16$) in Region 1 (Port Gregory to Geraldton). Region 3 (Perth) was the southern range limit of *P. occidentalis* on shallow coastal reef (Fig. 2). *P. victoriae* was present at 5 of the 7 regions sampled, from Region 3 (Perth) and along the south coast to Region 7 (Esperance). With the exception of Region 6 (Bremer Bay), where only 2 individuals were recorded, the density of *P. victoriae* was found to increase south and eastward from Region 3 to a maximum mean density of $5.1\text{ fish }1500\text{ m}^{-2}$ ($\pm 1.5\text{ SE}$, $n = 16$) at Region 7 (Esperance). Region 3 (Perth) was the northern range limit for this species on shallow coastal rocky reef in Western Australia.

Geographical relationship of density to SST and habitat

A model using 5 predictor variables to explain 33% of the variation in the population of *Parma* densities was generated from the DistLM procedure ($R^2 = 0.33$, $\text{AICc} = 737.83$). The environmental variables were: SST, height of reef or rocky outcrop above sea bottom, presence of vertical walls and overhangs, pres-

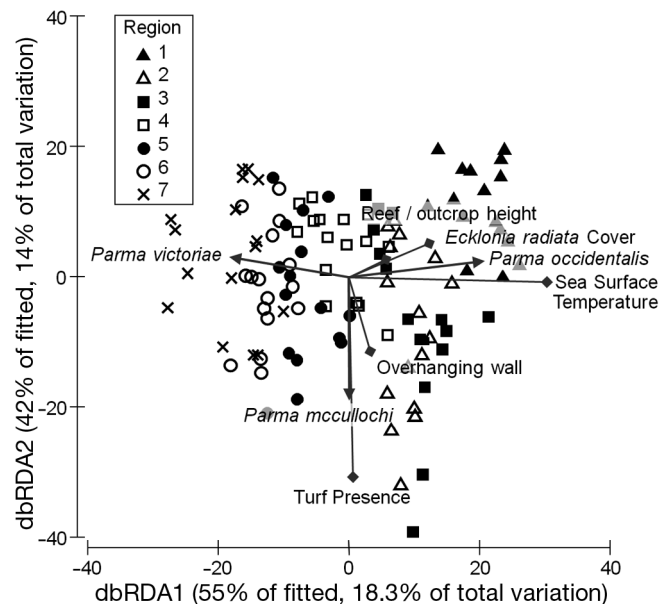


Fig. 3. Distance-based redundancy analysis (dbRDA) ordination of first and second fitted axes relating environmental variables to *Parma* density across the entire survey area. Vectors plotted show the strength and direction of multiple partial correlations of the environmental variables and Spearman rank correlations of *Parma* density to the first and second RDA axes. The first and second dbRDA axes explained 55 and 42% of the variation in the fitted model, respectively. Note that symbols overlapping with text are shown in grey for better readability

Table 2. Correlations to the first and second dbRDA (distance-based redundancy analysis) axes (Fig. 3) of selected environmental variables and *Parma* densities per reef site (1500 m²). Correlations >0.5 indicated in **bold**

Variable	dbRDA1	dbRDA2
Multiple partial correlation		
Turf presence	0.02	-0.92
Sea-surface temperature	0.91	-0.02
<i>Ecklonia</i> cover	0.37	0.16
Constant overhang	0.10	-0.34
Reef/outcrop height	0.17	0.08
Spearman rank correlation		
<i>P. mccullochi</i>	<0.01	-0.57
<i>P. occidentalis</i>	0.62	0.07
<i>P. victoriae</i>	-0.55	0.09

