

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

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20 Stereo-video

21

22 ABSTRACT:

23

24 Similarities and differences in the density, distribution and habitat associations of three
25 species from the pomacentrid genus *Parma* (*Parma mccullochi*, *Parma occidentalis*, *Parma*
26 *victoriae*) were identified across 2,000 kilometres of temperate coastline in Western
27 Australia. For *P. mccullochi*, fine-scale habitat associations were also assessed using the
28 position of individual fish as observation points. A fourth species, the endemic *Parma bicolor*
29 was rarely encountered. Satellite derived sea surface temperature was a good predictor of the
30 distribution of the three commonly encountered species over the survey area. *P. occidentalis*
31 were northerly distributed in warmer waters, *P. victoriae* southerly distributed in cooler
32 waters, while *P. mccullochi* were cosmopolitan over the survey area, with the highest
33 densities recorded towards the centre of the study area. These findings suggest that eco-
34 physiological theory may be applicable to describing the distribution of these, and similar,
35 species. Similar habitat associations were observed for the three commonly encountered
36 species, and in the case of *P. mccullochi* at a range of spatial scales. All species were
37 associated with vertical or overhanging rock walls, and avoided areas of continuous algal
38 canopy. *P. occidentalis* and *P. mccullochi* were associated with turfing and understory algal
39 forms. As the species use similar habitats, we suggest that where their distributions overlap
40 they will experience niche overlap and resource competition. While each species may occupy
41 different fundamental niches defined by different sea surface temperature requirements,
42 further study may reveal that competition for resources between these species leads to
43 competitive displacement on both local and geographical scales.

44

45 **INTRODUCTION**

46

47 Large-bodied territorial damselfish species are an abundant and prominent part of the fish
48 assemblage on rocky reefs in temperate Australian waters. This group is dominated by the
49 genus *Parma*. The genus is made up of 10 species, and is confined to Australasian waters
50 (Allen 1987). Damselfish species from the genus *Parma* are territorial and herbivorous
51 (Moran & Sale 1977, Jones 1999). In tropical systems the role of damselfish as agents of
52 biological disturbance is well documented (Hixon & Brostoff 1983, Lewis 1997, Ceccarelli et
53 al. 2001, Hata & Kato 2004, Ceccarelli et al. 2005). Many tropical damselfishes use and
54 defend algae within their territories as a food resource (Ceccarelli et al. 2001). The
55 composition of these food resources is variable, from small monocultural algal farms, to large
56 species rich assemblages (Montgomery 1980, Hixon & Brostoff 1983, Hixon & Brostoff
57 1996, Hata & Kato 2002). While research to assess the role of *Parma* in maintaining food
58 resources, and thus habitat heterogeneity in temperate Australasia is continuing, previous
59 studies have shown only limited effects of herbivory by territorial *Parma* on the algal
60 assemblage (Jones & Andrew 1990, Jones 1992). However, substantial small scale effects of
61 *Parma victoriae* and *Parma mccullochi* in the maintenance of spawning sites consisting of
62 short algal turf have been reported (Jones and Andrew 1990, Saunders et al. 2013).

63

64 The geographical distribution of species is influenced by their physiological tolerance along
65 environmental gradients such as water temperature (Pörtner et al. 2010, Langlois et al. 2012),
66 as well as oceanographic and recruitment processes. However, on smaller scales the
67 distribution of site-associated species such as territorial damselfish, may be more heavily
68 influenced by discrete local habitat variables (Galaiduk et al. 2013), such as the reef
69 topography, the algal community, or disturbance events. Individual damselfish species can

70 exhibit strong habitat preferences within their latitudinal range (Kingsford 1999, Galaiduk et
71 al. 2013). The habitat associations of territorial damselfish are likely to relate to their dietary
72 needs, their requirement for shelter and for a suitable substrate on which to lay eggs
73 (Tzioumis & Kingsford 1995). The requirement for shelter and suitable substrate upon which
74 to lay eggs should lead to an association with complex reef environments. Indeed, *Parma*
75 *mccullochi* have previously been shown to be more abundant on high relief reefs than low
76 relief reefs (Harman et al. 2003), and *Parma microlepis*, a species endemic to New South
77 Wales, were more abundant when shelter sites of 30cm or greater height were available
78 (Moran & Sale 1977). As a result of this need for shelter, substrate upon which to spawn and
79 their dietary requirements, another limiting factor in the distribution of temperate damselfish
80 species is likely to be macroalgal cover. Many damselfish species are herbivorous, preferring
81 to consume filamentous red algae (see review by Ceccarelli et al. 2001). Elsewhere in
82 Australasia *Parma* have been shown to be associated with small filamentous and foliose algal
83 patches on reefs (Moran & Sale 1977, Norman & Jones 1984, Jones 1992, Shepherd et al.
84 2008, Buckle & Booth 2009), or sea urchin barrens habitat (Anderson & Millar 2004,
85 Galaiduk et al. 2013). However, in temperate Western Australia reefs are dominated by
86 canopy forming algae (Wernberg et al. 2003, Toohey et al. 2007, Smale et al. 2010). Algal
87 canopies physically restrict feeding access to more palatable understory algae, and affect the
88 species composition and biomass of the associated understorey algae (Kennelly 1987b,
89 Kendrick et al. 1999, Wernberg et al. 2005). As a result, temperate damselfish may avoid reef
90 dominated by algal canopy. As examples, the abundance of *Parma mccullochi* on low relief
91 limestone reefs was higher when canopy forming algae *Ecklonia radiata* and *Sargassum* spp.
92 were not abundant (Harman et al. 2003). Western Australian *Parma* species might respond in
93 a similar fashion to their congeners elsewhere in Australasia by inhabiting patches in the
94 canopy caused by physical disturbance or other processes. An integrated sampling program

95 that measures the abundance patterns of *Parma* and considers both continuous environmental
96 variables and discrete habitat variables together may allow us to identify habitat associations,
97 and limiting resources for *Parma*.

98

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

119

120 This study aimed to identify similarities and differences in the habitat associations of each
121 species of *Parma* across the biogeographic scale of temperate Western Australia. Using the
122 most abundant of the study species, *Parma mccullochi*, the habitat associations of each
123 recorded fish were assessed at a single location. In addressing these aims we:

- 124 1) Describe the distribution and density of *Parma* species on shallow rocky reefs in temperate
125 Western Australia.
- 126 2) Quantify the correlations between discrete abiotic and biotic habitat variables and sea
127 surface temperature (as a proxy for water temperature) with geographical patterns in densities
128 of *Parma* spp.
- 129 3) Perform fine scale analyses to determine whether the habitat associations of individual *P.*
130 *mccullochi* are random or whether the fish ‘select’ for specific habitats.

131

132 **MATERIALS AND METHODS**

133

134 **Survey design**

135

136 This survey targeted shallow complex rocky reefs of between 4 and 12 metres depth, along
137 Western Australia’s warm temperate coastline. Surveys were performed between November
138 of 2005 and June of 2006. A nested hierarchical survey design was used, with seven
139 geographical regions (Figure 1). Within each region four locations were chosen and within
140 these four locations four different reef sites were selected. Twelve replicate 25 by 5 metre
141 belt transects were carried out at each reef site. Distance between samples varied on a
142 hierarchical spatial scale with regions being separated by thousands of kilometres to tens of
143 kilometres, locations within regions being separated by tens of kilometres to kilometres, reef
144 sites within locations being separated by kilometres to hundreds of metres and transects

145 within reef sites being separated by at least ten metres. Geographical regions and locations
146 within regions were positioned along a temperature gradient following the coastline of south-
147 western Australia (Figure 1). This design resulted in a total of 7 regions, 28 locations, 112
148 reef sites and 1344 transects, and spanned almost seven degrees of latitude and ten degrees of
149 longitude, or approximately 2000 kilometres of coastline.

