# Potential climate-mediated changes to the distribution and density of pomacentrid reef fishes in south-western Australia

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ABSTRACT: Climate change and associated increased water temperatures pose a substantial threat for the future of marine ecosystems. Temperate Australia is a global biodiversity hotspot which has experienced ocean warming rates 2 to 4 times faster than the global average. To better understand the effects of these temperature changes on marine fish distributions and densities, we surveyed territorial damselfishes across 2000 km of temperate coastline in south-western Australia. Diver-operated stereo-video was used to determine if the distribution and density of 4 pomacentrids (*Parma occidentalis*, *P. mccullochi*, *P. victoriae* and *Pomacentrus milleri*) and their biotic habitat changed between 2006 and 2015, a time period characterised by gradual warming trends and an extreme marine heatwave. Surveys showed that the density of the warm-water pomacentrids *P. milleri* and *P. occidentalis* increased, while cool-water *P. victoriae* and intermediate species *P. mccullochi* showed no changes in density. In northern, warmer waters, the density of habitat-forming algal species such as *Ecklonia radiata* decreased, while turf algae species increased. In general, 2015 was characterised by a shift toward non-canopy algae habitats when compared to 2006. The observed changes in fish assemblages were likely caused by a combination of increased temperatures and changes in habitat-forming algal species. These changes along the Western Australian coast provide insights into the different nature of cool- and warm-water affiliated species' responses to ocean warming and biogenic habitat changes associated with climate change.

KEY WORDS: Damselfishes · Pomacentridae · *Parma* · *Pomacentrus* · Global warming · Heatwave · Biological distribution · Range expansion · *Ecklonia radiata*

## INTRODUCTION

Temperature is an important driver of the productivity, distribution and abundance of species in the marine environment (Lüning 1984, Dayton et al. 1999). Changes to ocean temperatures (i.e. through climatic warming) have been observed globally over the past 5 decades, impacting and changing the distributions of marine organisms (Poloczanska et al. 2013, Pecl et al. 2017). In addition to the impacts of 'gradual' climate warming, abrupt extreme climatic events such as heat waves are also having adverse impacts on marine communities, exerting profound and lasting selective pressure on ecosystems given their relatively short duration (Wernberg et al. 2013, 2016, Bennett et al. 2016). It is predicted that heat

waves will occur more frequently, at increased durations and intensity (Meehl & Tebaldi 2004, Cai et al. 2015).

Biogeographical range shifts among marine species are increasing as a response to climate change and accompanying increases in sea surface temperature (SST) (Poloczanska et al. 2007, Galaiduk et al. 2013, IPCC 2014, Pecl et al. 2017). Range shifts can be driven by both discrete and gradual climatic events, which can be cumulative in nature (Smale & Wernberg 2013, Wernberg et al. 2013). The oceans surrounding Australia have experienced climatic and short-term temperature changes which have caused shifts in species distributions (Ling et al. 2009a,b, Smale & Wernberg 2013). Predicted range shifts of tropical species into temperate environments have the potential to increase competition between them and the existing local temperate species for resources, such as food and shelter, potentially to the detriment of endemic species in particular (Booth et al. 2011, Last et al. 2011). Although multiple examples of range shifts have been observed, it remains unclear how interactions between warming temperatures and corresponding changes to habitat structure interact to influence the distribution and abundance of affected organisms.

Temperate Australia has experienced ocean warming rates 2 to 4 times faster than the global average (Pearce & Feng 2007, Lough & Hobday 2011). Poleward-flowing boundary currents, like the Leeuwin Current in Western Australia (WA), create ocean warming hotspots which facilitate changes in tropical and temperate species distributions (Cheung et al. 2012, Vergés et al. 2014). In addition to gradual warming, south-western Australia has also been subject to discrete and extreme warming events. In 2011, an unprecedented 'marine heat wave' occurred across the west coast of Australia. The marine heat wave continued over 10 wk, affected approximately 2000 km of Western Australia's coastline and caused SST anomalies up to 5°C above normal (Abdo et al. 2012, Feng et al. 2013, Pearce & Feng 2013). This event caused significant impacts on marine ecosystems in WA (Wernberg et al. 2016).

Temperate reefs in Australia are largely characterised by the presence of habitat-forming *Ecklonia radiata* kelp forests, which provide important functions and resources to fishes such as food, shelter and spawning sites (Wernberg et al. 2016). Therefore, any changes to habitat-forming species are expected to have consequential impacts upon marine communities (Cheung et al. 2012). Distribution of turf-feeding herbivorous fish is often restricted by the presence of *E. radiata* canopy as it limits access to more palatable forms of algae (Kendrick et al. 1999, Wernberg & Thomsen 2005).

Following the 2011 heat wave, kelp canopy cover declined along the south-west coast, with the proportion of canopy area lost increasing toward warmer latitudes (Wernberg et al. 2016). In the northern, warm margin of the kelp distribution (~28°S), kelp canopies completely disappeared, compared to a 40% reduction around reef sites in warm temperate waters (~30°S), and no discernible impact in cooler temperate waters (~34°S) (Wernberg et al. 2013, 2016). Turf-forming algae are typically outcompeted by these subtidal habitat-forming canopy species, as they reduce light and sedimentation occurring on the reef surface (Wernberg et al. 2013). Areas which were high in canopy cover prior to the 2011 heat wave have subsequently become dominated by algal turfs (Wernberg et al. 2016). Such changes may have had further implications to other marine species including fish assemblages, particularly toward the northern margin of temperate reef distribution (i.e. ~28–30°S) (Wernberg et al. 2016).

Damselfishes (Pomacentridae) are among the most diverse fish families, containing many herbivores, and form abundant and conspicuous assemblages on tropical, subtropical and temperate reefs (Allen 1987). Changes to the benthic composition as a result of climatic events can lead to range shifts in herbivorous fishes (Langlois et al. 2012). In temperate Australia, territorial pomacentrids are dominated by the genus *Parma*, which contains 10 species that are confined to Australasian waters (Allen & Hoese 1975, Allen 1987).

