

Distributional responses to marine heat waves: insights from length frequencies across the geographic range of the endemic reef fish *Choerodon rubescens*

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Abstract Range shifts as a result of warming oceans call for evaluation of populations at the geographic range level, particularly for highly vulnerable species such as endemics and fisheries targets. We examined the influence of latitudinal temperature gradients and temperature anomalies during a 2011 marine heat wave on range-wide abundance, length frequency and recruitment of *Choerodon rubescens*, a reef associated fisheries target endemic to Western Australia. Diver-operated stereo-video surveys were conducted at shallow reefs (3–18 m) along 124 sites spanning the entire species' distribution (21°S–34°S), to obtain abundance, length frequency and habitat data. Models were used to assess the

influence of satellite-derived long-term average temperature (2002–2010) and 2011 temperature anomalies, compared to habitat, depth and distance to mainland, on the abundance of adult and juvenile fish and overall population size structure. Long-term temperature had the highest effect on adult *C. rubescens* abundance, with highest values recorded towards the centre of the temperature gradient investigated (22 °C). In contrast, juveniles were mostly influenced by 2011 temperature anomalies, with highest abundance recorded towards the cooler range edge, where anomalies were lowest. Length-frequency distributions showed recent recruitment towards the cooler range edge coupled with recruitment absence at the warmer edge. Recruitment differences were traced to 2011–2013 when ocean temperatures were up to 3.5 °C higher than average, via back-calculation of juvenile ages. These findings support predictions of a poleward distributional shift in response to ocean warming, and suggest that marine heatwaves can facilitate range shifts by affecting recruitment across latitudinal gradients.

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Introduction

Shifts in the distribution and abundance of species towards higher latitudes are occurring across the world oceans as a result of warming sea temperatures (Perry et al. 2005; Last et al. 2011; Poloczanska et al. 2016). Shifts have been reported across taxonomic groups including plankton (Behrenfeld et al. 2006; Beaugrand et al. 2012), habitat-forming species such as corals and kelp (Yamano et al. 2011; Wernberg et al. 2013), fish (Perry et al. 2005), crustaceans, echinoderms and molluscs (Zacherl et al. 2003; Ling 2008). These changes to the distribution of species have the potential to significantly alter the ecology of ecosystems by changing food web dynamics and benthic composition (Behrenfeld

et al. 2006; Johnson et al. 2011; Vergés et al. 2014). To develop management responses that can account for species distribution changes, marine resource managers first require information on range-wide variations in population abundance, the underlying processes responsible for these variations, and how they change in response to warming oceans (Sagarin and Gaines 2002).

The abundance, life history and demography of populations may vary depending on their position along a species' range (Brown et al. 1996; Purves 2009). These variations can be particularly clear when geographic ranges occur along a latitudinal gradient with high temperature variation (Compton et al. 2007). Across its latitudinal range, a species' abundance may increase towards the range centre (Brown 1984), close to one of the range edges (Sagarin and Gaines 2002; Langlois et al. 2012b), or show no pattern at all (Rivadeneira et al. 2010). Such variations in abundance are the result of variations in the demographic rates of local populations (Purves 2009), which respond to a series of environmental and ecological factors such as temperature (Choat et al. 2003), habitat (Baums et al. 2014), spatial location (e.g. coastal vs. island position) (Choat and Ayling 1987; Gust et al. 2001), larval dispersal patterns (Cowen 1985; Feary et al. 2014) and species interactions (e.g. competition, predation) (Price and Kirkpatrick 2009).

Temperature in particular is important for aquatic ectotherms because of its direct effect on metabolic functions (Phillips et al. 2014). Demographic metrics such as growth rates and recruitment increase with temperature to an optimal value and decline, often rapidly, once the optimal temperature is exceeded (Pörtner and Knust 2007; Kordas et al. 2011). At low temperatures, growth rates are reduced and maturation delayed (Atkinson 1994). Larval and juvenile stages show particular dependence on temperature, especially towards the cooler range edge of a species where low winter temperatures can result in high mortality rates (Figueira et al. 2009). Recruitment is generally low and sporadic towards both low and high temperature extremes along a species' geographic range, because of the physiological limitations of temperature extremes on recruits (Nantel and Gagnon 1999; Zacherl et al. 2003). These patterns, however, are recently changing in response to warming oceans, with unusually high recruitment of tropical species into temperate locations, particularly along regions influenced by poleward boundary currents (Booth et al. 2007; Johnson et al. 2011; Last et al. 2011; Vergés et al. 2014). In most cases, these intrusions into cooler waters occur during summer months and are only temporary, as recruits die after exposure to cold winter temperatures (Meister et al. 2005). However, as ocean temperatures continue to rise at a global scale, recruits have managed to survive at cooler locations (Figueira et al. 2009; Figueira and Booth 2010), establishing adult populations in novel environments and expanding the geographic range of

many marine species (Last et al. 2011; Poloczanska et al. 2016).

The coast of Western Australia (WA) spans approximately 22° of latitude from tropical coral reefs (13°S) to temperate rocky reefs (35°S) and presents a structured gradient in ocean temperature influenced by the southward flow of the Leeuwin Current (LC), which transports warm equatorial waters to temperate regions (Feng et al. 2008). WA is a hotspot for endemism (Roberts et al. 2002; Allen 2008) and at particular risk from rapid ocean warming, together with other temperate locations influenced by poleward boundary currents (Wu et al. 2012). Species distribution shifts as a result of increasing ocean temperatures in this region have been recorded by recent in situ observations (Pearce and Hutchins 2009) and geological studies (Greenstein and Pandolfi 2008). Recently, a marine heat wave (2011) in which temperature anomalies of 2–4 °C persisted for more than 10 weeks simulating predicted temperature increases for the next century, caused extensive fish die-offs (Pearce and Feng 2013), and an apparent shift in temperate communities to a more tropical species composition (Wernberg et al. 2013, 2016). Warmer temperatures are projected for WA in the future (Pearce and Feng 2007), together with changing intensity of ocean currents (Hobday and Lough 2011) and more frequent extreme weather events (Cai et al. 2015). Mathematical models predict that fish species along the WA coast will respond to these changes by shifting their distributions poleward (Cheung et al. 2012), but these models have not been empirically tested.