150

151 **Survey Method**

152

153 Diver-operated stereo-video, as originally described in Harvey and Shortis (1995), was used
154 to swim transects of dimensions 5 by 25 metres (sample area 125 m²), with a 10 metre
155 spacing between transects. All surveys were recorded in visibility of 7 metres or greater. A 25
156 metre transect length was selected due to the patchy nature of the complex reefs targeted by
157 this survey. By selecting a short transect length, each transect could be completed within the
158 target habitat type. Transects were swum by teams of two SCUBA divers. The first diver
159 swam the stereo-video system, while the second measured the transect length. The two divers
160 were separated by a 10 m rope. The rope allowed communication between the divers,
161 meaning that only one diver was present at the cameras, and so reduced the effects of diver
162 presence on the fish assemblages that were captured on the video. The effects of SCUBA
163 diver presence on the recorded fish abundance can be variable and species specific, possibly
164 attracting or repelling fish (see Watson & Harvey 2007). Each transect was as linear as
165 possible within the target habitat, and the 10 m distance between transects was measured
166 using the 10 m rope between divers. The stereo-video system allows accurate and precise
167 measurements of the length of fish, and the range and angle of a fish from the camera system
168 (Harvey & Shortis 1998, Harvey et al. 2001). This allowed us to exclude fish that were
169 outside the transect area. The video recording created a permanent record of each transect,

170 which allowed ex situ habitat analysis. The benefits of using this type of system for
171 measuring fish densities and lengths have been discussed elsewhere (Harvey et al. 2001,
172 2002, Harvey et al. 2004, Langlois et al. 2010, Watson et al. 2005).

173

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

184

185 **Image processing**

186

187 The video from the left and right cameras for each transect was captured onto a PC as an
188 audio video interlaced (.avi) file. The software package Vision Measurement System (VMS,
189 Robson et al. 2006) was used to measure fork length of each fish, and also the three
190 dimensional positions of fish relative to the camera system. These three dimensional
191 positions were used to exclude fish that were further than 7 m from the camera system (7 m
192 was the minimum usable visibility), or more than 2.5 m from the centre of the transect line.
193 This allowed standardisation of the field of view used to the minimum visibility (Harvey et
194 al. 2004) and control of the transect area to 125 m². Fish that were within the sample area, yet

195 were visible in only one camera as they were hidden by benthos or rugose substrate, could
196 not be measured, but were still counted and included in the density data.

197

198 **Broad scale habitat quantification**

199

200 Habitat analysis was undertaken from the video footage using a visual basic program in
201 Microsoft Excel. This program was modified from Holmes (2005). Five estimates of habitat
202 were made for each twenty five metre transect. The video file was split into five equal non-
203 overlapping sections and a frame from each section selected for analysis haphazardly, but at a
204 point where the field of view encompassed a wide view of the habitat. Therefore, the
205 categorisation of the habitat was done on a horizontal image, with a depth of field of
206 approximately five metres. Rather than to quantify percentage cover absolutely as is possible
207 with downward facing images with a consistent scale, we chose to categorise each
208 observation into percentage cover or reef height / slope bins, or by recording the presence /
209 absence of difficult to classify habitat variables. This approach was chosen to reduce any bias
210 associated with the horizontally facing image.

211

212 At each observation point the reef height and slope were estimated from the field of view and
213 assigned categorical values. The reef or outcrop height was ranked from one to four
214 according to the following categories: 1) Platform reef, 2) small outcrops (boulders or
215 outcrops less than 1 m in height), 3) large outcrops (boulders or outcrops greater than 1 m but
216 less than 3 m), and 4) massive outcrops (outcrops greater than 3 m in height). Slope was
217 estimated and assigned to one of the following categories: 1) Less than 30° (gentle slope), 2)
218 30° to 70° (steep slope), 3) 70° to 110° (vertical wall), 4) greater than 110° (overhanging wall),
219 and 5) overhead overhanging reef or cave. Benthic biota cover was estimated at each

220 observation point for the following variables; sessile invertebrates, *Ecklonia radiata* (kelp)
221 canopy, non-*Ecklonia* canopy forming algae (fucal species), and understory algae, which
222 included fucal, foliose, and turfing alga where a canopy was not present. These were
223 assigned a rank from zero to six according to the following estimated percentage cover
224 categories: 0) nil, 1) <1%, 2) 1-10%, 3) 10-25%, 4) 25-50%, 5) 50-75%, and 6) >75% cover.
225 The understory algae category was further divided into three groups; foliose algae, turf
226 algae, and seagrass, the presence or absence of each of these three groups at each observation
227 point were recorded. For geographical analysis these categorical observations were averaged
228 to give measures of mean habitat at the reef site level (60 measurements, 1500 m²).

229

230 As this survey encompassed both the warm and cold extremes of range for different *Parma*
231 species mean water temperature throughout the year was used instead of winter temperature.
232 Sea surface temperature (SST) data derived from the Moderate Resolution Imaging
233 Spectroradiometer (MODIS) instrument was obtained from ocean color web
234 (oceancolor.gsfc.nasa.gov). A level 3 product, annual mean SST was obtained for two
235 adjacent 9 km pixels at each location. The mean of these two pixels was calculated for each
236 of 5 years (2002 to 2006 inclusive). These were then averaged across the 5 years to give a 5
237 year mean sea surface temperature for each location. The 5 year mean SST was used as it
238 represented the historical record of water temperatures on a scale that was thought to be
239 relevant to long-lived, site-associated species such as those of the genus *Parma*.

240

241 **Fine scale habitat quantification**

242

243 *Parma mccullochi* have been reported as the most abundant and widely spread of the *Parma*
244 species in Western Australia (Hutchins 1994, 2001), so they were selected for habitat analysis

245 on a finer scale. This analysis was carried out using data from one location in region 3
246 (Marmion Lagoon, Perth) because densities of this species were found to be highest there.
247 Rather than averaging habitat observations to the site level, the data from each of the five
248 individual habitat observation points on each transect were used. These were compared to
249 similar observation points made where each *P. mccullochi* was encountered. These
250 observations were made from a single video frame, at the point in time where the fish was
251 measured. The habitat visible in the entire field of view at that frame was characterised
252 following the procedure described above.

253

254 **Statistical Analysis**

255

256 **Geographical patterns in density and range**

257 Total number of fish per reef site (1500 m²) for each *Parma* species at each of the seven
258 geographical regions were calculated and represented graphically. Univariate ANOVA
259 analysis were performed using MINITAB release 13 on square root transformed densities of
260 each species, using a three factor (Region, Location and Site) hierarchical nested model.
261 Region was a fixed factor with seven levels. The factor location had four levels and was
262 nested within region. The factor reef site also had four levels and was nested within location.
263 A square root transformation was applied as this resulted in the data most closely fitting a
264 normal distribution as tested using Anderson-Darling normality tests.

265

266 The distribution patterns for each species of *Parma* were plotted against sea surface
267 temperature. Following the method outlined in Langlois et al. (2012), quantile regression
268 spline models (Koenker & Bassett 1978) were used to fit 95th percentile splines of the density
269 of each species to mean sea surface temperature (after Anderson 2008). Models were fitted

270 using the function `rq()` (part of the ‘`quantreg`’ package, Koenker 2010) combined with the
271 function `bs()` in the ‘`splines`’ package in the R computer programming language (R Core
272 Team 2012). The appropriate degree of the polynomial for each spline was determined from a
273 set of models having polynomial of degree 1, 2, 3 or 4 using the corrected AIC selection
274 criteria (AICc). The quantile regression sandwich formula and Hall–Sheather bandwidth rule
275 were used to estimate goodness of fit and calculate *P*-values for each polynomial degree to
276 assess the polynomial degree that was selected using the AICc (after Cade et al. 2005).