ence of turfs and cover of the kelp *Ecklonia radiata* (Fig. 3). Marginal tests identified SST and the presence of turfing algae as the 2 most important predictor variables, accounting for 16 and 10% of the variability in densities of the *Parma* assemblage, respectively ($p < 0.001$). The first 2 dbRDA axes accounted for 55 and 42% of the variation in the fitted model, respectively, and together accounted for 32% of the total variation in *Parma* density data (Fig. 3). *P. occidentalis* and *P. victoriae* densities were positively and negatively correlated, respectively, to the first dbRDA axis. SST was strongly correlated to this axis. The southern and northern extremes, respectively, of these species were encompassed by the survey, at Region 3. At this region from 2002 to 2006 the yearly mean SST ranged between 17.6 and 20.7°C, with a mean of 19.9°C (oceancolor.gsfc.nasa.gov). *P. mccullochi* density was negatively correlated to the second dbRDA axis, as was turfing algal presence. Other predictor variables included in the model may play some role in explaining variation in *Parma* densities (Fig. 3). Yet these were not strongly correlated to the first 2 dbRDA axes which accounted for so much of the variation in the fitted model (Table 2). On a smaller scale these variables showed greater predictive power (Table 3). The variables associated with more complex reef, such as reef/outcrop height, and increasing cover of *Ecklonia radiata*, were correlated with *P. occidentalis* density (Fig. 3). The correlation vec-

tor for *P. victoriae* increased in the opposite direction, and *P. victoriae* appeared negatively correlated with *E. radiata* cover (Fig. 3). Across the geographical range surveyed, reef site scale patterns in densities of *Parma* were most strongly correlated to SST and the presence of turfing algae.

Habitat associations of each species

Further modelling of each species of *Parma* individually using the environmental variables revealed that vertical or overhanging walls explained a large proportion of the patterns in density of all species (Table 3). Turf algal presence, overhead reef or cave, overhanging wall, and reef or outcrop height above the seabed were selected by the model to best predict the abundance of *P. mccullochi* (Table 3). Turf algal presence, other algal cover and overhead reef or cave, and overhanging wall explained the largest proportions of the variation in the density of *P. mccullochi* across the whole survey area (Table 3). Marginal tests showed that these relationships were statistically significant (Table 3). Turf algal presence and overhanging wall were selected by the model to

Table 3. The 5 environmental variables that explained the greatest proportion of the variation in the densities of each of 3 species of *Parma*. The variables highlighted in **bold** were selected to best model the abundance of each species through DistLM using the best-selection procedure and AICc selection criteria (for details see the 'Materials and methods' section; *P. mccullochi* includes a sixth variable which was selected by the model but had low predictive power by itself)

Variable	SS (trace)	Pseudo- <i>F</i>	p	Proportion
<i>P. mccullochi</i> all regions (AICc = 87.5, R ² = 0.44, no. of variables = 4)				
Turf presence	105.23	39.64	<0.001	0.26
Other algal cover	56.29	18.16	<0.001	0.14
Overhead or cave	48.90	15.44	<0.001	0.12
Overhanging wall	33.64	10.18	0.003	0.08
Hard coral cover	13.79	3.95	0.048	0.03
Reef/Outcrop height	0.57	0.16	0.697	0.001
<i>P. occidentalis</i> Region 1 (AICc = 1.5, R ² = 0.29, no. of variables = 2)				
Hard coral cover	2.20	3.00	0.114	0.18
Turf presence	2.01	2.69	0.125	0.16
Overhanging wall	1.75	2.28	0.150	0.14
Other algal cover	1.06	1.30	0.274	0.09
Foliose presence	1.02	1.24	0.279	0.08
<i>P. victoriae</i> Region 7 (AICc = 3.0, R ² = 0.47, no. of variables = 2)				
Vertical wall	7.43	7.16	0.028	0.34
Overhanging wall	6.83	6.31	0.034	0.31
Seagrass presence	4.78	3.90	0.090	0.22
Non- <i>Ecklonia</i> canopy cover	3.80	2.93	0.111	0.17
Hard coral cover	2.46	1.77	0.211	0.11