*Parma* spp. are primarily herbivorous and use their turf algal territories for both reproductive and dietary purposes (Buckle & Booth 2009, Saunders et al. 2013, 2015). *Pomacentrus milleri* is an herbivorous and territorial pomacentrid that exhibits similar behaviour patterns as *Parma* species. Range shifts in response to warming water may increase competition with temperate species due to limited availability of resources, for example suitable turf algae species (Galaiduk et al. 2013). Conversely, if turf algae increase as a result of warming (Wernberg et al. 2013), competition for resources may decrease. Such compositional changes in fish communities have already been observed following the heat wave in 2011 (Wernberg et al. 2016). For example, the abundance of warm-water *Parma occidentalis* dramatically increased in temperate locations in WA (Wernberg et al. 2013, Caputi et al. 2014). The implications of these compositional changes remain

unexplored on a latitudinal scale and are important for understanding the full and long-term impacts on a larger scale.

We investigated the potential impacts of current ocean warming trends and an extreme marine heatwave on temperate, subtropical and tropical damselfishes in WA. Pomacentrids were chosen as a focal family as they are one of the most abundant and visually conspicuous groups on temperate west-Australian rocky reefs (Hutchins 1994, 2001, Saunders et al. 2013). The overall aim of this study was to compare the distribution and density of 4 territorial and herbivorous pomacentrids along the latitudinal biogeographic scale of temperate WA between 2006 and 2015. Against the background of changes in habitat and temperature extremes, field data were collected to address the following questions: (1) Has the distribution and density of 4 pomacentrids on these shallow rocky reefs changed since 2006? (2) Do the distribution and density patterns of warmer-water and cooler-water affiliated pomacentrids respond in a similar way? (3) Are any of the observed changes in the pomacentrid assemblages correlated to changes in algal cover?

## MATERIALS AND METHODS

### Survey design

Surveys were conducted between the mid-west and south-east of temperate WA, covering a distance of approximately 2000 km of coastline from Port Gregory (north) to Cape Le Grand (south) (Fig. 1A). The survey targeted shallow rocky reefs, between December 2014 and July 2015, following the survey design reported by Saunders et al. (2014) between November 2005 and June 2006. Survey sites were originally selected by Saunders et al. (2014) based on the known distribution of the territorial and herbivorous pomacentrid genus *Parma* along temperate rocky reefs of temperate
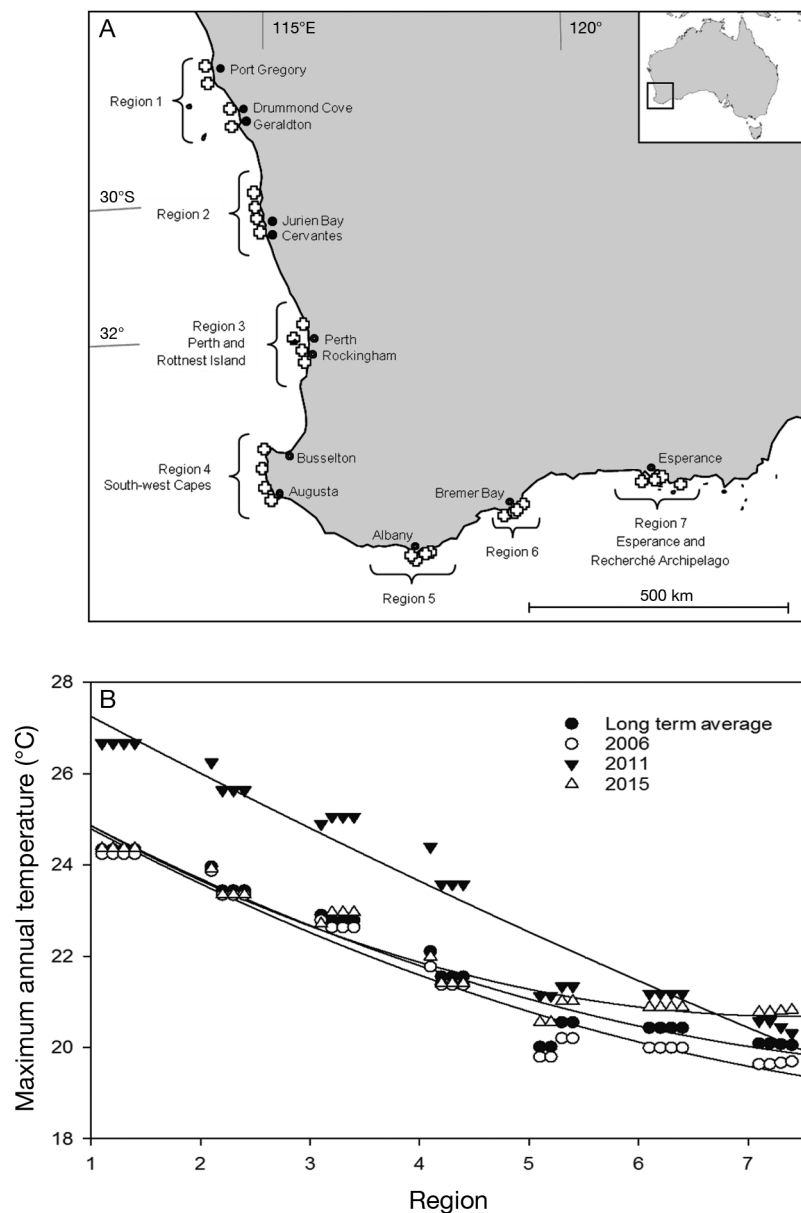


Fig. 1. (A) Survey design illustrating the 7 regions surveyed (as shown in Saunders et al. 2014). Within each region, 4 locations (white crosses) are illustrated. Regions are: (1) Port Gregory to Geraldton; (2) Jurien Bay; (3) Perth and Rottnest Island; (4) South-West Capes; (5) Albany; (6) Bremer Bay; (7) Esperance and inshore islands of the Recherché Archipelago. Inset: location of the study area in Australia. (B) Maximum annual temperatures for the years 2006, 2011, 2015 and the long-term average (1981–2015). Points represent the 4 locations within each of the 7 regions. Second-order polynomial regression lines were fitted to each year illustrating the relationship in temperatures among regions and years

WA. The survey area included locations that were influenced by the 2011 marine heat wave and gradually increasing ocean temperatures (Fig. 1B). Three *Parma* species (*P. occidentalis*, *P. mccullochi* and *P. victoriae*) and 1 *Pomacentrus* species (*P. milleri*) were surveyed.