277

278 **Geographical relationship of density to SST and habitat**

279 In order to elucidate the role of environmental variables in determining the distribution and
280 community structure of the three *Parma* species over the survey area a distance based linear
281 model (DistLM) was calculated using the PERMANOVA+ (Anderson et al. 2008) package in
282 PRIMER 6 (Clarke & Gorley 2006). This analysis selects the environmental variables that
283 best explain the variation in the density of the three *Parma* species over the entire survey
284 area. A resemblance matrix of the densities per reef site (1500 m²) of each of the three *Parma*
285 species was constructed from square root transformed data using the zero-adjusted Bray-
286 Curtis coefficient (Clarke et al. 2006). The Bray-Curtis coefficient was selected as it has the
287 property of independence of joint absences. However, this property results in an undefined
288 value where samples contain no individuals at all. To avoid this difficulty the zero-adjusted
289 Bray-Curtis includes a dummy species of value one in all samples. Habitat predictor variable
290 data were not transformed. Where habitat variables were strongly correlated ($> \pm 80\%$) one
291 variable was excluded. Sand cover was negatively correlated to reef cover so was excluded
292 from analysis. Mean sea surface temperature data was also included in the model. No
293 environmental variables were strongly correlated with sea surface temperature. DistLM was
294 performed using the best selection procedure and the AICc. AICc was originally proposed by

295 Sugiura (1978) to reduce bias in linear regression models. It has since been shown to also
296 greatly improve model selection with small sample sizes (Hurvich & Tsai 1989, Hurvich et
297 al. 1990). For these reasons it was selected for use in our analysis. The variables selected to
298 make up the model were then plotted using distance based Redundancy Analysis (dbRDA).
299 Spearman rank correlations of the densities of each *Parma* species to the dbRDA axis were
300 calculated.

301

302 **Habitat associations of each species**

303 While the analysis above considered the three common species together, we also wanted to
304 assess the habitat associations of each species individually. For this analysis DistLM using
305 the best selection procedure and AICc criterion was used to model the distributions of each of
306 the three species individually using the environmental variables described above. Marginal
307 tests were used to identify the environmental variables that explained a significant portion of
308 the variation in the densities of each of these species. For *Parma mccullochi* DistLM and
309 marginal tests were performed across all seven regions as this species was ubiquitous. For
310 *Parma occidentalis* and *Parma victoriae* this analysis was carried out only using data from
311 the one region where they were most abundant (regions 1 and 7 respectively). This was to
312 reduce the likelihood of detecting spurious relationships with habitat, as these species were
313 rare in other regions.

314

315 **Fine scale habitat associations**

316 Fine scale habitat analysis for *Parma mccullochi* was performed at one location in region 3
317 (Marmion Lagoon, Perth). This analysis was designed to determine whether the distribution
318 of *P. mccullochi* along a transect was random or whether the fish were ‘selecting’ for specific
319 habitats. Observations of habitat were recorded from the point on the video where each *P.*

320 *mccullochi* was measured. These observations were compared to the available habitat, which
321 was calculated from five haphazard observations along each transect, as described previously.
322 The percentage of observations where each category of habitat variable was recorded was
323 plotted for the expected habitat and observed habitat when *P. mccullochi* were present. Chi-
324 square goodness of fit tests were calculated to test a hypothesised difference between
325 expected and observed observations. Categories where the expected values were very low
326 were summed together to allow testing.

327

328 **RESULTS**

329

330 **Geographical patterns in density and range**

331

332 Over the entire survey area only one *Parma bicolor* individual was recorded, in region 3 at
333 Rottnest Island. This species has been omitted from analysis due to its extreme rarity.

334 Differences in the densities of the three commonly observed *Parma* species per reef site
335 sampled (1500m²) were observed throughout the survey area (Figure 2). Significant
336 differences at $\alpha = 0.05$ in densities of all *Parma* species were observed between regions
337 (Table 1). While these were significant for each species, significant results were also returned
338 for locations within regions and reef sites within locations. There is a high degree of
339 variability expressed in the sums of squares at all levels of the ANOVA design. This
340 variability reflects the patchily distributed nature of these three species.

341

342 *Parma mccullochi* reached a maximum density of 96 individuals 1500 m⁻² (Figure 2) at a reef
343 site in region 3 (Wanneroo Reef, Marmion Lagoon, Perth). *Parma occidentalis* also reached
344 its maximum density of 21 individuals 1500m⁻² (Figure 2) at a site in region 3 (Cow Rocks,

345 Marmion Lagoon, Perth). Away from the Marmion Lagoon *P. occidentalis* was absent from
346 reefs surveyed in region 3, as a result of which the mean density per reef (3.3 ± 0.7 SE, $n =$
347 16) is highest in region 1 (Port Gregory to Geraldton) where it was consistently present.
348 *Parma victoriae* was found to reach its maximum density of 23 individuals 1500 m^{-2} in
349 region 7 (Esperance) at Cull Island (Figure 2).

350

351 *P. mccullochi* showed a unimodal distribution across the geographical range studied here,
352 with high densities at both region 3 and region 5 (Perth and Albany, Figure 2). At both the
353 northern and south-eastern extremes of the survey area the mean density of *P. mccullochi* was
354 very low, less than two and four individuals on average per 1500 m^2 respectively (region 1,
355 1.6 ± 0.5 SE, $n = 16$; region 7, 3.3 ± 0.9 SE, $n = 16$). The extremes of the survey area are
356 likely to be close to the range limits of *P. mccullochi*. *Parma occidentalis* was present only in
357 the three northernmost regions (Figure 2). It reached the highest mean density (3.3 ± 0.7 SE,
358 $n = 16$) in region 1 (Port Gregory to Geraldton). Region 3 (Perth) was the southern range
359 limit of *P. occidentalis* on shallow coastal reef (Figure 2). *Parma victoriae* was present at
360 five of the seven regions sampled, from region 3 (Perth), and along the south coast to region
361 7 (Esperance). With the exception of region 6 (Bremer Bay), where only two individuals
362 were recorded, the density of *P. victoriae* was found to increase south and eastward from
363 region 3 to a maximum mean density of 5.1 fish 1500 m^{-2} (± 1.5 SE, $n = 16$) at region 7
364 (Esperance). Region 3 (Perth) was the northern range limit for this species on shallow coastal
365 rocky reef in Western Australia.

