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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22   ABSTRACT:

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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 understorey 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

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, Hixon & Brostoff 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 *Parma victoriae* and *Parma mccullochi* in the maintenance of spawning sites consisting of short algal turf have been reported (Jones and 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

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 m^2), 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 m^2. 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 (fucalean species), and understorey algae, which

222   included fucalean, 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 understorey 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 m^{-2}).

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 m^2) 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 m^2) 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

12

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 ($1500m^2$) 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   α = 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 understorey

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

604

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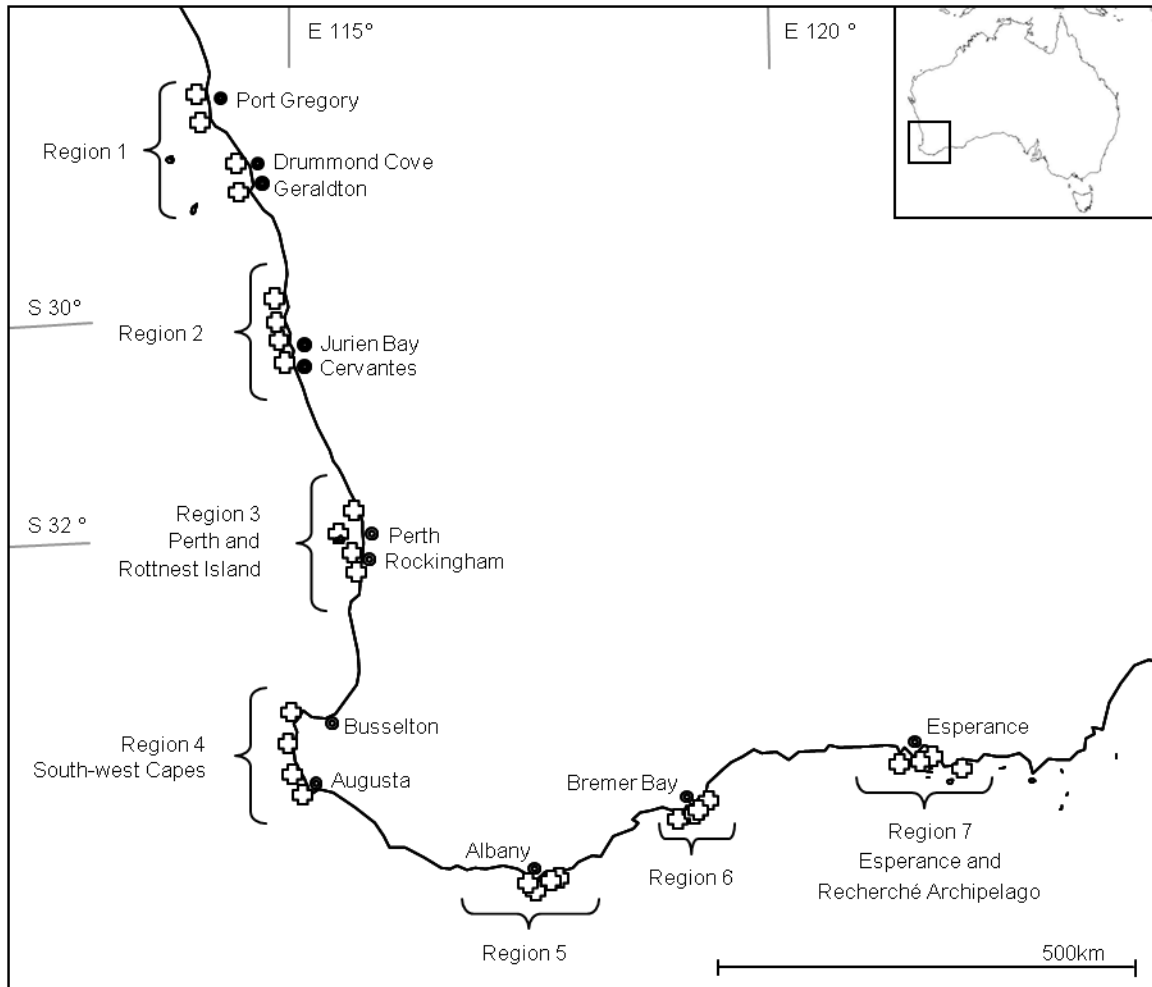
799 **Figure 1. Survey design illustrating the seven geographical regions surveyed. Within each region four**
800 **locations are illustrated. From northernmost through south to easternmost the regions (bold) and**
801 **locations are: 1 Port Gregory to Geraldton** locations were; Port Gregory North, Port Gregory South,
802 Drummond Cove and Geraldton. **2 Jurien Bay** locations were; Leeman, Green Head, Jurien Bay and Cervantes.
803 **3 Perth and Rottnest Island** locations were; Marmion Lagoon, Rottnest Island, Carnac Island and Shoalwater
804 Islands Marine Park. **4 South-West Capes** locations were; Geographe Bay, Cape Freycinet, Hamelin Bay and
805 Flinders Bay: **5 Albany** locations were; Cosy Corner, Albany, Two Peoples Bay West and Two Peoples Bay
806 East. **6 Bremer Bay** locations were; Dillon Bay, Point Henry, Back Beach Bommie and Peppermint Beach. **7**
807 **Esperance and inshore islands of the Recherché Archipelago** locations were; Observatory Island, Cull and
808 Black Islands, Thomas and Woody Islands, and Cape Le Grand.
809