The baldchin groper *Choerodon rubescens* (Günther, 1862) is a large subtropical wrasse (family Labridae) endemic to WA and targeted by recreational and commercial fisheries along its entire geographic range. A previous study identified unusually high recruitment towards the cooler range edge of *C. rubescens* associated with increasing water temperatures and suggestive of a future poleward range shift (Cure et al. 2015). However, the study lacked replication at the geographic range level crucial for identifying distributional change (Kerr et al. 2015), and offered little insight into the factors determining the abundance distributions of adult and juvenile populations across the species' range. In this study, we aim to provide information on how the distribution, abundance, size structure and recruitment of *C. rubescens* responds to temperature gradients along WA and temperature anomalies during the 2011 marine heat wave, to assist fisheries management for the species and the development of climate adaptive management strategies. Because many other endemic fish species along WA have similar distributions to *C. rubescens* (Edgar 2000; Hutchins 2001), this study also provides a useful model for predicting how the geographic ranges of other marine fishes in this endemism hotspot may respond to increasing sea temperatures. Such model can also further our understanding on the processes

behind distributional shifts at a global scale, particularly along continental margins with poleward flowing boundary currents where the impacts of distribution shifts are a major force changing the ecological dynamics of ecosystems (Johnson et al. 2011; Vergés et al. 2014).

Specifically, we tested whether there was significant latitudinal variation in the abundance and length frequencies of adult and juvenile baldchin groper *C. rubescens* across its geographic range, and examined the relationship of these patterns to a set of possible explanatory variables including long-term sea surface temperature (2002–2010), 2011 temperature anomalies, depth, habitat structure and distance from the mainland. We further used range-wide length frequencies to assess recruitment differences and their response to the 2011 marine heat wave, by comparing the abundance of juvenile vs. adult size classes, taking the latter as an indication of historical recruitment. Finally, we used back-calculated juvenile ages to estimate the settlement time of juveniles surveyed and relate recruitment events to temperature profiles in the region. We hypothesised that: (a) abundance of adult *C. rubescens* would be higher towards the warmer northern end rather than the cooler southern end of their geographic range, due to the positive effects of temperature on metabolism (Kordas et al. 2011) and the strong temperature gradient along WA; (b) historical recruitment (inferred from length frequency data) would be low and sporadic towards both range edges (Nantel and Gagnon 1999; Zacherl et al. 2003), and (c) recruitment following the 2011 marine heat wave would be highest towards the cooler range end in response to warmer ocean temperatures.

Materials and methods

Study organism

The distribution of *C. rubescens* spans approximately 1400 km, between the tropical coral reefs of Ningaloo (21°S) and the temperate rocky reefs of Cape Leeuwin (34°S) (Allen and Swainston 1988; Edgar 2000; Hutchins 2001) (Fig. 1a). Juveniles live in shallow (< 3 m) protected lagoons (Fairclough 2005; Hutchins and Swainston 2008; Cure et al. 2015) and adults inhabit deeper and more exposed reefs (up to 100 m), although they are also common in shallow waters (Fairclough et al. 2011b). Maximum size and age is 700 mm total length (L_T) (Hutchins and Swainston 2008) and 25 years (Fairclough et al. 2014). Juveniles attain sexual maturity as females at a minimum size of 226 mm L_T (Nardi et al. 2006). Sex change to males follows with some variation in size and age of sex change according to latitude (Fairclough 2005). Reproduction occurs mostly during the austral spring to mid-summer (October–January), larvae disperse via pelagic currents and juveniles settle onto the

reef during the austral summer and early autumn (December–March) (Fairclough 2005; Cure et al. 2015). The species is reef associated after settlement with movement of both juveniles and adults likely to occur at small spatial scales, and no evidence of north to south movement or migration (Fairclough et al. 2011a).

Survey methods

Diver-operated stereo-video surveys (stereo-DOVs) were used to obtain abundance and length estimates (L_T) of *C. rubescens* across its geographic range (Fig. 1a). The stereo-DOV system consisted of two SONY HDR CX12 video cameras mounted 0.7 m apart on a base bar and inwardly converged at 8°, to gain an optimised field of view of 7 m (Harvey and Shortis 1995). A synchronising diode was mounted in front of the cameras, and floats used to achieve neutral buoyancy. Two SCUBA divers conducted the stereo-DOV surveys: one operating the camera system and another measuring the distance swum using a cotton counter. Divers swam approximately 30 cm above the substrate pointing the camera system slightly downward, and maintaining a speed of about 3 m s⁻¹.

Stereo-DOV surveys were undertaken from January 2013 to March 2014 at 124 randomly selected sites along the WA coast at 14 locations (three island, 11 mainland) (Table 1). At each site, 12 replicate transects were swum (25 × 5 m) separated by at least 10 m, targeting reef habitat (coral and rocky) for standardisation. Surveys were conducted in depths of 3–18 m, targeting both protected inshore reefs and exposed reef slopes, to include both adults and juvenile *C. rubescens* in our fish counts; at each site, a single depth profile was selected. We included areas open and closed to fishing to account for fishing effects as much as possible, but were unable to include this as a factor in our sampling design, given that most of the latitudinal gradient surveyed is open to recreational fishing for *C. rubescens*. Nonetheless, we inspected data for any regional bias due to protection status, which may have skewed our interpretation of overall patterns.

Video analyses

Stereo-video imagery was calibrated (Harvey and Shortis 1998) using CAL (SeaGIS Pty. Ltd., Bacchus Marsh, Australia), and videos analysed using the software EVENTMEASURE (SeaGIS Pty. Ltd., Bacchus Marsh, Australia). EVENTMEASURE is a purpose built event logger that allows an operator to record the number of fish and their species identification, as well as enabling accurate and precise measurements of the total length (L_T) of each fish and its distance from the camera system. We used EVENTMEASURE to: (1) standardise the survey area to 125 m² per each 25 m transect,