366

367 **Geographical relationship of density to SST and habitat**

368

369 A model using five predictor variables to explain 33% of the variation in the population of
370 *Parma* densities was generated from the DistLM procedure ($R^2 = 0.33$, AICc = 737.83). The
371 environmental variables were: sea surface temperature, height of reef or rocky outcrop above
372 sea bottom, presence of vertical walls and overhangs, presence of turfs and cover of the kelp
373 *Ecklonia radiata* (Figure 3). Marginal tests identified sea surface temperature and the
374 presence of turfing algae as the two most important predictor variables, accounting for 16%
375 and 10% of the variability in densities of the *Parma* assemblage respectively ($P < 0.001$). The
376 first two dbRDA axis accounted for 55% and 42% of the variation in the fitted model
377 respectively, and together accounted for 32% of the total variation in *Parma* density data
378 (Figure 3). *Parma occidentalis* and *Parma victoriae* densities were positively and negatively
379 correlated respectively, to the first dbRDA axis. Sea surface temperature was strongly
380 correlated to this axis. The southern and northern extremes respectively of these species were
381 encompassed by the survey, at region 3. At this region from 2002 to 2006 the yearly mean
382 sea surface temperature ranged between 17.6°C and 20.7°C with a mean of 19.9°C
383 (oceancolor.gsfc.nasa.gov). *Parma mccullochi* density was negatively correlated to the
384 second dbRDA axis, as was turfing algae presence. Other predictor variables included in the
385 model, may play some role in explaining variation in *Parma* densities (Figure 3). Yet these
386 were not strongly correlated to the first two dbRDA axes which accounted for so much of the
387 variation in the fitted model (Table 2). On a smaller scale these variables showed greater
388 predictive power (Table 3). The variables associated with more complex reef, such as Reef /
389 outcrop height, and increasing cover of *Ecklonia radiata*, were correlated with *P. occidentalis*
390 density (Figure 3). The correlation vector for *P. victoriae* increased in the opposite direction,
391 and *P. victoriae* appeared negatively correlated with *E. radiata* cover (Figure 3). Across the
392 geographical range surveyed reef site scale patterns in densities of *Parma* were most strongly
393 correlated to sea surface temperature and the presence of turfing algae.

394
395 Habitat associations of each species
396 Further modelling of each species of *Parma* individually using the environmental variables
397 revealed that vertical or overhanging walls explained a large proportion of the patterns in
398 density of all species (Table 3). Turf algae presence, overhead reef or cave, overhanging wall,
399 and reef or outcrop height above the seabed were selected by the model to best predict the
400 abundance of *Parma mccullochi* (Table 3). Turf algae presence, other algae cover and
401 overhead reef or cave, and overhanging wall explained the largest proportions of the variation
402 in the density of *P. mccullochi* across the whole survey area (Table 3). Marginal tests showed
403 that these relationships were statistically significant (Table 3). Turf algae presence and
404 overhanging wall were selected by the model to best predict the abundance of *Parma*
405 *occidentalis* at region 1 (Table 3). Hard coral cover, turf algae presence and overhanging wall
406 all explained greater than 10% of the variation in *P. occidentalis* densities at region 1.
407 However, none of these relationships were statistically significant (Table 3). In the case of
408 *Parma victoriae*, the explanatory variables vertical wall and seagrass presence were selected
409 by the model to best explain the abundance of this species at Region 7 (Table 3). Vertical
410 wall and overhanging wall explained large and statistically significant proportion of the
411 variation in the densities of *P. victoriae* at region 7 at 34% and 31% respectively (Table 3).
412 Seagrass presence, non-*Ecklonia* canopy cover and hard coral cover all explained greater than
413 10% of the variation yet the relationships were not significant (Table 3). The inclusion of the
414 variable seagrass presence in the model suggests that *P. victoriae* are associated with the
415 edges of reef habitat, near soft seabed where seagrass beds are established.

416

417 **Fine scale habitat correlations with *Parma mccullochi***

418

419 At the fine scale there was evidence of association of *Parma mccullochi* to certain habitat
420 types. All χ^2 comparisons of expected and observed habitat observations proved significant at
421 $\alpha = 0.05$ (Table 4). An association of individual *Parma mccullochi* with reef or outcrop
422 greater than 3 metres in height was apparent (Figure 4a). Greater than 45 % of fish were
423 observed here, while this habitat accounted for only 8 % of expected observations. A trend of
424 association with reef of increasing height was demonstrated by *P. mccullochi*. *P. mccullochi*
425 also demonstrated a clear association with reef classed as vertical wall. 43 % of fish of this
426 species were observed on vertical walls, while this accounted for only 19 % of expected
427 observations. *P. mccullochi* also demonstrated an association with low to medium (1-25 %)
428 *Ecklonia radiata* cover and areas with nil or with low non-*Ecklonia* canopy cover (Figure
429 4d). *P. mccullochi* were most often recorded where higher covers of understorey macroalgae
430 were recorded (Figure 4e).

431

432 **Length frequency distributions**

433

434 The fork length frequency distributions of *Parma mccullochi* were broadly similar in shape
435 (Figure 5), although at region 3 the median length classes were more evenly populated than at
436 other regions. The length frequency distribution at region 3 differed significantly to those at
437 regions 2, 4, 5, and 6 (two sample Kolmogorov-Smirnov tests; all $P < 0.014$). At regions 2, 3,
438 and 4 the range of lengths recorded was similar, whilst at regions 1, 5, 6, and 7 fewer very
439 large or very small *P. mccullochi* were recorded (Figure 5). Statistical comparisons of length
440 frequency distributions were not conducted at regions 1 or 7 due to the low number of lengths
441 measured at these regions. Similarly, statistical tests of the length frequency distributions of
442 *Parma occidentalis* and *Parma victoriae* were not conducted due to low numbers of length
443 measurements. The length frequency distributions for *Parma occidentalis* generally covered a
444 similar range to those of *P. mccullochi*, however the maximum fork length recorded for *P.*

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

448

449 **DISCUSSION**

450 Our study described the distributions of three congeneric pomacentrid species throughout
451 temperate south-western Australia. The fourth species, *Parma bicolor*, is endemic to Western
452 Australia (Hutchins 2001). However, in our survey only one individual was recorded. This
453 species is often observed on deeper reefs along the south coast of Western Australia, with a
454 preferred depth range of 30 metres or greater (Hutchins 1994). This depth range was beyond
455 the scope of this survey. It may be that *P. bicolor* inhabits similar habitat to other *Parma*
456 species, simply shifted to a deeper water environment, possibly as a result of competition
457 with con-generics in the shallow complex rocky reefs. Identification of the ecological niches
458 of coexisting species aids in the detection and discussion of any interspecific competition
459 (Sale 1974, Ebersole 1985, Huston 1999). The three common species were found to have
460 overlapping distributions, *Parma occidentalis* was northerly (warm water) distributed, *Parma*
461 *mccullochi* was found across the survey area, and *Parma victoriae* was southerly (cool water)
462 distributed.

463

464 Sampling occurred over 7 months (November of 2005 until June of 2006, the Austral summer
465 and autumn) encompassing the main recruitment period for these fishes (Saunders et al.
466 2013). While it is possible that the density patterns may have been affected by seasonal
467 recruitment, our length information shows no evidence of a seasonal increase in the number
468 of recruits. Very few recruits were counted. Only eleven *P. mccullochi* and one *P.*
469 *occidentalis* were measured at less than 100 mm in length. The smallest *P. victoriae* was

470 measured at 109 mm in length. Very small recruits of these species are cryptic and find
471 refuge in small cracks in the reef. Therefore, they may not have been detected by our video
472 based sampling method.