Region 6 ◐   Region 4 ●   Region 1 ○
Region 7 ● Region 5 ⊗   Region 3 ⊖   Region 2 ◉
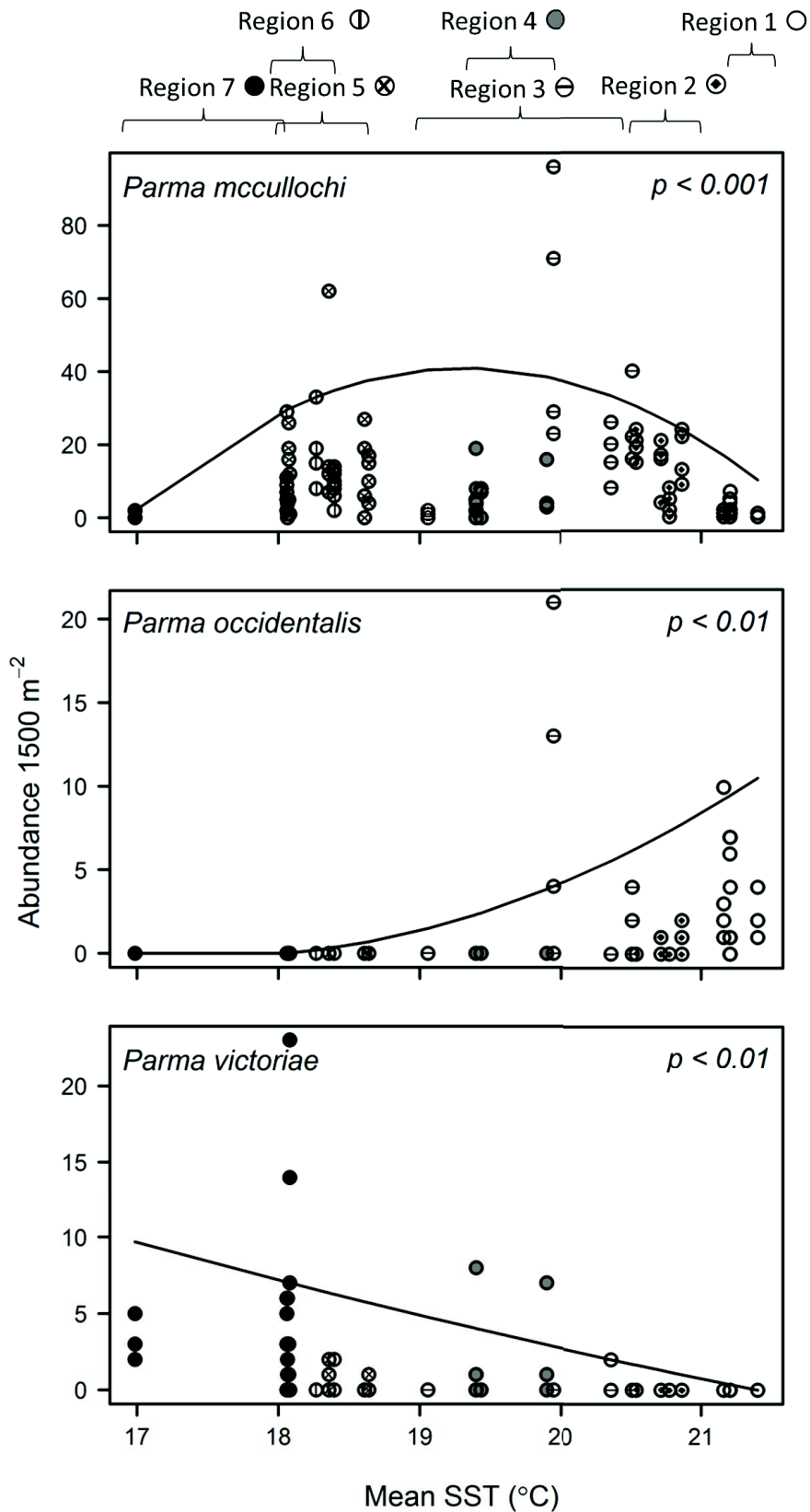
Figure 2. Abundance (fish 1500m⁻²) and 95th percentile regression spline models for each *Parma* species and the mean SST at each location. *P* values for the fit of the polynomials are overlaid.