best predict the abundance of *P. occidentalis* at Region 1 (Table 3). Hard coral cover, turf algal presence and overhanging wall all explained >10% of the variation in *P. occidentalis* densities at Region 1. However, none of these relationships were statistically significant (Table 3). In the case of *P. victoriae*, the explanatory variables vertical wall and seagrass presence were selected by the model to best explain the abundance of this species at Region 7 (Table 3). Vertical wall and overhanging wall explained large and statistically significant proportions of the variation in the densities of *P. victoriae* at Region 7 (34 and 31%, respectively; Table 3). Seagrass presence, non-*Ecklonia* canopy cover and hard coral cover all explained >10% of the variation, yet the relationships were not significant (Table 3). The inclusion of the variable seagrass presence in the model suggests that *P. victoriae* are associated with the edges of reef habitat, near soft seabed where seagrass beds are established.

Fine-scale habitat correlations with *P. mccullochi*

At the fine scale, there was evidence of association of *P. mccullochi* to certain habitat types. All χ^2 comparisons of expected and observed habitat observations proved significant at $\alpha = 0.05$ (Table 4). An association of individual *P. mccullochi* with reefs or outcrops >3 m in height was apparent (Fig. 4A). Greater than 45% of fish were observed here, while this habitat accounted for only 8% of expected observations. A trend of association with reefs of increasing height was demonstrated by *P. mccullochi*. *P. mccullochi* also demonstrated a clear association with reefs classed as vertical wall; 43% of fish of this species were observed on vertical walls, while this accounted for only 19% of expected observations. *P. mccullochi* also demonstrated an association with low to medium (1–25%) *E. radiata* cover and areas with nil or with low non-*Ecklonia* canopy cover (Fig. 4D). *P. mccullochi* were most often recorded where higher covers of understory macroalgae were recorded (Fig. 4E).

Length-frequency distributions

The fork-length frequency distributions of *P. mccullochi* were broadly similar in shape (Fig. 5), although at Region 3 the median length classes were more evenly populated than at other regions. The length-frequency distribution at Region 3 differed significantly to those at Regions 2, 4, 5 and 6 (2-sam-

Table 4. Chi-squared goodness-of-fit tests comparing observed frequencies of habitat at points where *Parma mccullochi* were present (Observed freq., % in parentheses) to the expected proportion of randomly sampled habitat observations (Expected prop.) calculated at 5 points along each transect, for each of 5 habitat classes

	Observed freq.	Expected prop. (%)
Reef or outcrop height		
Platform reef	4 (1.81)	20.4
0–1 m	28 (12.67)	7.9
1–3 m	86 (38.91)	62.9
>3 m	103 (46.61)	8.8
	$\chi^2 = 425.98$, df = 3, p < 0.001	
Reef slope		
Gentle slope	19 (8.60)	27.9
Steep slope	35 (15.84)	15.4
Vertical wall	97 (43.89)	19.2
Overhanging wall	47 (21.27)	21.3
Overhead overhang/cave	23 (10.41)	16.3
	$\chi^2 = 104.70$, df = 4, p < 0.001	
<i>Ecklonia radiata</i> canopy cover		
<1%	88 (39.8)	48.8
1–10%	36 (16.3)	7.5
10–25%	41 (18.6)	14.2
25–50%	28 (12.7)	9.6
50–75%	21 (9.5)	8.3
>75%	7 (3.2)	11.7
	$\chi^2 = 45.62$, df = 5, p < 0.001	
Non-<i>Ecklonia</i> canopy cover		
<10%	186 (84.2)	61.3
10–25%	20 (9.1)	8.3
25–50%	4 (1.8)	6.7
50–75%	9 (4.1)	5.8
>75%	2 (0.9)	17.9
	$\chi^2 = 63.77$, df = 4, p < 0.001	
Understorey algal cover		
<10%	15 (6.8)	27.9
10–25%	15 (6.8)	11.7
25–50%	41 (18.6)	8.8
50–75%	50 (22.6)	10.4
>75%	100 (45.3)	41.3
	$\chi^2 = 96.59$, df = 4, p < 0.001	