473

474 Sea surface temperature decreased from north to south-east over the survey area. Our
475 geographical scale modelling found that sea surface temperature was an important predictor
476 for both *Parma occidentalis* and *Parma victoriae* densities over the survey area. However,
477 some components of the pattern in density in our survey suggest that local habitat variables
478 may be just as important as water temperature in determining the density of these species. For
479 example, *P. occidentalis* is a sub-tropical / warm temperate species that has been suggested to
480 be expanding southward in response to warming trends (Wernberg et al 2013). Yet the
481 maximum density of this species was at a site in region 3. This region also encompassed the
482 southern range limit of this species. Another example is evident in the density of *P. victoriae*
483 in region 6. The density of this species was high at region 5 to the west and region 7 to the
484 east, but only two individuals were recorded at region 6. A similar importance of local habitat
485 over water temperature in determining the abundance of *Parma* was suggested by Galaiduk et
486 al. (2013). However, on broad geographical scales SST was a good predictor of the density of
487 *Parma* in south-western Australia. Temperature changes can increase stress levels and inhibit
488 growth rates in fishes (Wendelaar Bonga 1997) including pomacentrids (for example see;
489 Nakano et al. 2004, Figueira et al. 2009). The southern and northern extremes of range of *P.*
490 *occidentalis* and *P. victoriae* respectively were found around region 3. The range in sea
491 surface temperature at this region may encompass the minimum and maximum temperature
492 respectively that allows successful population processes for these species. Highest densities
493 of *Parma mccullochi* were found at region 3, although *P. mccullochi* was cosmopolitan over
494 the survey area. Density of *P. mccullochi* was generally high over the survey area, but did

495 decrease quickly at the warm and cool extremes of the survey range. This pattern is broadly
496 similar to the abundant centre distribution of this species which was described by Tuya et al.
497 (2008). The abundant centre hypothesis has been a common assumption in ecology (Austin
498 1987, Cox & Moore 1993, Sagarin & Gaines 2002). However, the generality of this
499 hypothesis in real world applications has been increasingly questioned (Austin 1987, Sagarin
500 & Gaines 2002, Sagarin et al. 2006, Tuya et al. 2008, Langlois et al. 2012). An abundant
501 centre distribution was described in only 39% of literature that was reviewed by Sagarin and
502 Gaines (2002). Langlois et al. (2012) modelled the distributions of 20 abundant fish species
503 over the south-west of Australia, and demonstrated that 15 of the 20 had unimodal
504 distributions, while four had ramped distributions. Over our survey area, *P. mccullochi* had a
505 unimodal distribution, *P. victoriae* a ramped distribution favouring cooler waters, and *P.*
506 *occidentalis* were more abundant in warmer waters. Langlois et al. (2012) conclude that eco-
507 physiological theory (Pauly, 2010; Pörtner et al., 2010) is appropriate for application to
508 predictive models of the abundance distribution of marine species, and our observations
509 support this conclusion, at least over broad geographical scales in Western Australia.

510

511 In addition to possible physiological effects, sea surface temperature may be a proxy for
512 physical and biological oceanographic processes. Such patterns could influence survivorship
513 of fish larvae and the feeding of reef fish (Kingsford 1989) which may in turn influence
514 patterns of reef fish assemblages. While sea surface temperature appears to separate *Parma*
515 *victoriae* from other species on the south coast of W.A. other environmental factors may be at
516 play. For example, the dominance of the canopy algae *Ecklonia radiata* decreases along the
517 south coast as it is replaced by other fucalean canopy species (Wernberg et al. 2003). This
518 pattern may be reflected in the correlation of *E. radiata* in a similar direction to *P.*
519 *occidentalis*. Rather than indicating a causal relationship, this correlation may simply be due

520 to *P. occidentalis* only being recorded on the west coast, where *E. radiata* canopy is more
521 dominant.

522

523 Regional scale modelling of the habitat to each species separately revealed similarities in
524 habitat associations between species. All three species were associated with vertical or
525 overhanging rock walls. Fine scale observations showed that *Parma mccullochi* were
526 associated with complex reef habitat, typified by a reef height greater than three metres and
527 with a vertical reef face. These observations are supported by (Harman et al. 2003) who
528 found similar patterns for this species.

529

530 In modelling the relationships of *Parma* to environmental variables over the survey area, we
531 found that the presence of turfing algae predicted the density of *Parma mccullochi* well.

532 Regional scale modelling of the species separately also outlined associations of *Parma* to
533 certain algal morphologies. *P. mccullochi* and *Parma occidentalis* were both associated with
534 turf algae presence and understorey algal cover. In addition, our fine scale habitat
535 observations for *P. mccullochi* revealed an association with high understorey algae cover and
536 low canopy cover (both *Ecklonia radiata* and otherwise). While little published information
537 is available on *P. mccullochi* and *P. occidentalis*, as territorial herbivores (Jones 1999) they
538 are likely to eat turfing algae and understorey algal species. Published information is
539 available for *P. victoriae*, which has a strong preference for red algal understorey species
540 such as from the genera *Champia* and *Rhodoglossum* (Jones 1999). Other *Parma* species
541 have been shown to feed on red understorey algae, or within breaks in algae canopy within
542 their territories (Norman & Jones 1984, Jones & Norman 1986, Andrew & Jones 1990, Jones
543 & Andrew 1990, Jones 1992, Shepherd et al. 2008). Additionally, the maintenance of turfing
544 algae (usually red, polysiphonious algae) as a food resource has been recorded in many

545 tropical herbivorous pomacentrids (Hixon & Brostoff 1983, Ceccarelli et al. 2001, Hata &
546 Kato 2004, Barneche et al. 2009). In addition to food, both *P. mccullochi* and *P. victoriae*
547 have been shown to maintain small patches of turfing algae as nest sites (Jones & Andrew
548 1990, Saunders et al. 2013), this may be another driver for the association with turf algae that
549 we observed. Our observed association of *Parma* with understorey algae may be due to
550 *Parma* taking advantage of breaks in the algal canopy. A similar pattern has been reported for
551 *Parma* species in New Zealand, that inhabit breaks in algal canopy caused by sea urchins
552 (urchin barrens) (Anderson & Millar 2004). Breaks in the algal canopy are rarely caused by
553 sea urchins in south-western Australia (Vanderklift & Kendrick 2005), probably due to low
554 sea urchin abundances (Fowler-Walker & Connell 2002, Vanderklift & Kendrick 2004).
555 However, breaks can occur as a result of storm disturbance (Kennelly 1987a).
556
557 Similar habitat use suggests that where the distributions of the three common species of
558 *Parma* in south-western Australia overlap, they can be considered to occupy a similar post-
559 interaction ecological niche. In areas where the species co-occurred they were often recorded
560 on the same transect. On a fine scale, the biogeographic density patterns are likely to be
561 directed by local scale processes such as recruitment, or by the availability of resources,
562 territorial interactions and competition for use of these resources (Chase & Myers 2011,
563 Wiens 2011). In addition, species competition should be considered in connection with the
564 niche concept, since some similarity and overlap in niches is a prerequisite of competition
565 (Alley 1982). Where the distributions and habitat use of *Parma* species overlap, competition
566 for resources is likely to be important in determining their realised niches. Indirect evidence
567 of such processes is suggested by our study. Earlier in this discussion we have highlighted the
568 importance of local scale habitat variables in determining the density of *Parma* in south-
569 western Australia. Such small scale habitat variation may lead to interspecific competition for

570 resources. For example, at regions 5 and 6 the density of *P. mccullochi* was high, while the
571 density of *P. victoriae* was comparatively low. By contrast at both the northern and southern
572 adjacent regions (regions 4 and 7) this pattern was reversed. While these density patterns
573 were undoubtedly influenced by other factors, such as recruitment and oceanographic
574 processes, and habitat variation, they suggest interspecific interactions and competition. To
575 tease out the separate influences of these processes would require well designed targeted
576 research. Further investigation of *Parma* spp. behaviour and resource utilisation may clarify
577 any niche overlap or resource competition between species.

