# Successful establishment of range-shifting, warm-water Labridae in temperate South Western Australia

## Jack R. C. Parker[1],[*], Benjamin J. Saunders[1], Scott Bennett[2], Euan S. Harvey[1]

[1]School of Molecular and Life Sciences, Curtin University, Perth, WA 6102, Australia
[2]Institute of Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7000, Australia

ABSTRACT: Climate change is rapidly altering the distributions of species and the composition of communities that have evolved over evolutionary time scales. Quantifying changes in species distributions and abundance in response to warming is critical to understanding how these changes modify structure, function and services provided by recipient communities. Changes in size structure of warm- and cool-affiliated species is an important indicator for climate-driven species redistributions over time, and has received relatively little attention. We quantified changes in length and biomass distributions of 25 species of Labridae fishes from 112 sites spanning 2000 km across a warm–cool temperate transition zone in south Western Australia. Length and biomass data were collected in 2005–2006 and 2014–2015 using diver operated stereo-video. In the decade between sampling events, south Western Australia experienced an extreme marine heatwave followed by repeated summers of anomalously warm ocean temperatures. Biomass of tropical and subtropical species increased 10-fold and 3-fold, respectively, between 2006 and 2015, whereas temperate species biomass remained relatively stable. In 2014–2015, the abundance and biomass of tropical species (e.g. *Scarus ghobban*) increased in the warmest regions and established multiple size classes poleward of their recorded 2005–2006 distributions, suggesting successful overwintering and recruitment where viable populations were not recorded in 2005–2006. Large, slow-growing temperate species such as *Achoerodus gouldii* and *Bodianus frenchii* decreased in small and medium size classes in warm regions. Our findings report a substantial change in the size structure and composition of labrid assemblages over a decade of climatic variability.

KEY WORDS: Temperate reefs · Climate change · Diver operated stereo-video · Range shift · Functional groups

## 1. INTRODUCTION

Increasing oceanic temperature is an important driver of changes in the distribution of marine species (Seabra et al. 2015, Lenoir et al. 2020). Temperature can be directly and indirectly responsible for altering marine assemblages (Stuart-Smith et al. 2017), modifying species interactions (Kordas et al. 2011) and disrupting the function of marine ecosystems (Ling et al. 2009, Wernberg et al. 2016). Such effects are becoming increasingly prevalent in response to the poleward redistribution of species around the globe (Poloczanska et al. 2013, Vergés et al. 2014, Cure et al. 2018).

A range shift can be defined as the expansion or contraction (or both) of the distribution of a species (Sorte et al. 2010). Life-history traits, such as growth rate, length at maturity and recruitment, can vary among species and between populations across a species' range, implying that species' responses to

warming may be diverse and plastic (Booth et al. 2011, Poloczanska et al. 2016). Tracking changes in the size distribution of species over time can help infer mechanisms underlying range shifts of species and the ecological significance of such changes. For example, high abundances of juveniles, without any larger individuals, might suggest successful recruitment of a species, but an inability to overwinter. Alternatively, a few large individuals, but no small individuals might suggest adult migration but limited reproductive success. Quantifying size structure and biomass of species in addition to patterns of abundance is therefore important to understanding the ecological consequences of range shifts.

Temperature has a fundamental control over an organism's physiological and ecological performance. When combined with other processes such as available food, temperature can directly influence individual biomass production (Brown et al. 2004, Duffy et al. 2016, Audzijonyte et al. 2020). Increases in temperature can result in differing responses depending where within a species' range the increase in temperature occurs. At an assemblage level, increase in oceanic temperature can cause a biomass increase over a short period of time as metabolism increases, or conversely biomass crashes, as a species' thermal tolerance is exceeded and individuals die off. Even when consumer species biomass increases, it is often followed by a corresponding crash as food sources are exhausted (Forster et al. 2012, Pörtner et al. 2014, Bruno et al. 2015, Duffy et al. 2016). Monitoring changes in the biomass of a species is important for predicting the impact of temperature on both that marine species and more widely, in marine food webs (O'Connor et al. 2009). Biomass can also be used to identify a species' optimum distribution and to determine whether a species occurring outside its natural range is adapting and using resources effectively (Duffy et al. 2016).