ple Kolmogorov-Smirnov tests; all p < 0.014). At Regions 2, 3 and 4, the range of lengths recorded was similar, whilst at Regions 1, 5, 6 and 7 fewer very large or very small *P. mccullochi* were recorded (Fig. 5). Statistical comparisons of length-frequency distributions were not conducted at Region 1 or 7 due to the low number of lengths measured at these regions. Similarly, statistical tests of the length-frequency distributions of *P. occidentalis* and *P. victoriae* were not conducted due to low numbers of length measurements. The length-frequency distributions for *P. occidentalis* generally covered a similar range to those of *P. mccullochi*; however, the

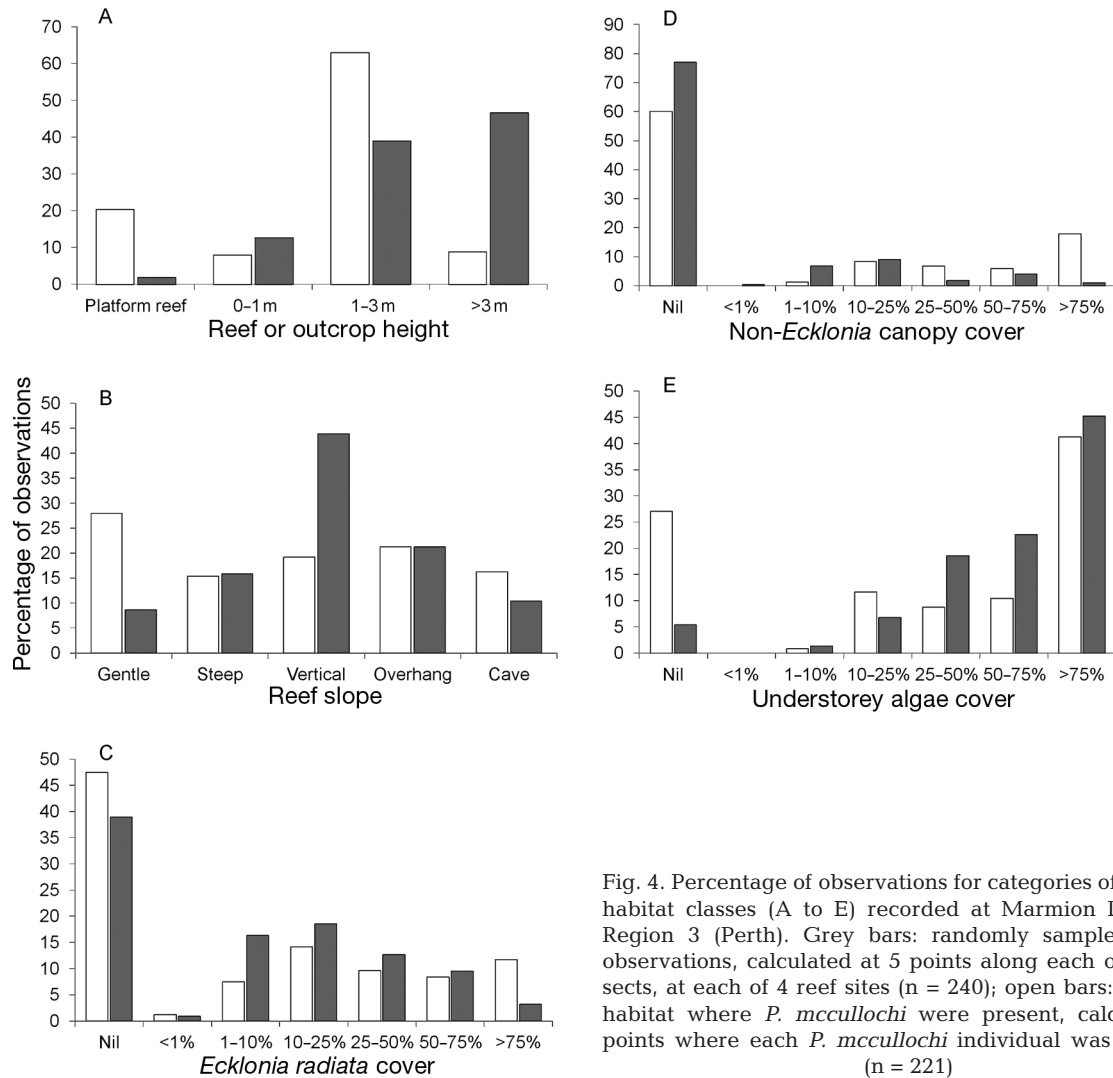


Fig. 4. Percentage of observations for categories of each of 5 habitat classes (A to E) recorded at Marmion Lagoon in Region 3 (Perth). Grey bars: randomly sampled habitat observations, calculated at 5 points along each of 12 transects, at each of 4 reef sites ($n = 240$); open bars: observed habitat where *P. mccullochi* were present, calculated at points where each *P. mccullochi* individual was observed ($n = 221$).

maximum fork length recorded for *P. occidentalis* was 299 mm, compared to 346 mm for *P. mccullochi*. *P. victoriae* were generally smaller than the other 2 common species. The maximum fork length recorded for *P. victoriae* was 262 mm.

DISCUSSION

Our study described the distributions of 3 congeneric pomacentrid species throughout temperate south-western Australia. The fourth species, *Parma bicolor*, is endemic to Western Australia (Hutchins 2001). However, in our survey only 1 individual was recorded. This species is often observed on deeper reefs along the south coast of Western Australia, with a preferred depth range of 30 m or greater (Hutchins 1994). This depth range was beyond the scope of our

survey. It may be that *P. bicolor* inhabits similar habitat to other *Parma* species, simply shifted to a deeper water environment, possibly as a result of competition with con-generics in the shallow complex rocky reefs. Identification of the ecological niches of coexisting species aids in the detection and discussion of any interspecific competition (Sale 1974, Ebersole 1985, Huston 1999). The 3 common species were found to have overlapping distributions, *P. occidentalis* was northerly (warm water) distributed, *P. mccullochi* was found across the survey area and *P. victoriae* was southerly (cool water) distributed.

Sampling occurred over 7 mo (November of 2005 until June of 2006, the austral summer and autumn), encompassing the main recruitment period for these fishes (Saunders et al. 2013). While it is possible that the density patterns may have been affected by seasonal recruitment, our length information shows no