Each region comprised 4 locations, within which 4 different reef sites were sampled. The survey design consisted of a total of 7 regions, 28 locations and 112 reef sites, spanning approximately 7 degrees of latitude and 10 degrees of longitude. This surveying design allowed samples to vary on both temporal and spatial scales. Twelve replicate belt transects of 25 by 5 m (sample area of 125 m$^2$) were conducted at each reef site. These transects were surveyed using diver-operated stereo video (stereo-DOV) in a depth range of 4 to 12 m, resulting in a total of 1344 transects both in 2006 and 2015.

## SST

NOAA Optimum Interpolation SST (OISST) (https:// www.ncdc.noaa.gov, accessed 6 October 2015) was used to examine temperature differences among years and regions along the west-Australian coastline. OISST is a blended product, computed on a 1° grid, combining satellite data and *in situ* observations from 1981 to present. Annual monthly maximum temperatures were extracted for each cell grid corresponding to the study locations along the WA coast. Average maximum annual temperatures over the past 33 yr temperature record were used to calculate long-term maximum temperatures for each location.

The trajectory of climatological temperature anomalies within each of the 7 regions along the west-Australian coastline was examined using the OISST. Mean monthly temperatures were extracted for each cell grid corresponding to the study locations along the WA coast. Anomalies were calculated for each cell by comparing mean monthly SST with the long term (1981–2015) average temperature for that month. Monthly anomalies were averaged among sites within each region. Linear regression was used to examine the trajectory of climatological anomalies over the past 33 yr within each region.

## Survey method

The stereo-DOV system consisted of 2 digital video cameras in underwater housings mounted on an aluminium frame. Saunders et al. (2014) used Sony TRV 900, while Sony CX700 cameras were used for the 2015 surveys. Cameras were converged at an angle of 8° and securely mounted on the base bar 70 cm apart. The stereo-DOV system, including an explanation of how they are configured and cali-brated, was described by Harvey & Shortis (1995, 1998). Calibration of the cameras allowed accurate range and angle measurements to be taken from the cameras' stereo images. Calibration of the cameras was undertaken a number of times over the surveying period to ensure that any alterations in camera position due to transportation and use were accounted for. Cameras were calibrated with the software packages Vision Measurement System (Robson et al. 2006) and CAL (Seager 2014) in 2006 and 2015, respectively. These software packages use the same algorithms and general approaches for bundle adjustments.

All surveys were conducted in a minimum of 7 m visibility with 10 m breaks between transects. Cameras were positioned approximately 0.5 m above the reef and angled in a straight-forward position. Transects were swum at a rate of approximately 10 m min$^{-1}$. A team of 2 SCUBA divers swam transects; one of the divers swam with the stereo-DOVs and simultaneously measured transect length using a Chainman cotton counter. Effects of SCUBA diver presence upon fish assemblages was minimised, as only 1 diver was present with the cameras (Watson & Harvey 2007). The stereo-video system allows accurate and precise measurements of fish length, range and angle (Harvey & Shortis 1998, Harvey et al. 2001, 2002, 2004).

## Image processing

All 2015 footage from both left and right cameras was converted from AVCHD (.mts) format to Xvid (.avi) format using Xilisoft Video Converter Ultimate (www.xilisoft.com). The software package Event Measure (Stereo; www.seagis.com.au) was used to measure both the 3-D positions of each fish relative to the camera system along with their fork length. The preparation and analysis of 2006 footage was outlined by Saunders et al. (2014). The 3-D positions were used to enable individuals more than 7 m from the camera system (the minimum useable visibility was 7 m), or >2.5 m from the transect line to be excluded from the data set. This allowed the field of view to be standardised to the minimum sampled visibility while maintaining a transect area of 125 m$^2$ (Harvey et al. 2004). Fish which were not visible in both cameras were unable to be measured but were still included in the density data. This included all individuals within the transect area that were partially or completely concealed by benthos and rugose substrate.

## Habitat analysis

An estimation of habitat was made from the stereo-DOV footage by taking 5 equally spaced frames from each 25 m transect. Habitat analysis was undertaken following the procedures outlined by Saunders et al. (2014). Benthic habitat composition was analysed for each frame using a modified version of a Visual Basic program in Microsoft Excel originally designed by Holmes (2005).

For each field of view, the benthic biota was assessed as either bare or populated substrate. Populated substrate was then further assessed for estimations of the percentage cover of vegetation. Categories of vegetation included *Ecklonia radiata*, non-*Ecklonia* canopy (i.e. *Sargassum* spp. and *Scytothalia dorycarpa*) and understorey algae. Categorical percentage cover of vegetation was evaluated using the following values: 0 (nil); 1 (trace, <1%); 2 (sparse, 1–10%); 3 (low, 10–25%); 4 (medium, 25–50%); 5 (dense, 50–75%); and 6 (very dense, 75–100%).

The category of percent cover of understorey algae was further differentiated by recording the presence or absence of foliose algae and turf algae. The presence or absence data were compiled and analysed using the percentage of observations where the presence of each algal class was recorded.