578

579 This study reveals similarities in the habitat use of three related species of territorial
580 pomacentrid. We propose that increased reef complexity results in greater availability of
581 shelter sites, and that the association of *Parma mccullochi* and *Parma occidentalis* with
582 turfing algae and low or absent canopy cover is due to the use of turfing and understory
583 algae as food and nesting resources in a similar fashion to many other pomacentrids. The
584 species however were found to have different geographical distributions. It is likely that
585 competition for resources between these species leads to competitive displacement on both
586 local and geographical scales. In comparison to elsewhere, both globally and nationally, the
587 south-western Australian marine environment has been geologically stable and isolated, and
588 free of glaciation events and mass extinctions throughout the Cainozoic era (see Phillips 2001
589 and Langlois et al. 2012 for review). The marine environment has been moderated by the
590 warm Leeuwin current for 40 million years (McGowran et al. 1997), and this stability, in
591 combination with its switching on and off periodically (McGowran et al. 1997), may have
592 contributed to the high diversity and degree of endemism in south-western Australia (Phillips
593 2001). In this environment our three common *Parma* species may have evolved over time to

594 occupy differing fundamental niches, as sea surface temperature is strongly correlated to the
595 distribution of these species over the geographical area surveyed.

596

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604

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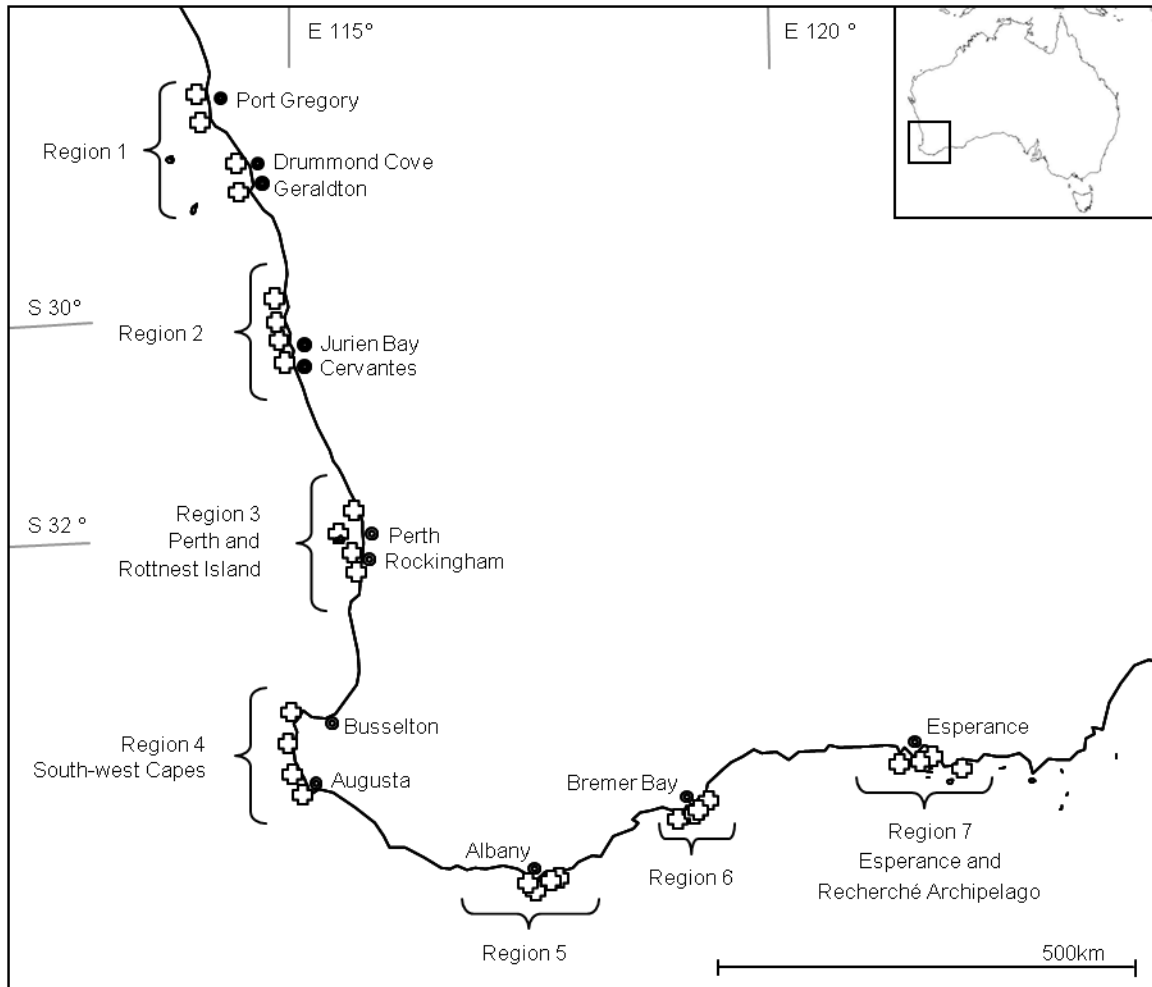
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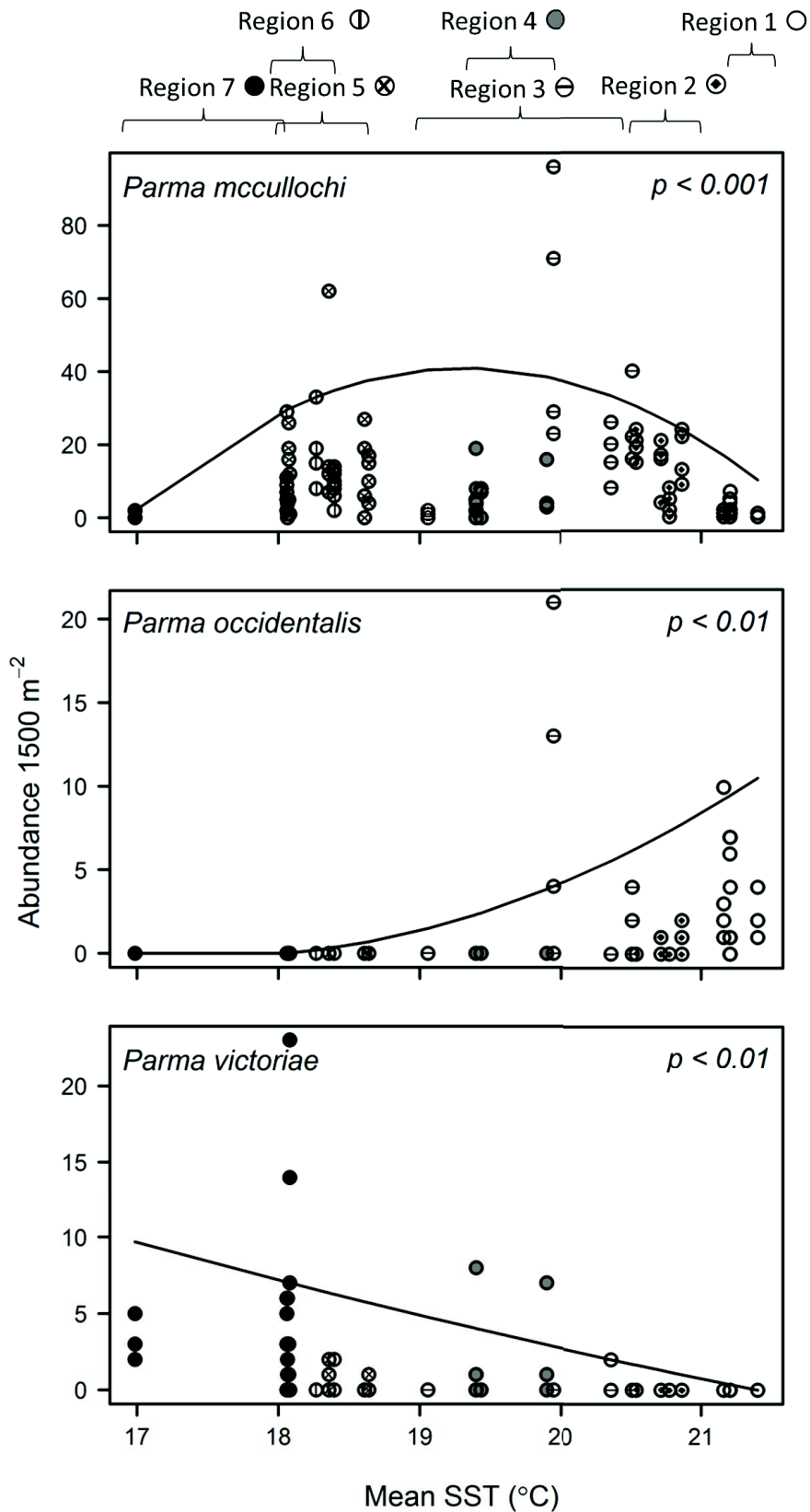
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Figure 1. Survey design illustrating the seven geographical regions surveyed. Within each region four locations are illustrated. From northernmost through south to easternmost the regions (bold) and locations are: **1 Port Gregory to Geraldton** locations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