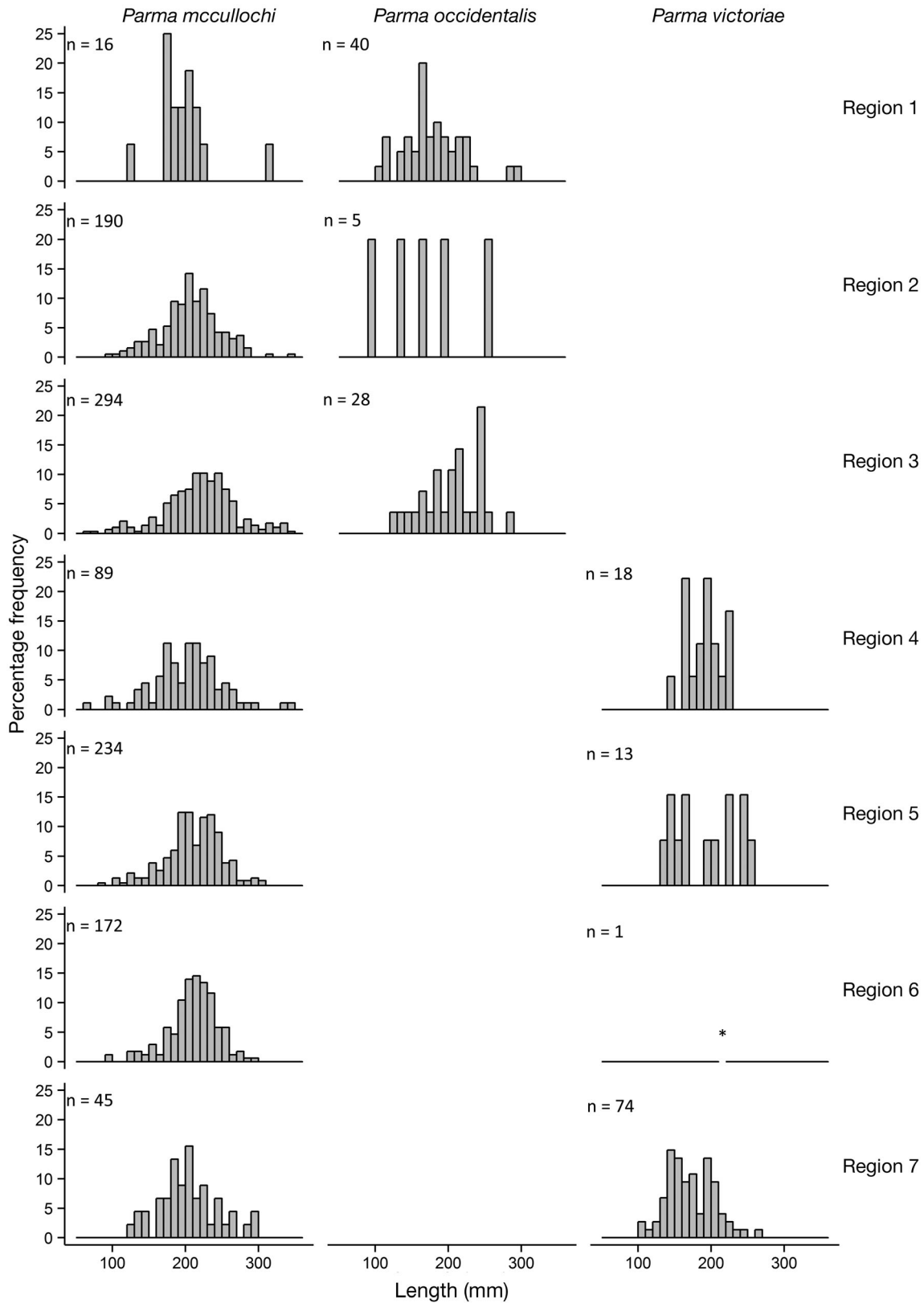


Fig. 5. Length to percentage frequency for each of the 3 common species of *Parma* at each region. Asterisk indicates that only 1 individual was measured at this region, so 100% of length measurements were in this length bin. 'n' represents the number of lengths measured, and is not representative of the density of fish recorded

evidence of a seasonal increase in the number of recruits. Very few recruits were counted. Only 11 *P. mccullochi* and 1 *P. occidentalis* were measured at <100 mm in length. The smallest *P. victoriae* was measured at 109 mm in length. Very small recruits of these species are cryptic and find refuge in small cracks in the reef. Therefore, they may not have been detected by our video-based sampling method.