## Statistical analysis

Sea surface temperature plots were created using R (R Core Team 2015) in the package ggplot2 (Wickham 2009). Univariate ANOVA ($\alpha$ = 0.05) was performed using the PERMANOVA+ (Anderson et al. 2008) package in PRIMER 6 (Clarke & Gorley 2006) on square-root-transformed mean densities per reef site (1500 m$^2$) of each species using a 3-factor (year, region and location) hierarchical nested model. Factors 'year' and 'region' were fixed with 2 and 7 levels, respectively. The factor 'location' had 28 levels, with 4 locations nested within each region. The interaction terms 'year × region' and 'year × location' were the terms of interest in assessing any shifts in distribution or changes in abundance over time. A square root transformation was applied, as abundances of *Parma* were generally low; this allowed the data to most closely meet the assumptions of homogeneity of variance distribution. PERMANOVA is robust to deviation from normality (Anderson et al. 2008). Following the univariate ANOVA, a pairwise *t*-test with Monte Carlo bootstrapping (Manly 2006) was performed in PERMANOVA to investigate the signifi-

cant interaction between the factors year and location. The habitat data were normalised, and changes in the multivariate algal categories were tested in PERMANOVA using the same design. Multivariate patterns were illustrated using non-metric multidimensional scaling (nMDS) plots. The relationship between algal habitat and the pomacentrid species was investigated using distance-based linear models (DistLM) and illustrated using distance-based redundancy analysis (dbRDA) in PERMANOVA+. The corrected Akaike's information criterion (AIC$_c$) was used to select the best model. For each sampling year, the correlations of each pomacentrid species to the algal habitat variables were investigated using Pearson's correlations.

## RESULTS

Second-order polynomial regression showed a negative linear relationship between maximum summer temperatures and distance along the coast (Fig. 1B). A steep decreasing SST gradient along the west coast (~24.4–21.4°C) developed into a more gradual gradient along the south coast (~19.8–20.5°C). An exception to this pattern was evident in 2011, where large anomalies were observed along the west coast and small anomalies along the south coast (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m604p223_supp.pdf). A gradual long-term warming trend was evident across all regions between 1981 and 2015, but was most evident along the south coast (Fig. S1). A clear 4–5 yr El Niño Southern Oscillation (ENSO) cycle was evident in long-term climatological anomalies (Fig. S1), highlighting the shift between warm La Niña phases and cool El Niño phases along the WA coast. The period from 2010 through 2014 was characterised by successive La Niña phases, resulting in the high temperatures of the 2011 marine heat wave and subsequent high temperatures in 2012 and 2013 (Fig. S1).

Significant interactions were found for year × region and year × location for density of *Pomacentrus milleri* and *Parma occidentalis* (Table 1). These significant interactions indicate changes in distributions between years, across both regions and locations. *Parma mccullochi* showed significant main effects of years and both regions and locations, which indicate a change in abundance, but not distribution. *Parma victoriae* was the only species that did not show a change in abundance or distribution over time, with differences in density between regions and locations only (Fig. 2, Table 1). nMDS plots illustrate this tem-

Table 1. Results of 4-factor mixed model ANOVA on square-root-transformed densities of territorial and herbivorous pomacentrid species across 7 regions. Year and region are fixed factors. Significant differences at $\alpha = 0.05$ are shown in **bold**

|  | df | SS | F | p |
|---|---|---|---|---|
| ***Pomacentrus milleri*** |  |  |  |  |
| Year | 1 | 106.17 | 17.66 | **0.001** |
| Region | 6 | 418.10 | 7.64 | **0.001** |
| Location (region) | 21 | 191.55 | 3.58 | **<0.001** |
| Year × region | 6 | 251.73 | 6.98 | **0.001** |
| Year × location (region) | 16 821 | 126.25 | 2.36 | **0.001** |
| Residuals | 168 | 427.92 |  |  |
| Total | 223 | 1521.70 |  |  |
| ***Parma occidentalis*** |  |  |  |  |
| Year | 1 | 39.97 | 30.45 | **<0.001** |
| Region | 6 | 201.58 | 15.33 | **<0.001** |
| Location (region) | 21 | 46.03 | 3.03 | **<0.001** |
| Year × region | 6 | 55.27 | 7.02 | **<0.001** |
| Year × location (region) | 21 | 27.56 | 1.82 | **0.021** |
| Residuals | 168 | 121.4 |  |  |
| Total | 223 | 491.81 |  |  |
| ***Parma mccullochi*** |  |  |  |  |
| Year | 1 | 11.46 | 5.21 | **0.038** |
| Region | 6 | 261.72 | 5.14 | **0.002** |
| Location (region) | 21 | 178.13 | 3.98 | **<0.001** |
| Year × region | 6 | 10.74 | 0.81 | 0.565 |
| Year × location (region) | 21 | 46.18 | 1.03 | 0.423 |
| Residuals | 168 | 357.75 |  |  |
| Total | 223 | 865.97 |  |  |
| ***Parma victoriae*** |  |  |  |  |
| Year | 1 | 0.01 | 0.04 | 0.85 |
| Region | 6 | 96.21 | 20.49 | **<0.001** |
| Location (region) | 21 | 16.44 | 2.25 | **0.002** |
| Year × region | 6 | 4.60 | 2.39 | 0.06 |
| Year × location (region) | 21 | 6.72 | 0.92 | 0.57 |
| Residuals | 168 | 58.36 |  |  |
| Total | 223 | 182.33 |  |  |

poral shift in the pomacentrid assemblage, with increasing abundances of *P. milleri* and *P. occidentalis* in 2015 at the 2 most northern regions and a decrease of *P. victoriae* in region 5 (Fig. 2). Further pairwise tests on the interaction between year and location confirm an increase in density of warm-water affiliated species at the poleward ends of their distribution between 2006 and 2015 (Fig. 2, Table 2). Significant increases in the density of the warm-water species *P. milleri* from 2006 to 2015 were detected in region 1 (2 locations) and region 2 (2 locations) (Table 2). The density of *P. occidentalis*, a warmer-water species, increased between 2006 and 2015 in region 1 (1 location), region 2 (3 locations) and region 3 (1 location) (Table 2). In 2006, *P. occidentalis* was only observed as far south as region 3, while 2015 surveys recorded this species at the southernmost location of region 4. A significant de-

crease in the density of *P. victoriae*, a cool-water species, was detected between 2006 and 2015 in region 5 (3 locations) (Table 2). In this region, *P. victoriae* was not recorded in 2015. However, this species was rare in 2006, with only 13 individuals being recorded in region 5. The density of *P. victoriae* increased in the coolest region (region 7, 1 location) (Table 2). For the cosmopolitan species *P. mccullochi*, no such consistent patterns were detected. The density of this species increased between 2006 and 2015 in region 1 (1 location) and region 3 (2 locations), but not in any of the other regions (Table 2).