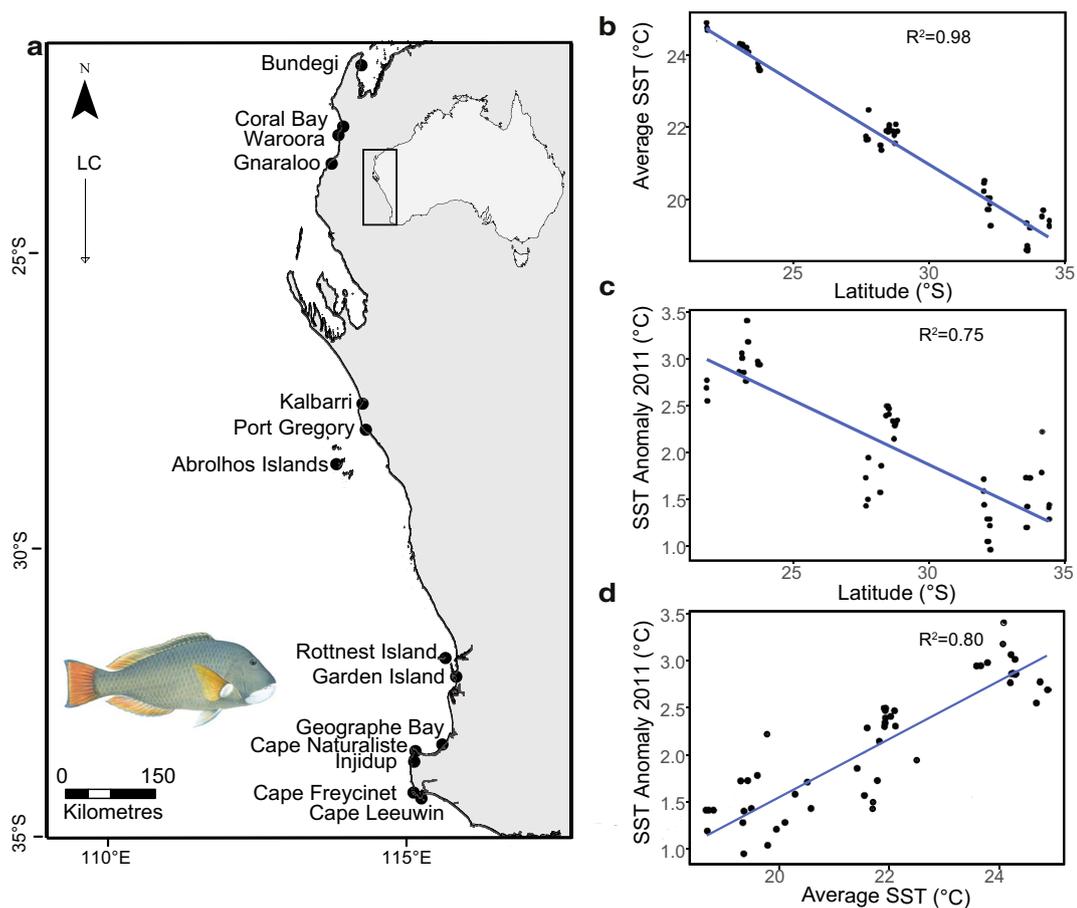


Fig. 1 Map of Western Australia (WA) showing: **a** the geographic range of *Choerodon rubescens* (square with black margin) and the 14 locations surveyed, **b** average sea surface temperature (SST, 2002–2010) gradient along the range of latitudes sampled across the WA coast, **c** SST anomalies during the marine heat wave of 2011 (summer) and their relationship to the range of latitudes sampled, and **d**

SST anomalies (summer 2011) and their relationship to the average temperature gradient surveyed. LC: poleward flowing Leeuwin Current. Temperature data courtesy of C. Rousseaux (National Aeronautics and Space Administration, NASA). Baldchin groper illustration © R. Swainston/<http://www.anima.net.au>

by setting the maximum distance from the camera system to each fish logged as 2.5 m at either side of the stereo-DOV system (Harvey et al. 2004), and (2) count and measure all *C. rubescens* encountered in the transect area. Abundance per transect was then calculated from the sum of individuals counted.

Habitat was determined at the transect level via modification of the point intercept method, which records habitat observed directly under set intervals along a transect line (McCormick 1994). To simulate the method, a fixed point was set in the middle of the video screen and used as a reference point. Video was stopped every 3 s along each transect and habitat type recorded at the reference point according to 11 categories (see Table 2). Records were then tallied and percentage cover of each category per transect estimated. Rugosity, a measure of habitat complexity, was assessed at each individual transect on a scale from zero to five following methods in Polunin and Roberts (1993). Habitat and

rugosity measures per transect were then used together with other variables measured (Table 2, variables 5–8) to model fish abundance and size structure (see “Statistical methods” below).

Temperature data

Average monthly sea surface temperatures (SST) were obtained from MODIS-AQUA at 4-km resolution. Annual average SST (2002–2010) and 2011 SST summer anomalies were used to represent long-term temperature gradients and temperature anomalies during the 2011 marine heat wave, respectively. Temperature anomalies during the 2011 marine heat wave were calculated as the difference between the average temperature during the summer of 2011 and the long-term average temperature during 2002–2010, which was taken as a baseline (Wernberg et al. 2013). Both variables were used as explanatory variables in models of

Table 1 Summary of surveys by location along the coast of Western Australia including sampling date, average sea surface temperature (SST) (2002–2010, °C), SST anomaly during the summer of 2011 (average across sites per location), number of sites surveyed, total number of transects (samples), and mean abundance (per 125 m²) of *Choerodon rubescens* (\pm SE)

Location	Sampling date	Mean SST (°C)	SST anomaly summer 2011 (°C)	No. of sites	Total no. of samples	Mean <i>C. rubescens</i> (per 125 m ² \pm SE)
Bundegi	Aug 13	24.49	2.61	8	100	0
Coral Bay	Aug 13	23.97	2.91	12	146	0.12 \pm 0.32
Warroora	Aug 13	23.80	3.08	12	145	0.30 \pm 0.05
Gnaraloo	Aug 13	23.28	2.94	11	127	0.21 \pm 0.06
Kalbarri	May 13	21.69	1.71	5	60	0.20 \pm 0.07
Port Gregory	Nov 13	21.16	1.74	9	106	0.48 \pm 0.09
Abrolhos	Apr 13, Mar 14	21.59	2.36	13	151	2.81 \pm 0.50
Rottnest Island	Mar 14	20.13	1.59	12	145	0.49 \pm 0.08
Garden Island	Feb 14, Apr 14	19.59	1.18	16	189	0.12 \pm 0.03
Geographe Bay	Feb 14	18.40	1.37	10	98	0.19 \pm 0.05
Cape Naturaliste	Mar 13	19.06	1.73	4	48	0
Indjidup Point	Mar 13	18.96	1.73	4	48	0
Cape Freycinet	Mar 13	19.28	2.00	4	48	0
Cape Leeuwin	Mar 13	19.07	1.39	4	48	0
Total				124	1459	

Table 2 Summary of variables used to model *Choerodon rubescens* length and abundance (adult and juvenile) at 124 sites along the coast of Western Australia

Variable	Replication	Type	Value
1. Abundance of <i>C. rubescens</i> (total #/125 m ²)	T	N	0–50
2. Length of <i>C. rubescens</i> (L_T , mm)	T	N	29.3–767.9
3. Habitat (11 categories, % cover)	T	C, N	Canopy forming algae (<i>Ecklonia</i> sp., <i>Sargassum</i> sp., <i>Scyathothalia</i> sp.), Green Algae, Red Algae, Brown Algae, Turf, Seagrass, Sand, Rubble, Rock, Live Coral (mound, encrusting, plate, branch, soft), Filter feeders (soft coral, sponges, bivalves)
4. Rugosity	T	N	0–5
5. Depth (m)	S	N	3–18
6. Distance to mainland (km)	S	N	0.05–81.19
7. Temperature (avg. SST 2002–2010, °C)	S	N	18.35–24.87
8. SST anomaly summer 2011 (°C)	S	N	0.98–3.4

Replication refers to the level at which the variable was measured T = transect (125 m², $n = 1459$), S = site ($n = 124$). Type of variable is either C = categorical or N = numeric. The 'value' column lists the types (C) or range (N) of observed values for each variable

L_T total length

fish abundance and size structure (see “[Statistical methods](#)” below).