SST decreased from north to south-east over the survey area. Our geographical scale modelling found that SST was an important predictor for both *P. occidentalis* and *P. victoriae* densities over the survey area. However, some components of the pattern in density in our survey suggest that local habitat variables may be just as important as water temperature in determining the density of these species. For example, *P. occidentalis* is a sub-tropical/warm temperate species that has been suggested to be expanding southward in response to warming trends (Wernberg et al. 2013). Yet the maximum density of this species was at a site in Region 3. This region also encompassed the southern range limit of this species. Another example is evident in the density of *P. victoriae* in Region 6. The density of this species was high at Region 5 to the west and Region 7 to the east, but only 2 individuals were recorded at Region 6. A similar importance of local habitat over water temperature in determining the abundance of *Parma* was suggested by Galaiduk et al. (2013). However, on broad geographical scales SST was a good predictor of the density of *Parma* in south-western Australia. Temperature changes can increase stress levels and inhibit growth rates in fishes (Wendelaar Bonga 1997), including pomacentrids (see e.g. Nakano et al. 2004, Figueira et al. 2009). The southern and northern extremes of range of *P. occidentalis* and *P. victoriae*, respectively, were found around Region 3. The range in SST at this region may encompass the minimum and maximum temperatures, respectively, that allow successful population processes for these species. Highest densities of *P. mccullochi* were found at Region 3, although *P. mccullochi* was cosmopolitan over the survey area. Density of *P. mccullochi* was generally high over the survey area, but did decrease quickly at the warm and cool extremes of the survey range. This pattern is broadly similar to the abundant centre distribution of this species which was described by Tuya et al. (2008). The abundant centre hypothesis has been a common assumption in ecology (Austin 1987, Cox & Moore 1993, Sagarin & Gaines 2002). However, the generality of this hypothesis in real-world applications has been increasingly questioned (Austin 1987, Sagarin & Gaines 2002, Sagarin et al. 2006,

Tuya et al. 2008, Langlois et al. 2012). An abundant centre distribution was described in only 39% of the literature that was reviewed by Sagarin & Gaines (2002). Langlois et al. (2012) modelled the distributions of 20 abundant fish species over the south-west of Australia, and demonstrated that 15 of the 20 had unimodal distributions, while 4 had ramped distributions. Over our survey area, *P. mccullochi* had a unimodal distribution, *P. victoriae* had a ramped distribution favouring cooler waters, and *P. occidentalis* were more abundant in warmer waters. Langlois et al. (2012) conclude that eco-physiological theory (Pauly 2010, Pörtner et al. 2010) is appropriate for application to predictive models of the abundance distribution of marine species, and our observations support this conclusion, at least over broad geographical scales in Western Australia.

In addition to possible physiological effects, SST may be a proxy for physical and biological oceanographic processes. Such patterns could influence survivorship of fish larvae and the feeding of reef fish (Kingsford 1989) which may, in turn, influence patterns of reef fish assemblages. While SST appears to separate *P. victoriae* from other species on the south coast of Western Australia other environmental factors may be at play. For example, the dominance of the canopy algae *Ecklonia radiata* decreases along the south coast as it is replaced by other fucal canopy species (Wernberg et al. 2003). This pattern may be reflected in the correlation of *E. radiata* in a similar direction to *P. occidentalis*. Rather than indicating a causal relationship, this correlation may simply be due to *P. occidentalis* only being recorded on the west coast, where *E. radiata* canopy is more dominant.

Regional scale modelling of the habitat to each species separately revealed similarities in habitat associations between species. All 3 species were associated with vertical or overhanging rock walls. Fine-scale observations showed that *P. mccullochi* were associated with complex reef habitat, typified by a reef height >3 m and with a vertical reef face. These observations are supported by (Harman et al. 2003) who found similar patterns for this species.

In modelling the relationships of *Parma* to environmental variables over the survey area, we found that the presence of turfing algae predicted the density of *P. mccullochi* well. Regional scale modelling of the species separately also outlined associations of *Parma* to certain algal morphologies. *P. mccullochi* and *P. occidentalis* were both associated with turf algal presence and understory algal cover. In addition, our fine-scale habitat observations for *P. mccullochi* re-