Algal habitat variables differed significantly between 2006 and 2015 (Table 3). Throughout the surveyed area, significant differences were observed between regions and locations (Table 3). Significant interactions for the multivariate algal habitat variables were observed between both year × region and year × location (Table 3). These interactions indicate a change in the composition and distribution of biotic habitat over time. A shift from canopy algae cover in 2006 toward small understorey and turf algae cover in 2015 was observed (Fig. 3).

The relationship between algal habitat and the pomacentrid species was further investigated using DistLM and illustrated using a dbRDA. The most parsimonious DistLM model used turf algae *Ecklonia radiata* and non-*Ecklonia* canopy to explain 20% ($R^2 = 0.20$) of the variation in fish assemblages. Alternative models within 2 $AIC_c$ included additional variables: understorey algae or both understorey algae and foliose algae. Vectors illustrating the strength and direction of the relationship between *E. radiata* and non-*Ecklonia* canopy and the pomacentrid assemblage are correlated more toward 2006 samples than 2015 samples (Fig. 4). Pearson's correlations between each pomacentrid species and algae habitat supported this relationship between the pomacentrid density and algal habitats (Table 4). These relationships were temporally consistent. All pomacentrid species showed a negative correlation with *E. radiata* canopy. *P. milleri, P. occidentalis* and *P. mccullochi* were positively
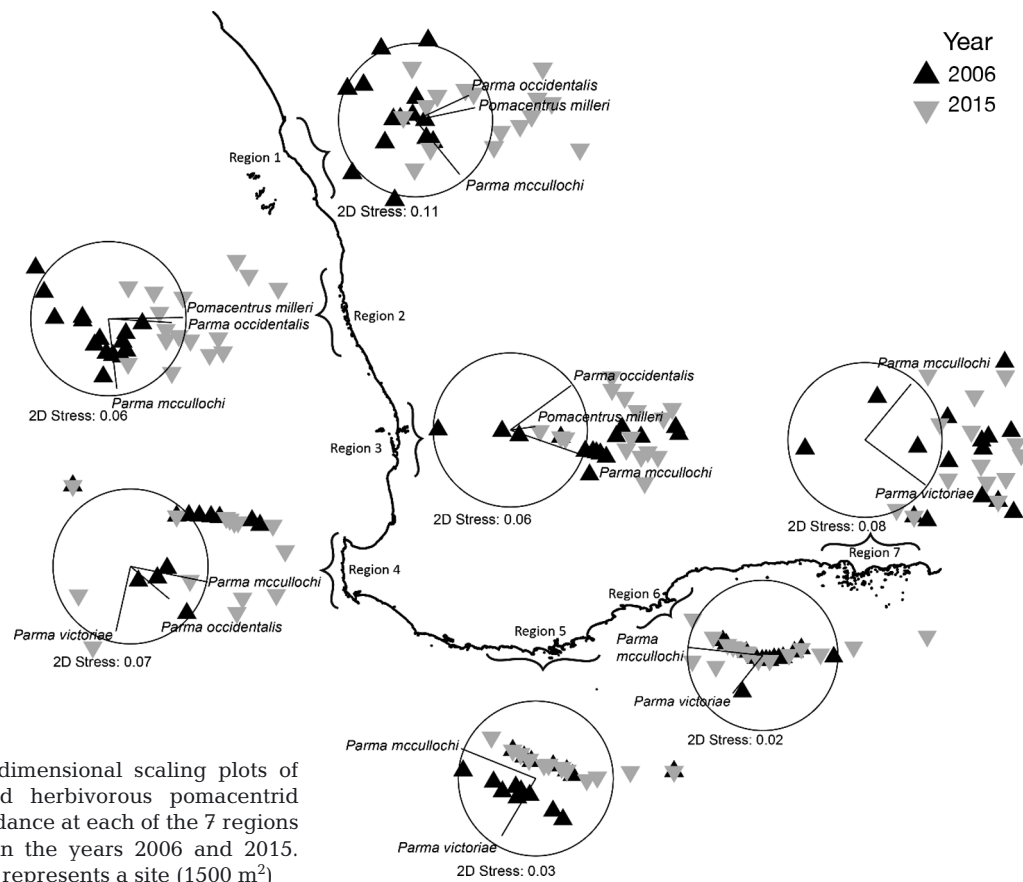
Fig. 2. Multidimensional scaling plots of territorial and herbivorous pomacentrid species abundance at each of the 7 regions (see Fig. 1) in the years 2006 and 2015. Each point represents a site (1500 m²)

correlated with turf algae, while *P. victoriae* was positively correlated with non-*Ecklonia* canopy (Table 4).

Length frequency plots indicate length ranges of between 30 and 350 mm for the 3 *Parma* species and between 20 and 160 mm for *P. milleri* (Figs. S2–S5 in the Supplement). There were no changes in the length frequency distributions between years in each region. However, in region 1, *P. milleri* were abundant enough that length frequency plots could be produced during 2015, and likewise in region 4 for *P. occidentalis*. In contrast, length frequency distributions could not be produced for *P. victoriae* individuals, as they were not measured in region 5 in 2015.

## DISCUSSION

Climate change is expected to cause changes in global fish assemblages (Cheung et al. 2012, Poloczanska et al. 2013, Wernberg et al. 2016). This study has indicated that such changes are already occurring in temperate rocky reef systems in Australia. In the past decade, the densities of 2 warm-water

pomacentrids in WA have increased at the leading cool edge of their geographical distribution. By comparison, a cool-water species showed a decrease in density at the warmest edge of its distribution. The widest-ranging species in the surveyed area showed no clear patterns of change, despite extensive changes to habitat structure in the surveyed area.