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811 **Figure 2. Abundance (fish 1500m⁻²) and 95th percentile regression spline models for each *Parma* species**

812 **and the mean SST at each location. *P* values for the fit of the polynomials are overlaid.**

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814 **Table 1. Results of a three factor fully nested analysis of variance on square root transformed densities of**
 815 **three *Parma* species across seven regions. Region is a fixed factor**
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Parma mccullochi

	DF	SS	MS	<i>F</i>	<i>P</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			

Parma occidentalis

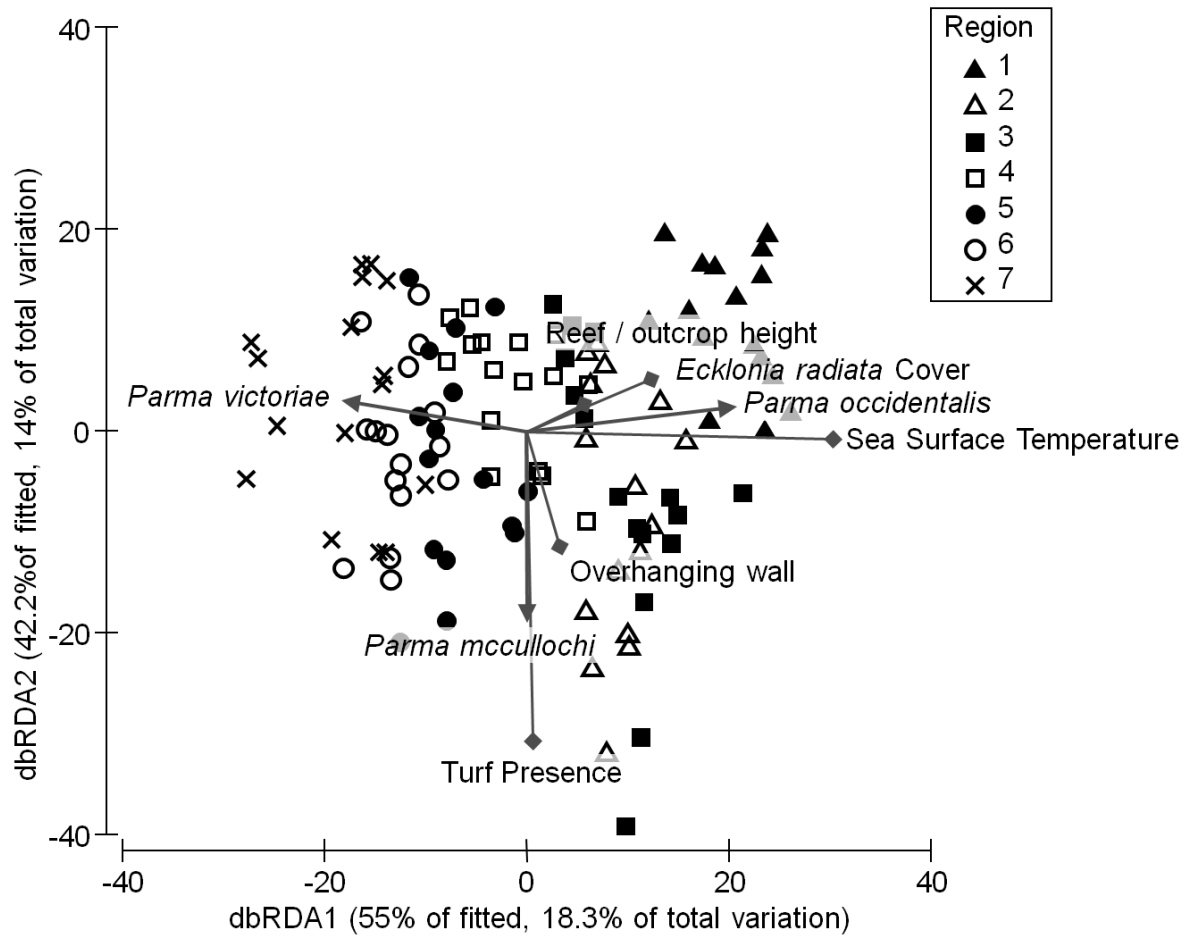
	DF	SS	MS	<i>F</i>	<i>P</i>
Region	6	8.88	1.48	4.633	0.004
Location (Region)	21	6.71	0.32	2.232	0.005
Reef site (Location (Region))	84	12.02	0.14	2.504	<0.001
Error	1232	70.41	0.06		
Total	1343	98.02			

Parma victoriae

	DF	SS	MS	<i>F</i>	<i>P</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			

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Figure 3. Distance based RDA ordination of first and second fitted axis 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 axis. The first and second dbRDA axis explained 55% and 42% of the variation in the fitted model respectively

826 **Table 2. Correlations to the first and second dbRDA axis (Figure 3) of selected environmental variables**
 827 **and *Parma* densities per reef site (1500m²)**

Multiple partial correlation		
Variable	dbRDA1	dbRDA2
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		
Variable	dbRDA1	dbRDA2
<i>Parma mccullochi</i>	<0.01	-0.57
<i>Parma occidentalis</i>	0.62	0.07
<i>Parma victoriae</i>	-0.55	0.09