Statistical methods

The influence of annual average SST, 2011 SST summer anomalies, habitat and other explanatory variables (Table 2, variables four to six) on the abundance of *C. rubescens* adults (> 226 mm L_T) and juveniles (< 226 mm L_T), was examined using generalised additive mixed models (GAMM), with package ‘mgcv’ in R version 3.1.2 (R Development Core Team 2014). Latitude was almost perfectly

correlated with annual average SST and for this reason was not included as a variable in our models ($r_s = 0.98$, $p = 0.001$; Fig. 1b). All other variables with a correlation < 0.80 were included in the models, but settings in our full subsets model fitting approach prevented variables with strong collinearity to appear in the same model (i.e. variables with correlation < 0.40).

Cut-off sizes for adult vs. juvenile life stages were based on the minimum size at sexual maturity reported for *C. rubescens* populations along the centre of the species’ range (Nardi et al. 2006). This is expected to be an average measure for all populations along the latitudinal gradient

examined given that size-at-maturity estimates for populations at the range edges are not available. Size measurements for each individual fish were obtained from stereo imagery as described in the “[Video analyses](#)”.

GAMMs are an extension of a generalised additive model, which use a sum of smooth functions to model covariate effects instead of a linear or other type of parametric form (Lin and Zhang 1999). As such, they are useful for explaining the shape of relationships between variables, without making an assumption about their parametric form. GAMMs were chosen due to non-linear relationships between dependent and continuous predictor variables (Austin 2007), and to include random effects accounting for correlation between observations on the same sampling unit (e.g. transects within site), thus avoiding issues with pseudo-replication.

In all GAMMs, habitat data were represented via two principal component (PC) scores from a principal components analysis (PCA) on all percent cover data (Green 1979; Wilson et al. 2012), which provided an ordination method for representing multivariate habitat data in one dimension (Anderson et al. 2008). This approach was used as a data reduction tool to reduce collinearity issues associated with multivariate habitat data that can cause problems in model selection (Graham 2003). A biological interpretation of what PC1 and PC2 represent can be found in the results section (see “[Habitat gradients](#)”). PCA analyses were completed using ‘vegan’ and ‘ade4’ packages in R version 3.1.2 (R Development Core Team 2014).

GAMMs with all possible variable subsets were fitted to untransformed fish abundance data (separate models for adult and juvenile *C. rubescens*) with package ‘mgcv’ in R version 3.1.2 using a Tweedie distribution ($k = 4$) (R Development Core Team 2014). This distribution provided the best fit to our data as assessed via diagnostic plots of residuals, allowing us to adequately model abundance data that did not follow a normal distribution. Model selection was based on Akaike’s information criterion corrected for finite sample sizes (AICc), which was used to compare models and select the most parsimonious one (fewer number of predictors and within two AICc units of the model with the lowest AICc value). Diagnostics on the selected model were completed via visual assessment of residuals with model validation procedures following Zuur (2012). Variable importance metrics were also calculated for each predictor variable based on a weighted AICc (wAICc) (Burnham and Anderson 2002), in order to assist model interpretation and further identify the most important predictors of juvenile and adult fish abundance. Prior to analyses, the explanatory variable ‘distance to mainland’ was $\log_{10}(x + 1)$ transformed to minimise the influence of outlying values and better represent relationships with fish abundance.

In a manner similar to GAMMs, we used a distance-based linear model (DistLM) (Legendre and Anderson 1999) to

assess the influence of explanatory variables (Table 2, variables three to eight; habitat as PC1, PC2) on population size structure. As with GAMMs above, PC components were used to represent multivariate habitat data. For this analysis, length data collected via stereo-video measurements were first pooled at the location level to produce length-frequency distributions. Bin widths for these distributions were selected via the Sheather–Jones procedure (see Langlois et al. 2012a), using package ‘KernSmooth’ in R version 3.1.2 (R Development Core Team 2014). Each size class was then treated as a separate variable in a multivariate approach to assess the influence of explanatory variables on population size structure. Prior to multivariate analyses, size class frequencies were standardised by total sample abundance and cumulated by site to remove variations due to abundance. A dissimilarity matrix using Manhattan distance was calculated for the transformed data and related to explanatory variables via a DistLM, which was fitted using a full subsets approach excluding models with correlated variables (> 0.40). Model selection procedures to choose the most parsimonious model were based on a multivariate analogue of the AICc in a manner equivalent to that described for GAMMs above (see Anderson et al. 2008). Analyses used the PERMANOVA+ add-on package for PRIMER v.6 (Anderson et al. 2008). Distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999), a form of ordination, was used to visualise the chosen model with vectors overlaid for each environmental variable and size class.

Recruitment assessment

We assessed recruitment differences across the geographic range indirectly via evaluation of juvenile (< 226 mm L_T) length-frequency distributions. Age data at different latitudes across *C. rubescens* range indicate that irrespective of their location and variations in growth patterns according to latitude (Fairclough 2005), juvenile fish are less than 2 years old across the species’ range (Fairclough 2005; Nardi et al. 2006). Therefore, we assumed that comparison of juvenile abundances between locations was indicative of three consecutive recruitment events (0 +, 1 + and 2 + fish). For more precise tracing of recruitment events, we also back-calculated the age (t) of each juvenile fish in our surveys using fish size at the time of survey (L_T), and available von Bertalanffy growth model parameters (K , L_{inf} and t_0) for the closest location (Abrolhos Islands 28°S or Shark Bay 25°S) (Fairclough 2005). Back-calculations were made via simplification of the von Bertalanffy growth function (VBGF):

$$t = 1/K \times \ln(1 - L_t/L_\infty) + t_0,$$

where t is the back-calculated age at the time of measurement, K is a curvature parameter, L_t is the measured standard length at age t , L_∞ is the mean asymptotic standard length,

and t_0 is the age at which fish have theoretical length of 0. Posteriorly, based on calculated age (t) and sampling date (when fish were captured on video), we traced back the settlement date for each individual fish.