Two different temperature trends occurred between 2006 and 2015. The 2011 marine heat wave caused extreme temperatures across the northern regions of this study area. These temperatures did not extend to the cooler southern regions (Pearce & Feng 2013), which displayed a gradual warming trend. Similarly, habitat-forming algae experienced significant changes in the warmest northern regions of the survey area (28°–32° S), yet remained unchanged along the south coast. The dense macroalgal canopy of *Ecklonia radiata* restricts access to the food resource of turfing algae (Shepherd et al. 2008, Saunders et al. 2015, Vitelli et al. 2015). Thus, resource availability for pomacentrid species along the cooler southern coast in 2015 remained similar to 2006. Northern areas, however, experienced a shift from habitats dominated by *E. radiata* canopy to turf

Table 2. Mean (±SE) density and pairwise tests on the interaction between year and location (on square-root-transformed densities) by species. Asterisk (*) indicates significantly different means between years; significant p-values at α = 0.05 are shown in **bold**; – indicates species were not detected in surveys

| Region | Location | *Pomacentrus milleri* Mean 2006 | 2015 | t p | *Parma occidentalis* Mean 2006 | 2015 | t p | *Parma mccullochi* Mean 2006 | 2015 | t p | *Parma victoriae* Mean 2006 | 2015 | t p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1: Port Gregory and Geraldton | 1 | 0.5 (0.3) | 90.25* (32.9) | 2.73 **0.033** | 2.75 (0.8) | 26* (6.9) | 4.53 **0.003** | 0.5 (0.3) | 2 (1.4) | 0.70 0.513 | – | – | – |
| | 2 | 1 (1) | 138* (93.2) | 2.68 **0.039** | 4 (2) | 4.75 (1.6) | 0.41 0.691 | 0.75 (0.5) | 7.5* (1.6) | 4.30 **0.005** | – | – | – |
| | 3 | – | 0.25 (0.3) | 1.00 0.364 | 3 (1.6) | 16.75* (5.3) | 2.81 **0.028** | 2.75 (1.4) | 3.5 (1.9) | 0.28 0.795 | – | – | – |
| | 4 | – | 30.5 (29.8) | 1.17 0.281 | 3.5 (1.8) | 11.25) (6.7 | 1.20 0.273 | 2.5 (1.2) | 5 (1.7) | 1.21 0.268 | – | – | – |
| 2: Jurien Bay | 1 | 2.5 (1.6) | 42 (27.7) | 2.22 0.067 | 1 (0.4) | 5 (1.9) | 2.32 0.059 | 17.25 (3.8) | 9 (5.4) | 1.51 0.184 | – | – | – |
| | 2 | 3.5 (1.2) | 75.75* (24.4) | 4.97 **0.003** | – | 15* (6.7) | 3.41 **0.015** | 20.5 (1.9) | 22.75 (13.1) | 0.58 0.572 | – | – | – |
| | 3 | 2.25 (1.1) | 28.25* (11.6) | 3.07 **0.024** | 0.25 (0.3) | 12.75 (7.9) | 1.98 0.091 | 15.75 (4.3) | 22.5 (3.0) | 1.27 0.254 | – | – | – |
| | 4 | 0.25 (0.3) | 8.5 (3.8) | 3.53 0.073 | – | 14.5* (7.0) | 4.09 **0.007** | 5 (1.7) | 13.75 (3.8) | 2.14 0.075 | – | – | – |
| 3: Perth and Rottnest Island | 1 | – | 0.5 (0.3) | 1.73 0.137 | 9.5 (4.7) | 16.5 (7.2) | 0.56 0.602 | 54.75 (17.4) | 47.5 (11.8) | 0.25 0.809 | – | – | – |
| | 2 | 0.5 (0.5) | 1 (1) | 0.24 0.821 | 1.5 (1) | 1.5 (0.3) | 0.68 0.526 | 25 (5.2) | 46.75* (4.6) | 3.11 **0.019** | – | – | – |
| | 3 | – | 0.25 (0.3) | 1.00 0.360 | – | 8.5* (2.1) | 7.09 **<0.001** | 17 (3.4) | 15.25 (5.8) | 0.41 0.694 | – | – | – |
| | 4 | – | – | – | – | – | – | 1 (0.4) | 6.25* (1.3) | 3.99 **0.007** | – | – | – |
| 4: South–West Capes | 1 | – | – | – | – | 0.5 (0.5) | 1.00 0.354 | 6.5 (3.2) | 9.25 (2.1) | 0.86 0.417 | 2 (1.7) | 0.5 (0.5) | 0.78 0.472 |
| | 2 | – | – | – | – | – | – | 5.5 (1.8) | 3.25 (2.4) | 0.79 0.460 | – | 0.25 (0.3) | 1.00 0.363 |
| | 3 | – | – | – | – | 0.5 (0.5) | 1.00 0.362 | 3.75 (1.5) | 11 (5.2) | 0.88 0.403 | 0.5 (0.3) | 2.5 (1.4) | 0.87 0.422 |
| | 4 | – | – | – | – | 0.75 (0.5) | 1.68 0.146 | 6.5 (4.3) | 17.25 (6.1) | 1.64 0.156 | 0.25 (0.3) | 0.75 (0.5) | 0.81 0.446 |
| 5: Albany | 1 | – | – | – | – | – | – | 11.5 (2.9) | 23.5 (7.1) | 1.69 0.140 | 0.75 (0.3) | – | 3.00 **0.022** |
| | 2 | – | – | – | – | – | – | 16.75 (4.2) | 9.25 (1.0) | 1.63 0.154 | 1.5 (0.6) | – | 2.75 **0.034** |
| | 3 | – | – | – | – | – | – | 23.75 (12.8) | 12.5 (6.5) | 0.94 0.385 | 1 (0.4) | – | 2.84 **0.033** |
| | 4 | – | – | – | – | – | – | 12.75 (5.9) | 8.25 (3.6) | 0.28 0.797 | – | – | – |
| 6: Bremer Bay | 1 | – | – | – | – | – | – | 12 (6.3) | 14.25 (6.0) | 0.29 0.783 | – | – | – |
| | 2 | – | – | – | – | – | – | 18.75 (5.3) | 31.5 (15.9) | 0.35 0.736 | – | 0.5 (0.5) | 1.00 0.366 |
| | 3 | – | – | – | – | – | – | 11 (0.9) | 23 (6.1) | 2.28 0.060 | – | – | – |
| | 4 | – | – | – | – | – | – | 7.5 (2.5) | 15.75 (7.2) | 0.52 0.626 | 0.5 (0.5) | 0.25 (0.3) | 0.24 0.821 |
| 7: Esperance | 1 | – | – | – | – | – | – | 5.75 (1.5) | 9 (4.8) | 0.13 0.899 | 3.5 (1.3) | 3.5 (2.5) | 0.19 0.855 |
| | 2 | – | – | – | – | – | – | 3.75 (2.8) | 5.25 (1.9) | 0.68 0.525 | 11 (4.9) | 7.75 (3.9) | 0.30 0.771 |
| | 3 | – | – | – | – | – | – | 1.25 (1) | 4.75 (1.8) | 2.00 0.093 | 0.5 (0.3) | 3.75* (1.3) | 3.01 **0.024** |
| | 4 | – | – | – | – | – | – | 1.75 (1.4) | 2 (0.7) | 0.50 0.623 | 5.5 (1.6) | 8.5 (2.3) | 1.02 0.352 |