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**
816

Parma mccullochi

	DF	SS	MS	*F*	*P*
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	*F*	*P*
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	*F*	*P*
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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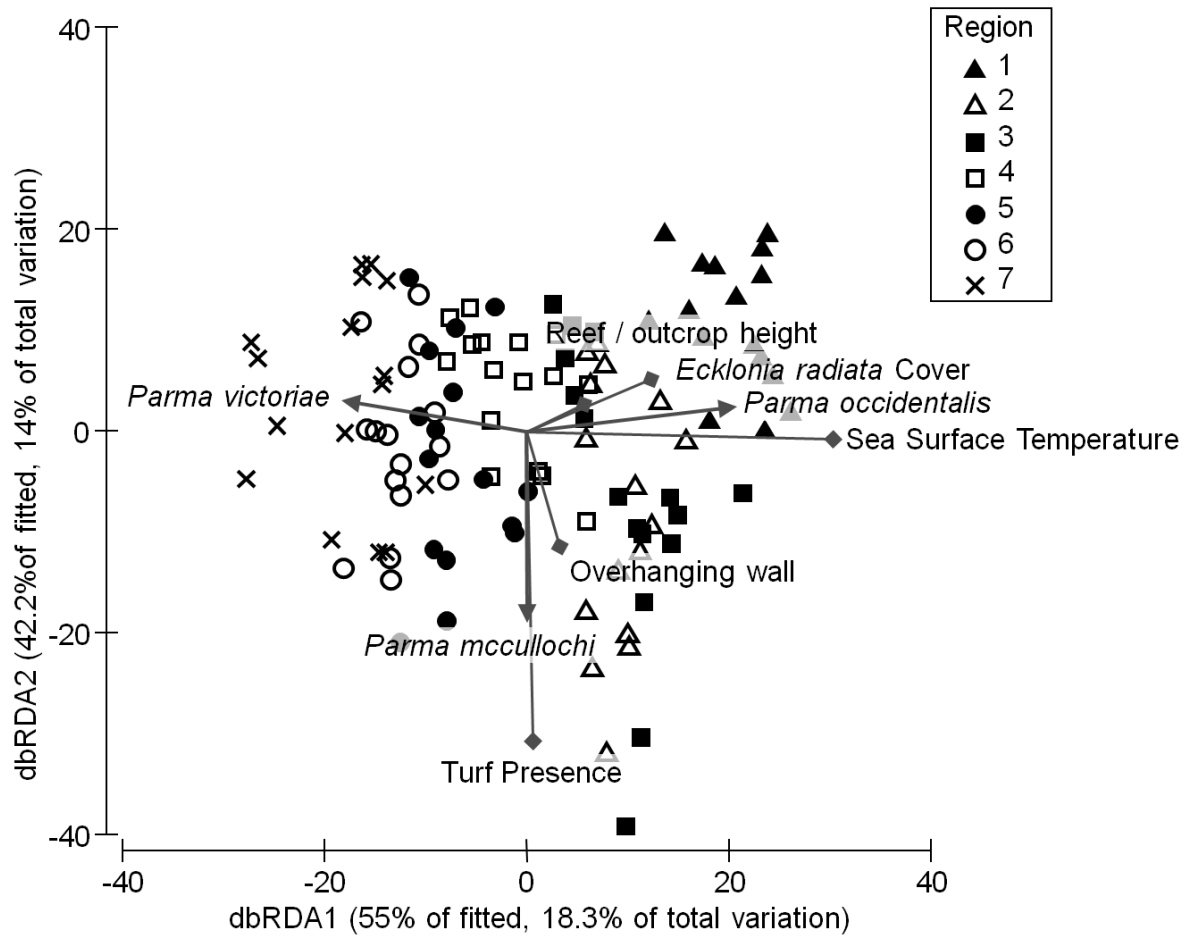
Figure 3. Distance based RDA ordination of first and second fitted axis relating environmental variables to *Parma* density across the entire survey area. Vectors plotted show the strength and direction of multiple partial correlations of the environmental variables and Spearman rank correlations of *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 (1500m^2)**