Results

Temperature gradients

Annual average SST (2002–2010) showed an approximate 6 °C gradient across the latitudinal range surveyed (Table 1; Fig. 1b). During the summer of 2011 when the WA coast experienced a marine heat wave, temperature anomalies of 0.96–3.40 °C were recorded across survey sites (Fig. 1c, d), causing a short-term shift in long-term temperature profiles along the range of *C. rubescens*. SST recorded along the range centre (Kalbarri to Abrolhos) was similar to the 2002–2010 average at the northern range edge (Bundegi to Gnaraloo), and SST recorded along the southern range edge (Rottnest Island to Cape Leeuwin) was similar to the 2002–2010 average at the range centre. SST remained higher than average during 2012 and 2013 (Supplementary material, S1). The temperature anomalies recorded during the summer of 2011 were significantly correlated with long-term average temperature profiles along WA (2002–2010) ($r_s = 0.80$, $p = 0.002$; Fig. 1d). Therefore, models (GAMMs, DistLMs) including both of these variables together as predictors of fish abundance and size structure were not included in the full subset of models explored (see “Materials and methods”).

Habitat gradients

We found a clear north–south habitat gradient along *C. rubescens* range with northern sites dominated by coral reefs and southern sites by rocky reefs covered in canopy forming algae (*Ecklonia* sp., *Sargassum* sp., and *Scyathothalia* sp.) (Fig. 2). In total, 68.17% of the variance in habitat was represented by the first two principal components (PC1 and PC2, used for GAMMs and DistLM). PC1 (42.50%) mainly discriminated between sites dominated by canopy forming algae (more negative values; Pearson’s product-moment correlation coefficient $r = -0.88$) and sites dominated by bare rock (more positive values; $r = 0.34$), and PC2 (25.67%) discriminated between brown algae (more negative values; $r = -0.72$) and live hard coral (more positive values; $r = 0.54$). Other habitat variables had loadings that were less important in the ordination (r values < 0.25).

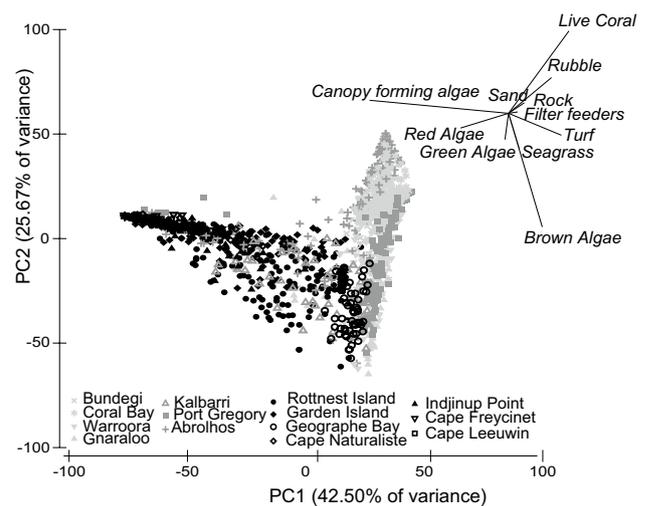


Fig. 2 Range-wide principal component analysis (PCA) showing habitat differences at the 14 locations sampled via diver-operated stereo-video surveys (stereo-DOVs) along *Choerodon rubescens* geographic range. Each point represents an individual transect (125 m²), and benthic variables (% cover) are overlaid as vectors. Principal components (PC1 and PC2) were used as a summarising variable of habitat in modelling juvenile and adult fish abundance (via generalised additive mixed models, GAMMs) and length (via distance-based linear model, DistLM) with respect to the set of explanatory variables measured

Abundance patterns

Range-wide surveys recorded 689 fishes from Coral Bay (23°S) to Geographe Bay (33°S). Although *C. rubescens* occurs at Bundegi (northern range edge) and the southwest Capes (southern range edge) (Hutchins 2001), individuals were not observed in surveys at these locations. Abundance for the species was highest at the Abrolhos Islands (28°S) towards the range centre, and consistently low at all other locations reaching minimum values towards the most northern (Coral Bay) and southern sites (Garden Island and Geographe Bay) (Table 1). This range-wide pattern in the abundance of *C. rubescens* differed between juvenile and adult life stages (Fig. 3). Adult *C. rubescens* followed the general distribution pattern for the species (Hutchins 2001; Table 1), with highest adult densities recorded towards the geographic range centre at the Abrolhos Islands (28°S), where annual SST average was approximately 22 °C (Figs. 1b, 3); this distribution followed a unimodal pattern along the temperature gradient sampled (Fig. 4). In contrast, the abundance of *C. rubescens* juveniles was highest towards the species’ southern range edge (Rottnest Island to Geographe Bay, 32°S–33°S; Fig. 3), where long-term annual SST average was 19–20 °C (Fig. 1b), but increased by 1–2 °C during the 2011 marine heat wave (Figs. 1c, 4).

Variation in the abundance of *C. rubescens* adults was best explained by a model including only long-term annual