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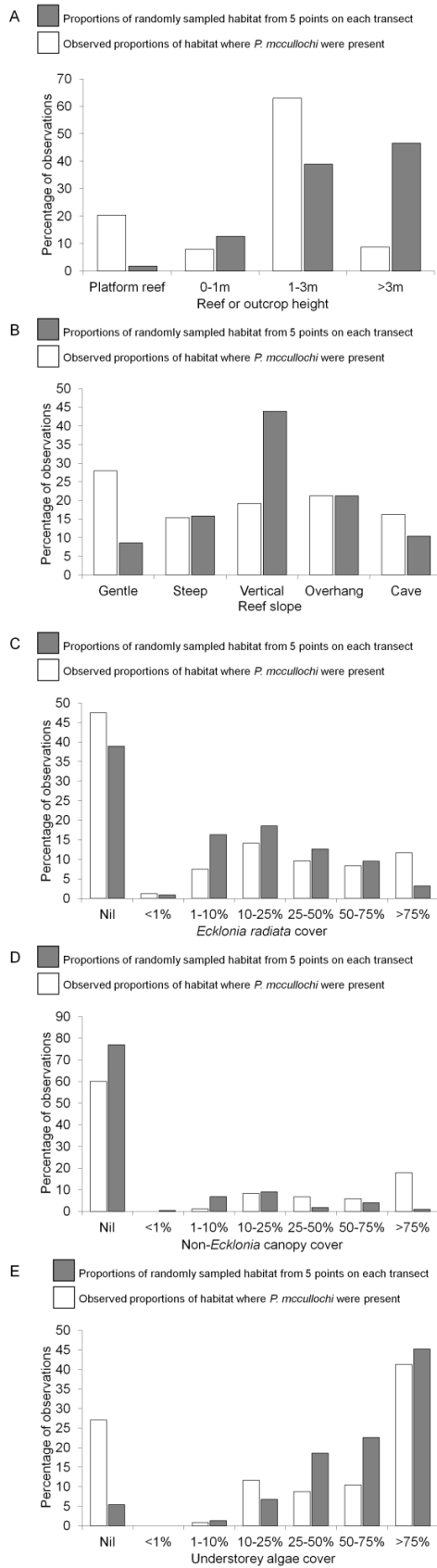
830 **Table 3** The five environmental variables that explained the greatest proportion of the variation in the
 831 densities of each of three species of *Parma*. The variables highlighted in bold were selected to best model
 832 the abundance of each species through DistLM using best selection procedure and AICc selection criteria
 833 (*P. mccullochi* includes a sixth variable which was selected by the model but had low predictive power by
 834 itself).
 835

<i>P. mccullochi</i> all regions		AICc 87.5, R ² 0.44 Number of variables: 4		
Variable	SS(trace)	Pseudo- <i>F</i>	<i>P</i>	Proportion
Turf Presence	105.23	39.64	<0.001	0.26
Other Algae 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 Number of variables: 2		
Variable	SS(trace)	Pseudo- <i>F</i>	<i>P</i>	Proportion
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 Algae 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 Number of variables: 2		
Variable	SS(trace)	Pseudo- <i>F</i>	<i>P</i>	Proportion
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

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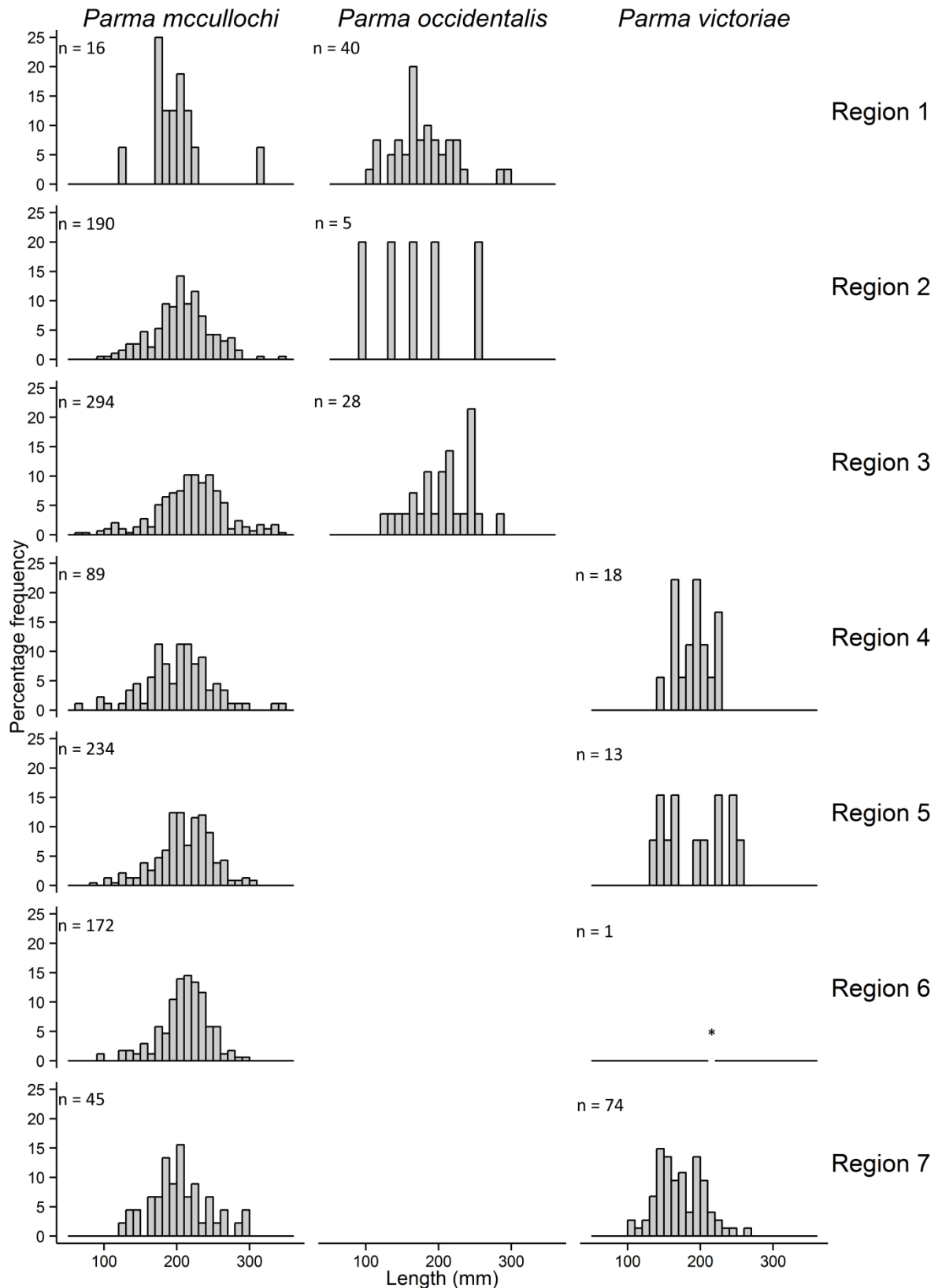
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Figure 4. Plots showing percentage of observations for categories of each of five habitat classes recorded at Marmion Lagoon in region 3 (Perth). Observations are illustrated for: Randomly sampled habitat observations, calculated at five points along each of twelve transects, at each of four reef-sites (n = 240) and observed habitat where *P. mccullochi* were present, calculated at points where each *P. mccullochi* individual was observed (n = 221)

843 **Table 4. Chi-square goodness of fit tests comparing observed frequencies of habitat at points where**
 844 ***Parma mccullochi* were present to the expected proportion of randomly sampled habitat observations**
 845 **calculated at five points along each transect, for each of five habitat classes. Degrees of freedom are in**
 846 **parentheses.**
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	Observed frequencies of habitat where <i>P. mccullochi</i> were present	Expected proportions of randomly sampled habitat observations
Reef or outcrop height		
Platform reef	4 (1.81%)	20.4%
0-1m	28 (12.67%)	7.9%
1-3m	86 (38.91%)	62.9%
>3m	103 (46.61%)	8.8%
$\chi^2_{(3)} = 425.98, P < 0.001$		
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%
$\chi^2_{(4)} = 104.70, P < 0.001$		
<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%
$\chi^2_{(5)} = 45.62, P < 0.001$		
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%
$\chi^2_{(4)} = 63.77, P < 0.001$		
Understorey algae 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%
$\chi^2_{(4)} = 96.59, P < 0.001$		

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850 **Figure 5. Length percentage frequency histograms for each of the three common species of *Parma* at each**
 851 **region. ‘*’ indicates that only one individual was measured at this region, so 100% of length**
 852 **measurements were in this length bin. ‘n’ represents the number of lengths measured, and is not**
 853 **representative of the density of fish recorded.**
 854