Table 3. Results of 4-factor mixed model analysis of variance on algal habitat variables (all values were significant at p < 0.001). Year and region are fixed factors

|                              | df  | SS     | F     |
|------------------------------|-----|--------|-------|
| Year                         | 1   | 134.67 | 29.47 |
| Region                       | 6   | 247.89 | 4.80  |
| Location (region)            | 21  | 180.83 | 3.97  |
| Year × region                | 6   | 91.33  | 3.33  |
| Year × location (region)     | 21  | 95.96  | 2.11  |
| Residuals                    | 168 | 364.32 |       |
| Total                        | 223 | 1115   |       |

algae (Smale & Wernberg 2013, Wernberg et al. 2013, 2016, Bennett et al. 2016), which opened up the turf algae resource and may have increased suitable habitat for pomacentrids in these areas.

Environments that are newly colonised by fish larvae must be able to provide adequate food and habitat to support survival at all life stages and the establishment of a permanent population (Figueira & Booth 2010). Since 2006, the observed increase in the abundance of warm-water pomacentrids coincided with an increase in turf algal presence and a decrease in *E. radiata* cover in northern areas. The presence of *E. radiata* is known to limit the abundance of dietary algae species and forms a barrier to restrict access to this understorey algal resource (Jones 1992, Shepherd et al. 2008). In addition, a

dense macroalgal canopy may hide cracks and crevices in the rocky reef habitat that might form potential shelter sites. The observed reduction in algal canopy is likely to have increased habitat and resource availability, thereby supporting higher pomacentrid density. It is plausible that the southward movement of warm-water species may have previously been limited by established competition for suitable food, shelter and other essential resources, rather than temperature alone (Thomas et al. 2004, Saunders et al. 2014).

The patterns of increased abundance observed in our study were not influenced by pulses of new recruits which may not survive over winter. The low seasonal SST variability in WA facilitates overwintering of warm-affiliated species (Cure et al. 2018). Moreover, *Parma* juveniles of age 1+ have a fork length between 60 and 100 mm (T. C. Shalders unpubl. data), and fish of these size classes or smaller were recorded with very low frequency. The great majority of fish observed during surveys were overwintering sub-adults or adults. Reef fishes establishing new populations in typically cooler environments often have an extremely high mortality (Smith et al. 2016). As the majority of *Parma* recorded in this study were overwintering survivors, it is likely that they are establishing viable populations in new areas. This is likely to be a result of warming trends facilitating range expansions, by allowing new populations to successfully overwinter (Figueira & Booth 2010).

In contrast to the 2 warm-water species that increased in density, no changes were detected in the widely distributed species *Parma mccullochi*. Despite potentially increased niche competition with *Pomacentrus milleri* and *Parma occidentalis* at the northern edge of its distribution (sensu Hixon & Jones 2005, Saunders et al. 2014), no evidence of displacement of *P. mccullochi* was found. While the abundance of the warmer-water species increased, the potential for increased interspecific competition may have been reduced by an increase in available resources in the form of turf algae and shelter. Additionally, *P. mccullochi* may be nearing the end of its maximum thermal range in the north (Hutchins 2001, Saunders et al. 2014), impairing survival and growth rates (Munday et al. 2008). Finally,
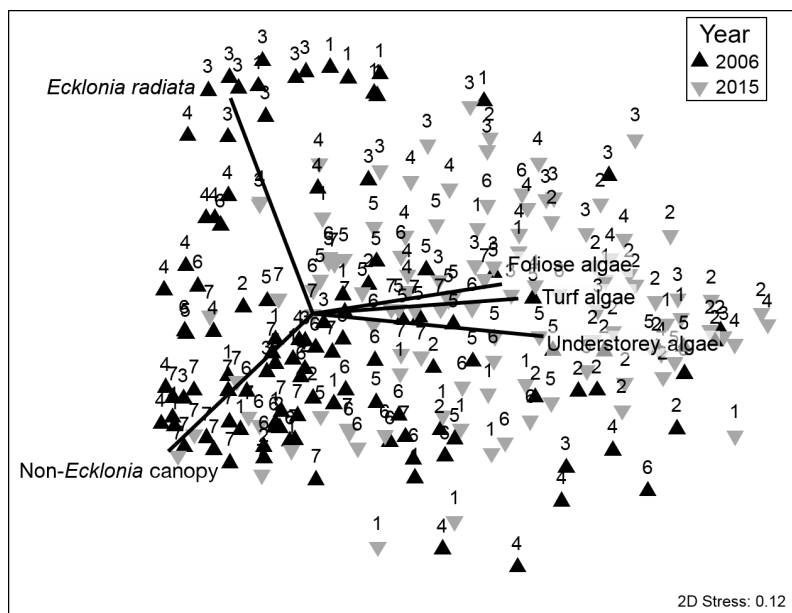