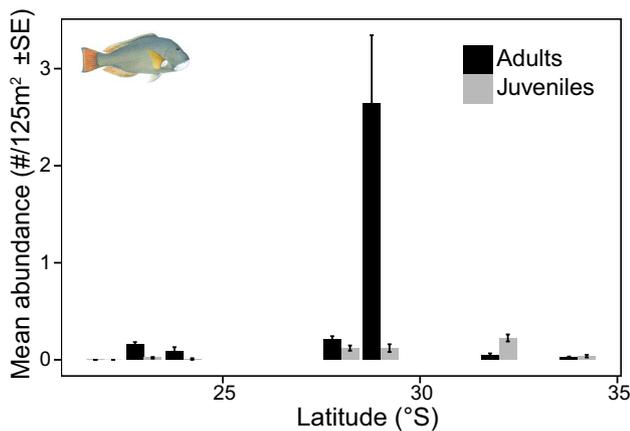
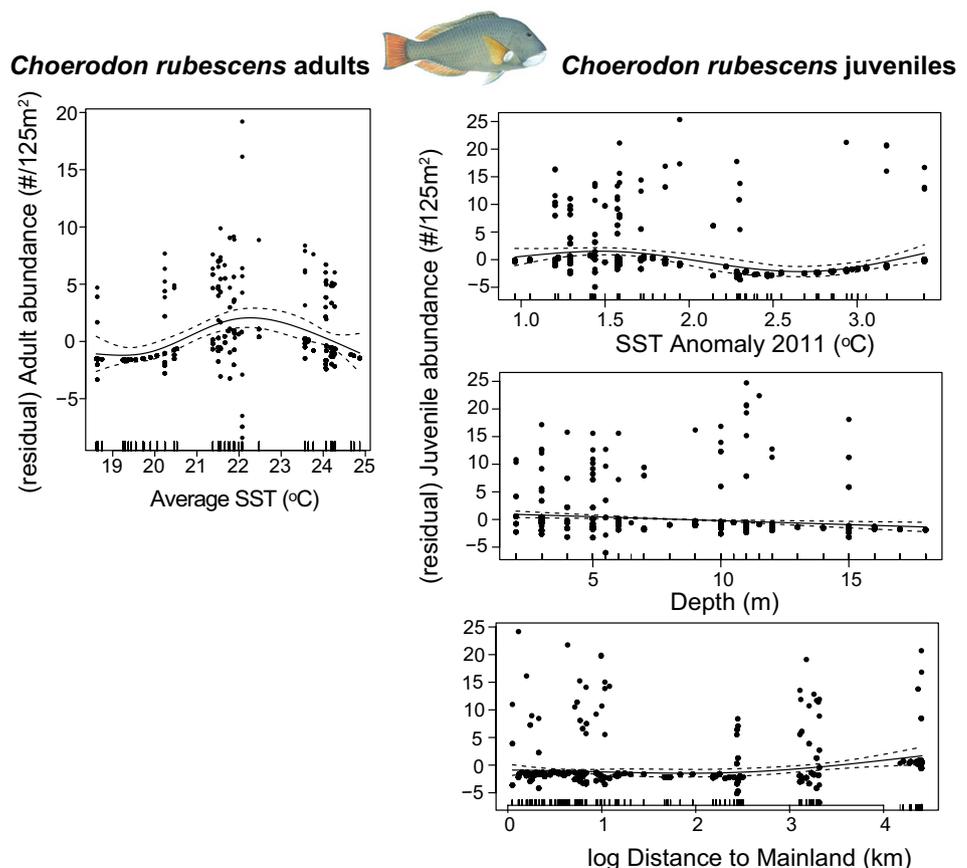


Fig. 3 Average abundance (# fish per 125 m² transect ± SE) of juvenile (grey) and adult (black) *Choerodon rubescens* across the latitudinal gradient sampled (21°S–34°S). Baldchin groper illustration © R. Swainston/<http://www.anima.net.au>

average SST (2002–2010) as a predictor, explaining 69% of variation in the data (Figs. 4, 5; Table 3; for model selection see Supplementary material S2). In contrast, variation in the abundance of *C. rubescens* juveniles was best explained by a model including SST anomaly during the summer of 2011, depth and distance to mainland (Figs. 4, 5; Table 3;

Fig. 4 Residual abundance of juvenile and adult *Choerodon rubescens* across their geographic range as a response to their most important explanatory variables identified via the most parsimonious generalized additive mixed models (GAMMs) for explaining observed latitudinal variations in fish abundance. Solid black line represents the estimated smoothing curve and dashed lines represent ± 2 × SE of the estimate. Baldchin groper illustration © R. Swainston/<http://www.anima.net.au>



for model selection see Supplementary material S2). These three variables explained 51% of the variation in the abundance of juvenile *C. rubescens*. Models that included long-term annual average SST rather than SST anomalies for juvenile *C. rubescens* were not chosen because they had higher AICc values by two or more units (see Supplementary material S2). In general, juvenile *C. rubescens* occurred in higher abundance in areas with lower temperature anomalies (1–2 °C, which generally occur towards the southern end of their range—see Fig. 1c), in shallower depths (< 7 m), and further from the mainland (> 20 km) (Fig. 4).

Size structure and recruitment patterns

A total of 463 fishes ranging from 29.3 to 767.9 mm *L_T* were measured. We found a clear latitudinal difference in both population size structure and overall mean length in the habitats surveyed (Fig. 6). Largest mean and maximum lengths were found towards the warmer northern range edge (Coral Bay to Gnaraloo) and smallest towards the cooler southern range edge (Rottneest Island to Geographe Bay). Size classes were more evenly represented towards the range centre (Kalbarri to Abrolhos). Size-structure differences were most evident when comparing juvenile abundance at northern vs. southern range edges. The proportion of fish under 226 mm

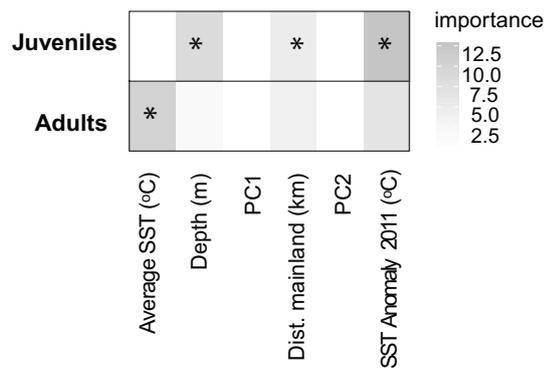


Fig. 5 Heatmap showing a comparison between the relative importance of each explanatory variable in predicting juvenile vs. adult *Choerodon rubescens* abundance, based on the full subset of fitted GAMMs (generalized additive mixed models). Each importance value was calculated as the average Akaike weight of all subsets of models containing that variable, scaled between 0 and 1 and multiplied by the R^2 value of the best fitted model. Only variables chosen in the top five models are presented (see Supplementary material S2). Asterisks embedded inside the squares denote that the variable was present in the top model selected for each life stage

Table 3 Results from the most parsimonious generalized additive mixed model (GAMM) relating the abundance of adult ($R^2 = 0.69$) and juvenile ($R^2 = 0.51$) *Choerodon rubescens* to explanatory variables measured (Table 2, variables three to eight)

Dependent variable	Explanatory variables	edf	F	p
Abundance of adult <i>C. rubescens</i> (#/125 m ²)	Average SST	3.33	7.35	< 0.001
	Site	61.79	3.09	< 0.001
Abundance of juvenile <i>C. rubescens</i> (#/125 m ²)	SST Anomaly summer 2011	3.48	6.42	< 0.001
	Depth	1	10.18	0.001
	Distance to mainland	2.39	3.94	0.010
	Site	36.31	0.81	< 0.001

(Habitat input as principal components PC1, PC2)

edf estimated degrees of freedom (from smoothing terms)

L_T was 11 times higher in the cooler southern edge than in the north (0.77 vs. 0.07). Age estimates for these juveniles (< 226 mm L_T) ranged from 2 months to 2.5 years at the cooler southern edge and 1–2 years at the warmer northern edge (Supplementary material S3). Based on sampling dates (Table 1) and estimated age, juvenile settlement was traced back to 2011–2013 (Supplementary material S3), when the WA coastline experienced a heat wave (2011) followed by 2 years of sustained higher than average SSTs during both summer and winter (Supplementary material S1).