vealed an association with high understorey algal cover and low canopy cover (both *E. radiata* and otherwise). While little published information is available on *P. mccullochi* and *P. occidentalis*, as territorial herbivores (Jones 1999) they are likely to eat turfing algae and understorey algal species. Published information is available for *P. victoriae*, which has a strong preference for red algal understorey species such as those from the genera *Champia* and *Rhodoglossum* (Jones 1999). Other *Parma* species have been shown to feed on red understorey algae, or within breaks in algal canopy within their territories (Norman & Jones 1984, Jones & Norman 1986, Andrew & Jones 1990, Jones & Andrew 1990, Jones 1992, Shepherd et al. 2008). Additionally, the maintenance of turfing algae (usually red, polysiphonious algae) as a food resource has been recorded in many tropical herbivorous pomacentrids (Hixon & Brostoff 1983, Ceccarelli et al. 2001, Hata & Kato 2004, Barneche et al. 2009). In addition to food, both *P. mccullochi* and *P. victoriae* have been shown to maintain small patches of turfing algae as nest sites (Jones & Andrew 1990, Saunders et al. 2013); this may be another driver for the association with turf algae that we observed. Our observed association of *Parma* with understorey algae may be due to *Parma* taking advantage of breaks in the algal canopy. A similar pattern has been reported for *Parma* species in New Zealand, which inhabit breaks in algal canopy caused by sea urchins (urchin barrens) (Anderson & Millar 2004). Breaks in the algal canopy are rarely caused by sea urchins in south-western Australia (Vanderklift & Kendrick 2005), probably due to low sea urchin abundances (Fowler-Walker & Connell 2002, Vanderklift & Kendrick 2004). However, breaks can occur as a result of storm disturbance (Kennelly 1987a).

Similar habitat use suggests that where the distributions of the 3 common species of *Parma* in south-western Australia overlap, they can be considered to occupy a similar post-interaction ecological niche. In areas where the species co-occurred they were often recorded on the same transect. On a fine scale, the biogeographic density patterns are likely to be directed by local-scale processes such as recruitment, or by the availability of resources, territorial interactions and competition for use of these resources (Chase & Myers 2011, Wiens 2011). In addition, species competition should be considered in connection with the niche concept, since some similarity and overlap in niches is a prerequisite of competition (Alley 1982). Where the distributions and habitat use of *Parma* species overlap, competition for resources is likely to be important in deter-

mining their realised niches. Indirect evidence of such processes is suggested by our study. Earlier in this discussion we have highlighted the importance of local-scale habitat variables in determining the density of *Parma* in south-western Australia. Such small-scale habitat variation may lead to interspecific competition for resources. For example, at Regions 5 and 6 the density of *P. mccullochi* was high, while the density of *P. victoriae* was comparatively low. By contrast at both the northern and southern adjacent regions (Regions 4 and 7) this pattern was reversed. While these density patterns were undoubtedly influenced by other factors, such as recruitment and oceanographic processes, and habitat variation, they suggest interspecific interactions and competition. To tease out the separate influences of these processes would require well-designed targeted research. Further investigation of *Parma* spp. behaviour and resource utilisation may clarify any niche overlap or resource competition between species.

This study reveals similarities in the habitat use of 3 related species of territorial pomacentrid. We propose that increased reef complexity results in greater availability of shelter sites, and that the association of *P. mccullochi* and *P. occidentalis* with turfing algae and low or absent canopy cover is due to the use of turfing and understorey algae as food and nesting resources in a similar fashion to many other pomacentrids. The species, however, were found to have different geographical distributions. It is likely that competition for resources between these species leads to competitive displacement on both local and geographical scales. In comparison to elsewhere, both globally and nationally, the south-western Australian marine environment has been geologically stable and isolated, and free of glaciation events and mass extinctions throughout the Cainozoic era (for review see Phillips 2001, Langlois et al. 2012). The marine environment has been moderated by the warm Leeuwin current for 40 million years (McGowran et al. 1997), and this stability, in combination with its switching on and off periodically (McGowran et al. 1997), may have contributed to the high diversity and degree of endemism in south-western Australia (Phillips 2001). In this environment our 3 common *Parma* species may have evolved over time to occupy differing fundamental niches, as SST is strongly correlated to the distribution of these species over the geographical area surveyed.

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