Fig. 3. Non-metric multidimensional scaling plots of the algal composition at each of the 7 regions in the years 2006 and 2015. Numbers represent the region (see Fig. 1), and each point represents a site (1500 m²)
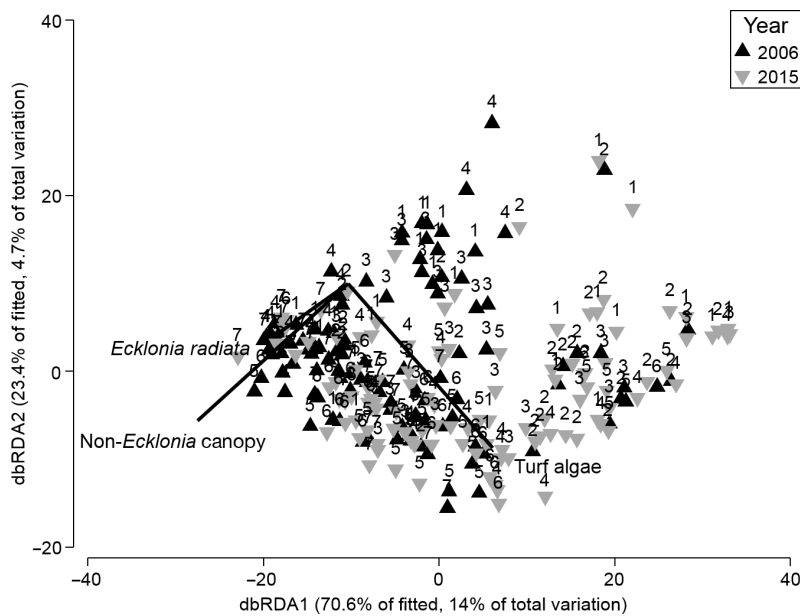
Fig. 4. Distance-based redundancy analysis (dbRDA) illustrating the influence of macroalgal cover variables on the pomacentrid fish assemblage. Length and direction of the vectors illustrate the strength and direction of correlation to the dbRDA axes. Numbers represent the region (see Fig. 1), and each point represents a site (1500 m²)

2006 survey, so it seems most likely that it was simply not encountered during the 2015 surveys. The algal assemblage was not observed to change along the south coast (Wernberg et al. 2013), and the temperature change has been much more gradual than the change experienced on the west coast. These relatively constant environmental conditions are likely to have supported the stable distribution of pomacentrid species along the south coast.

Our findings support previous studies that have demonstrated biological and physical changes to tropical-temperate transition zones as a result of increasing water temperatures (Pearce & Feng 2013, Wernberg et al. 2013, 2016). Major warming events such as marine heat waves are predicted to occur again in the future (Pearce & Feng 2013, Cai et al. 2015). Further impacts along Australia's temperate coastline are expected to result in permanent changes such as species extirpation or even extinction (Wernberg et al. 2011). Our study highlights the importance of understanding the nature of interactions between species, as well as the temperature tolerance of both fish and algal species. Further research is required to create a better understanding of the temperature tolerance profiles of warm- and cool-water species and the range of conditions these warm- and cool-affiliated species could potentially survive under. It further remains to be determined whether the observed changes in fish density were indeed the results of changes in algal habitat, or rather directly caused by elevated temperatures. Controlled experiments could be used to untangle the relative importance of temperature and habitat change. Impacts of climate-mediated changes on species assemblages are com-

any potential increased recruitment survival of *P. mccullochi* as a result of increased resource availability in the north may be restricted by prevailing southwards currents in the area (Benthuysen et al. 2014). Further research is required to disentangle the relative importance of negative effects caused by increased temperature stress, and the positive effects associated with increased habitat and resource availability.

The abundance of the cooler-water species *Parma victoriae* also did not change between the surveys. Toward the cooler south-eastern extent of its range, it remained the most abundant species. However, it was not recorded during our 2015 surveys in the warmer, westernmost region (Albany) on the south coast. *P. victoriae* was rare in this region during the

Table 4. Pearson's correlations (%) between each pomacentrid species and algal habitat variable for 2006 and 2015. **Bold** type indicates statistically significant correlations at α = 0.05

| | Pearson's correlations (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Pomacentrus milleri* | | *Parma occidentalis* | | *Parma mccullochi* | | *Parma victoriae* | |
| | 2006 | 2015 | 2006 | 2015 | 2006 | 2015 | 2006 | 2015 |
| *Ecklonia* | −10 | **−25** | 8 | **−25** | −11 | 0 | **−21** | −10 |
| Non-*Ecklonia* canopy | **−13** | **−35** | **−28** | **−39** | **−22** | **−19** | **25** | **40** |
| Turf algae | **19** | **27** | **17** | **31** | **37** | **24** | −12 | **−38** |

plex, depending on both the nature and direction of species and community interactions within the system (Westera et al. 2009, Bennett et al. 2015).

This study investigated 4 closely related pomacentrid species across a wide geographical area. Our results indicate that both marine fishes and algal communities are changing in response to the increasing temperatures and an unprecedented marine heat wave (Wernberg et al. 2016). The warm-water species displayed increased density at the cool edge of their distributions. The distribution of each of these species is restricted to Australian waters; *P. occidentalis* and *P. mccullochi* are endemic to WA, *P. victoriae* is endemic to southern Australia (Allen & Hoese 1975, Hutchins 1994, Hutchins 2001), and *P. milleri* ranges from tropical northern Australia and south down the west coast (Allen 1997, Hutchins & Swainston 1999). As the abundance of the warmer-water species increases in the south, we may in turn see changes in abundance or a southward retreat of the cooler-water species. However, the south coast of Australia is restricted to a narrow latitudinal band, and the possibility of retreat is limited. These changes along the west-Australian coast provide a unique insight into the nature of species' responses to a changing climate and highlight the importance of understanding the dynamic relationship between changing habitats and warming temperatures.

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