Range-wide differences in size structure were best explained by a model containing three predictors: annual average SST (46% of the variance), depth (7%), and habitat (PC1 6%), each of which had significant effects in observed

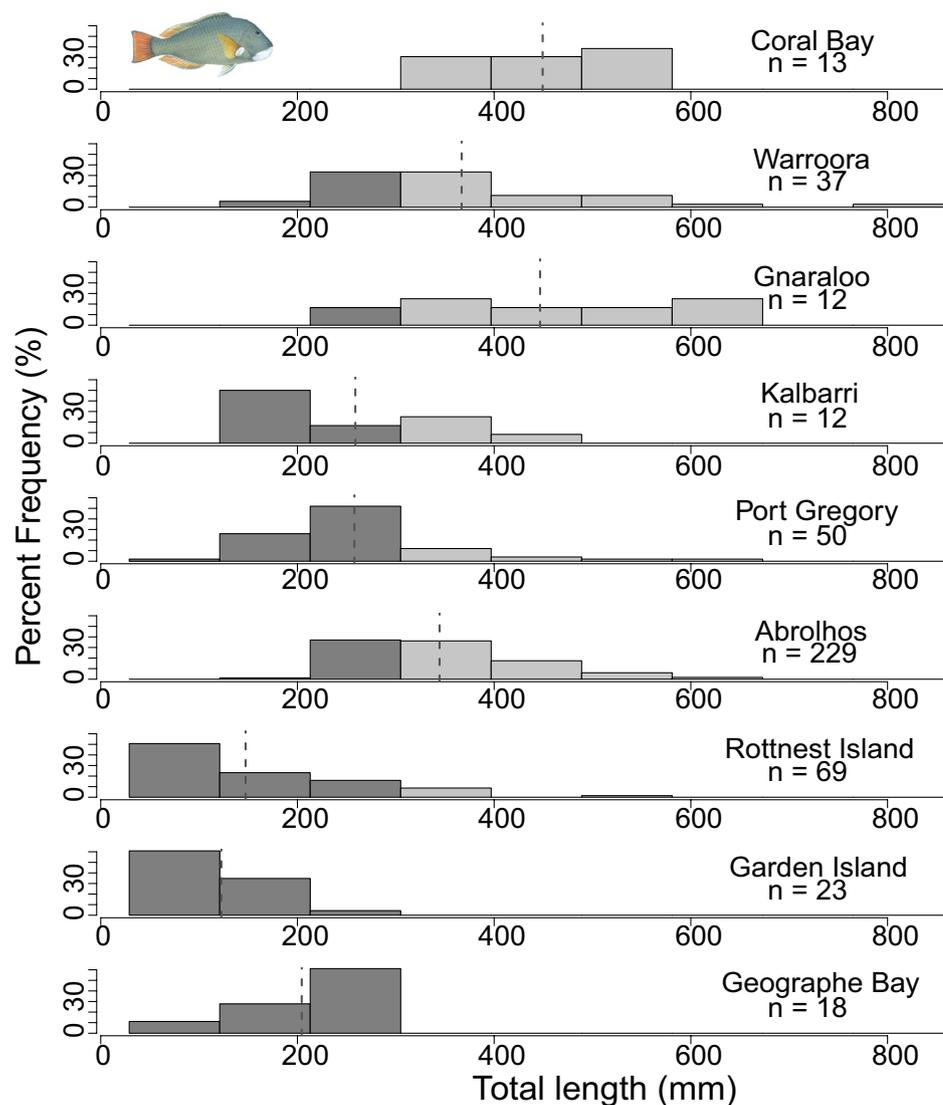
size structure patterns (Table 4; Supplementary material S4 and S5). This model accounted for 61% of variation in size structure data. In general, smallest fish (29–145 mm) were associated with lower average SSTs, shallow protected lagoons (< 7 m), and habitats dominated by canopy forming algae rather than bare rock (Supplementary material S5, Fig. 2). Largest fish showed the opposite pattern, being associated with higher average SST, deeper waters (> 10 m) and habitats dominated by bare rock (Supplementary material S5, Fig. 2).

Discussion

Latitudinal patterns in the abundance and size structure of *C. rubescens*, a fisheries target species endemic to WA, suggest that high ocean temperatures during and after a 2011 marine heat wave affected recruitment and shifted juvenile distribution southward with respect to that of adults. Populations of adult *C. rubescens* were in highest density at locations along the centre of the species' range where long-term average SST was approximately 22 °C. In contrast, juvenile abundance during and after the 2011 marine heat wave was highest towards the cooler southern range edge. Both adult and juvenile *C. rubescens* have limited movement capacity, with no evidence of north to south movement or migration (Fairclough et al. 2011a). During the time of the 2011 marine heat wave, long-term average SSTs increased by up to 3.5 °C raising water temperatures experienced by *C. rubescens* juveniles at southern sites from an average of 19 to up to 22 °C. Our models suggest that these warmer temperatures contributed to the successful establishment of *C. rubescens* recruits at the cooler range edge and their growth into juveniles, together with the presence of adequate food and habitat to sustain their populations.

Range-wide size structure of adult *C. rubescens* suggests that before the 2011 marine heat wave most recruitment occurred towards the central and warmer areas of the species' range, and was low at the cooler edge. In contrast, observed patterns in the size structure of juvenile *C. rubescens* show that after the 2011 marine heat wave, recruitment was absent at the northern warmer end and highest at the cooler southern end. These patterns in the distribution of recruits contradict the general assumption that the physiological constraints of recruits result in limited recruitment at both cooler and warmer edges of a species' distribution (Zacherl et al. 2003). Global observations on the effects of warming oceans to fish larvae and recruits highlight that warming oceans enhance larval survival and recruitment to cooler ends of species distributions but is detrimental to larval survival and growth at their warmer ends (Ling et al. 2008; Solmundsson et al. 2010; Beaugrand et al. 2012; Poloczanska et al. 2016). This study presents a unique