Multiple partial correlation

Variable	dbRDA1	dbRDA2
Turf Presence	0.02	**-0.92**
Sea Surface Temperature	**0.91**	-0.02
Ecklonia Cover	0.37	0.16
Constant Overhang	0.10	-0.34
Reef / outcrop height	0.17	0.08

Spearman rank correlation

| Variable	dbRDA1	dbRDA2
Parma mccullochi	<0.01	**-0.57**
Parma occidentalis	**0.62**	0.07
Parma victoriae	**-0.55**	0.09

828
829

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

P. mccullochi all regions	AICc 87.5, R^2 0.44 Number of variables: 4			
Variable	SS(trace)	Pseudo-*F*	*P*	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**

P. occidentalis region 1	AICc - 1.5, R^2 0.29 Number of variables: 2			
Variable	SS(trace)	Pseudo-*F*	*P*	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

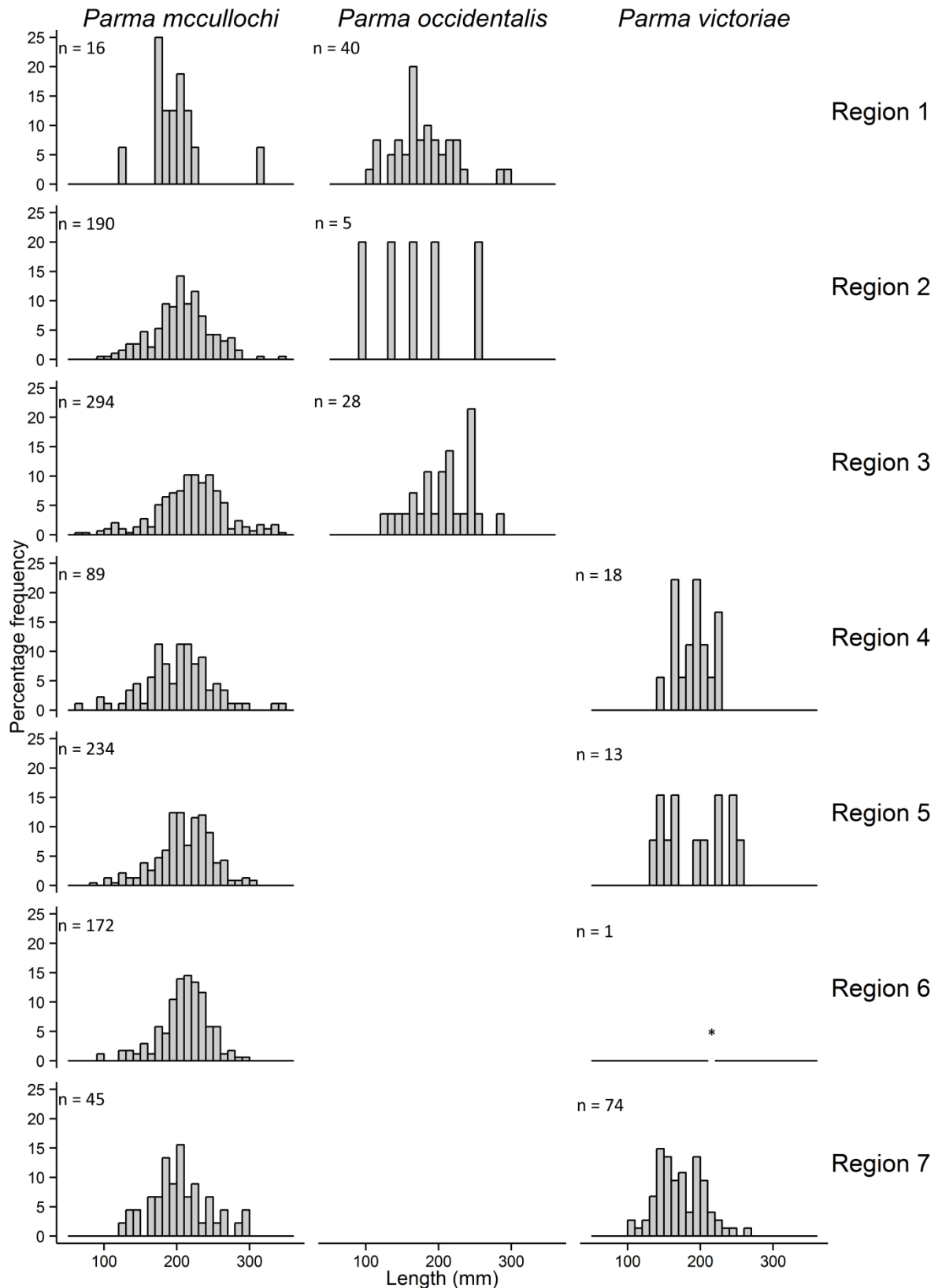| *P. victoriae* region 7	AICc 3.0, R^2 0.47 Number of variables: 2			
Variable	SS(trace)	Pseudo-*F*	*P*	Proportion
Vertical Wall	**7.43**	**7.16**	**0.028**	**0.34**
Overhanging wall	6.83	6.31	0.034	0.31
Seagrass Presence	**4.78**	**3.90**	**0.090**	**0.22**
Non-*Ecklonia* Canopy Cover	3.80	2.93	0.111	0.17
Hard Coral Cover	2.46	1.77	0.211	0.11