Fig. 6 Length-frequency distribution of *Choerodon rubescens* at the nine locations where fish were recorded during stereo-video surveys covering the range of the species along the western Australian coastline. Light grey bars represent adult fish (> 226 mm L_T) and dark grey bars juvenile fish (< 226 mm L_T , based on size at sexual maturity); dashed line represents mean length. Baldchin groper illustration © R. Swainston/<http://www.anima.net.au>



evaluation of these contrasting effects on recruitment at warmer vs. cooler range margins in response to rapid warming throughout the entire range of an important fisheries target species endemic to WA. An extension of sampling to include the full range of depth distribution of *C. rubescens*

Table 4 Results from the most parsimonious distance-based linear model (DistLM) relating *Choerodon rubescens* length (L_T) to explanatory variables measured (Table 2, variables three to eight)

Variable	<i>F</i>	<i>p</i>	Prop.	Cumul.
Average SST	46.77	< 0.001	0.460	0.460
Depth	14.16	< 0.001	0.112	0.572
PC1	5.99	0.012	0.044	0.615

(Habitat input as principal components PC1, PC2)

Prop. proportion of explained variance, Cumul. cumulative proportion of explained variance

is recommended, to further ascertain whether this pattern holds throughout the depth range of the species.

The lack of recruitment at the northern range edge of *C. rubescens* indicates that thermal conditions during anomalous summers may have exceeded the thermal tolerances of early life stages (Pearce and Feng 2013). Elevated sea temperatures can reduce the respiratory scope of reef fishes resulting in death (Nilsson et al. 2009). Consequently, sustained periods of elevated water temperatures can cause mass mortality of reef fishes (Hobbs and Mc Donald 2010), particularly during early life stages when oxygen requirements are greatest (Nilsson et al. 2007). Survivorship of new recruits at or beyond their range edge is determined by their physiological tolerance to conditions associated with temperatures beyond their usual experience (Figueira and Booth 2010). At the northern warmer range edge of *C. rubescens*, conditions during the 2011 marine heat wave may have exceeded the physiological tolerances of early life stages and

caused a recruitment failure. High temperatures during the 2011 marine heat wave, which resulted in adult mortality in at least some locations (Pearce et al. 2011a), may have also contributed to observed recruitment failure via reductions in the amount of larvae locally produced.

Latitudinal differences in recruitment were also probably influenced by the strong poleward flow of the LC during the 2011 marine heat wave (Pearce and Feng 2013) which could have pushed larvae south and prevented recruits from swimming northward. The close relationship between temperature along the WA coast and the strength of the LC (Feng et al. 2008) makes it difficult to determine the particular influence of these factors on recruitment. Most likely, a combination of warmer temperatures having a positive effect on recruitment (Figueira and Booth 2010) and a stronger LC pushing larvae south (Pearce et al. 2011b) resulted in the high recruitment event towards the cooler southern range edge and recruitment failure at the warmer northern edge. The combined effects of intensified poleward flowing boundary currents and warmer ocean temperatures have been identified as the primary mechanisms influencing recruitment changes leading to species distribution shifts at a global scale (Ling et al. 2008; Nye et al. 2009; Beaugrand et al. 2012).

Overall, the present distribution of *C. rubescens* shows that the species can maintain populations across a wide range of temperatures and habitats. This indicates a capacity to tolerate environmental variation. However, latitudinal differences in recruitment indicate that the species may be responding to abrupt warming in the region (Hobday and Lough 2011) by shifting its distribution poleward. Poleward shifts to escape warming oceans are becoming a common climate adaptation response in reef fishes (Perry et al. 2005; Last et al. 2011; Feary et al. 2014). Recent models predict that by 2055 the centroid of *C. rubescens* distribution will shift southward approximately 78 km (Cheung et al. 2012). This study provides the first empirical support for this prediction. We found contrasting patterns in the abundance of adult vs. juvenile *C. rubescens*, indicative of a poleward shift in recruitment patterns during years of high ocean temperatures associated with the 2011 marine heat wave. If warming trends continue as predicted (Hobday and Lough 2011), we expect recently recruited juveniles will grow, reproduce, and contribute to new recruitment events that could increase population abundance at the cooler southern edge pushing the species' range edge further south (see Cowen 1985; Pörtner et al. 2001). Anecdotal reports of juvenile *C. rubescens* as far south as Albany (270 km beyond the cooler edge) during summer months (G. Ellery pers. comm.), offer support for the possibility of a continued southern expansion if juveniles can survive over winter.

Distribution shifts are of biological and conservation importance for individual species and have significant ecological and socio-economic impacts by changing biotic

interactions and altering the balance of ecological communities (Kordas et al. 2011). For *C. rubescens* and other fisheries targets, a range shift would further result in significant impacts to the fisheries they support including shifts in location, intensity and species targeted (Sumaila et al. 2011; Cheung et al. 2013). Fisheries management regulations may, thus, require future changes to address latitudinal changes in abundance associated with a range shift. Given the importance of baldchin groper as a fisheries target and its limited range, further monitoring of range-wide populations along an extended depth gradient (to include the full range of depths where the species occurs) is recommended together with an assessment of possible ecological impacts to marine communities along WA as a result of a range shift. Monitoring recruitment at range edges in particular, is crucial for evaluation of range extension potential and should become priority for climate adaptive management strategies at subtropical locations around the world.

This study provides the first empirical test of models predicting southward shifts in the centroids of fish species in WA as a response to climate change (Cheung et al. 2012), and suggests that heat wave events may be important in facilitating such shifts by rapidly changing temperature profiles and recruitment success across latitudinal gradients. Because *C. rubescens* presents a similar distribution to numerous other fish species in WA (Edgar 2000; Hutchins 2001), our findings help predict how the geographic ranges of other WA endemic fishes may respond to increasing temperatures; in particular, other reef associated species with prolonged pelagic larval durations such as *C. rubescens* (~ 23 days; K. Cure unpublished data) that will have a high chance of arriving to new locations along the coast via the LC. These results also help understand the mechanisms behind range shifts of other species in response to ocean warming (Perry et al. 2005; Last et al. 2011), especially along continental margins with similar latitudinal temperature gradients and poleward flowing boundary currents (Vergés et al. 2014). It appears that short-term anomaly events such as marine heat waves can represent a stepping stone towards the more long-term changes associated with warming oceans, facilitating species range shifts. Analyses of the effects of similar rapid heating events such as those associated with strong *El Niño* on species recruitment distributions may provide further clarification.

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Compliance and ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors. Research surveys were approved by: Fisheries Exemption no. 2298 issued by the Department of Fisheries Western Australia, Licence Number SF009150 issued by the Department of Environment and Conservation Western Australia, and Animal Ethics Approval no. RA/3/100/1180 issued by the University of Western Australia.

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