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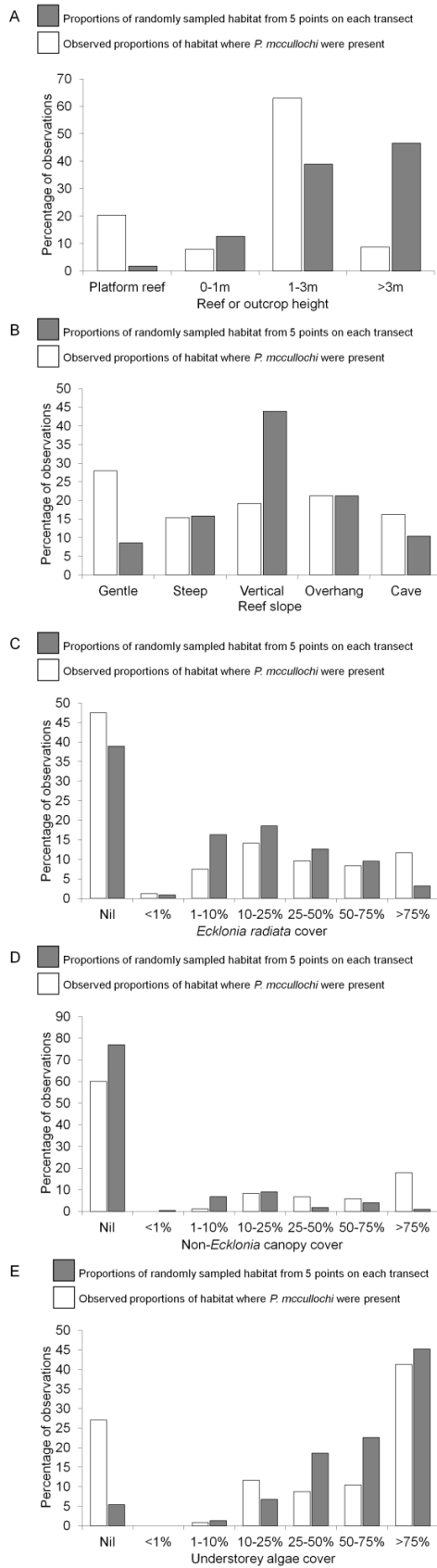
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838   **Figure 4. Plots showing percentage of observations for categories of each of five habitat classes recorded**
839   **at Marmion Lagoon in region 3 (Perth). Observations are illustrated for: Randomly sampled habitat**
840   **observations, calculated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

Table 4. Chi-square goodness of fit tests comparing observed frequencies of habitat at points where *Parma mccullochi* **were present to the expected proportion of randomly sampled habitat observations calculated at five points along each transect, for each of five habitat classes. Degrees of freedom are in parentheses.**

	Observed frequencies of habitat where *P. mccullochi* 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%
$\chi^2_{(4)} = 104.70$, $P<0.001$		
***Ecklonia radiata* 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-*Ecklonia* 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%
$\chi^2_{(4)} = 96.59$, $P<0.001$		

Figure 5. Length percentage frequency histograms for each of the three common species of *Parma* at each region. '*' indicates that only one 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.