Previous research has described how the larvae of tropical species are carried by currents into higher-latitude, temperate environments, where they survive over the warmer summer months until the colder winter conditions lead to temperature-induced reduction in physiological capacity, causing them to perish (Figueira & Booth 2010, Smith et al. 2016). Recently, warm-water species have been documented recruiting successfully into cooler-water ecosystems and overwintering (surviving the colder winter temperatures) (Vergés et al. 2014, Smith et al. 2016, Cure et al. 2018). The successful recruitment of warm-water species is seen most often in areas of poleward flowing currents (Last et al. 2011, Vergés et al. 2014, Cure et al. 2018), and is predicted to become more common with ocean warming and the increasing frequency of marine heatwaves (Figueira & Booth 2010, Vergés et al. 2014, Wernberg et al. 2016, Cure et al. 2018). Species length distributions can be used to track recruitment patterns and the life-history stages present in a habitat (Cure et al. 2018). Species length distributions can also be used to track cohorts of recruits over time (Russ et al. 1996) and help to identify whether juveniles settling into new areas are surviving in waters that have historically been too cold (Smith et al. 2016).

The Western Australian (WA) marine system is acknowledged as being the second richest multi-taxon centre of marine endemism in the world, with over 3000 species in total known to reside along the WA coast (Fox & Beckley 2005). The coastal marine system of WA has been described as an old, oligotrophic seascape that has been climatically buffered (Langlois et al. 2012b). The coast of South Western Australia (SWA) has had a relatively isolated and stable geological past compared to other areas around the world, being free from mass extinctions and glaciation events throughout the Cenozoic era (from 66.4 million years ago to the present) (Phillips 2001, Langlois et al. 2012b). An additional contributing factor to this stability in WA is the poleward flowing Leeuwin Current that has, over the past 40 million years, moderated the marine environment along SWA (McGowran et al. 1997). While geologically and climatically stable, the habitat along the WA coastline is highly variable, transitioning from warm tropical reefs in the north, to temperate cool water in the south that is dominated by kelp. Habitat-forming biota follow a temperature gradient decreasing linearly southward and then eastward (Langlois et al. 2012b), supporting tropical, subtropical and temperate species in SWA. The south Western Australian coast is dominated by limestone while the south coast is dominated by granite reefs. Although the heterogeneous nature of SWA marine habitat promotes endemism, it also can be detrimental for species that are displaced towards the poles, as they may be poorly adapted to the changing habitat types along the SWA coastline (Perry et al. 2005).

Species range shifts in SWA pose a risk to the diversity and abundance of endemic species, which can have wide-reaching impacts on ecosystems and services such as tourism and fisheries (Wernberg et al. 2011, Cheung et al. 2012, Harvey et al. 2013, Bennett et al. 2016). In 2011, a marine heatwave caused a 2–4°C anomaly in maximum summer temperatures over a period of 3 mo, causing habitat change and a subsequent regime shift that, in many areas, has yet to

recover (Wernberg et al. 2016, Cure et al. 2018). This disturbance resulted in mass die-offs of marine species (Caputi et al. 2014) and a dynamic shift in the composition of temperate reefs to a more tropical state (Cure et al. 2015, Wernberg et al. 2016, Parker et al. 2019).

Labridae are one of the most speciose, conspicuous and abundant families of reef-associated fish in temperate Australia (Morton et al. 2008a, Bray 2017). The family comprises more than 80 genera and 680 species globally, almost half of which occur in Australian waters (Western Australian Museum 2018). Labrids fulfil many functional roles including piscivory, invertivory and herbivory (Morton et al. 2008b, Lek et al. 2011), and representatives of the family inhabit all climatic zones from tropical and subtropical through to cold temperate waters. Some of the WA labrids are commercially important, including the western blue and baldchin groper (*Achoerodus gouldii* and *Choerodon rubescens*, respectively) (Coulson et al. 2009, Cure et al. 2015). Labrids have been shown to be affected by warming oceans in other geographic areas around the world, including the Mediterranean Sea (Bianchi 2007, Kruschel et al. 2012), and in SWA (Bennett et al. 2015b, Wernberg et al. 2016, Cure et al. 2018, Parker et al. 2019). Although the Labridae family is one of the most diverse in WA (Hutchins 2001), there is little information on changes in the distribution of labrids in SWA. This information is needed to determine the impacts that gradual warming and extreme events are having on reef ecosystems in SWA (Cure et al. 2018).

The goal of this research was to (1) determine if the geographic distributions of Labridae have changed from 2005–2006 to 2014–2015 along the SWA coastline, and identify which species have moved poleward; (2) examine whether the length–frequency structure has changed between 2005–2006 and 2014–2015 by climate affiliation and functional groups; and (3) quantify changes in biomass of different functional groups along the SWA coastline between 2005–2006 and 2014–2015.

# 2. MATERIALS AND METHODS

## 2.1. Site description

This study sampled complex, shallow, rocky reef systems from 4 to 12 m in depth across 2000 km of coastline from Port Gregory to Recherché Archipelago along the south Western Australia (Fig. 1). Surveys were conducted from December 2014 to July 2015 and replicated the areas that were previously sampled by Saunders et al. (2014) between November 2005 and June 2006. A total of 7 regions were sampled,
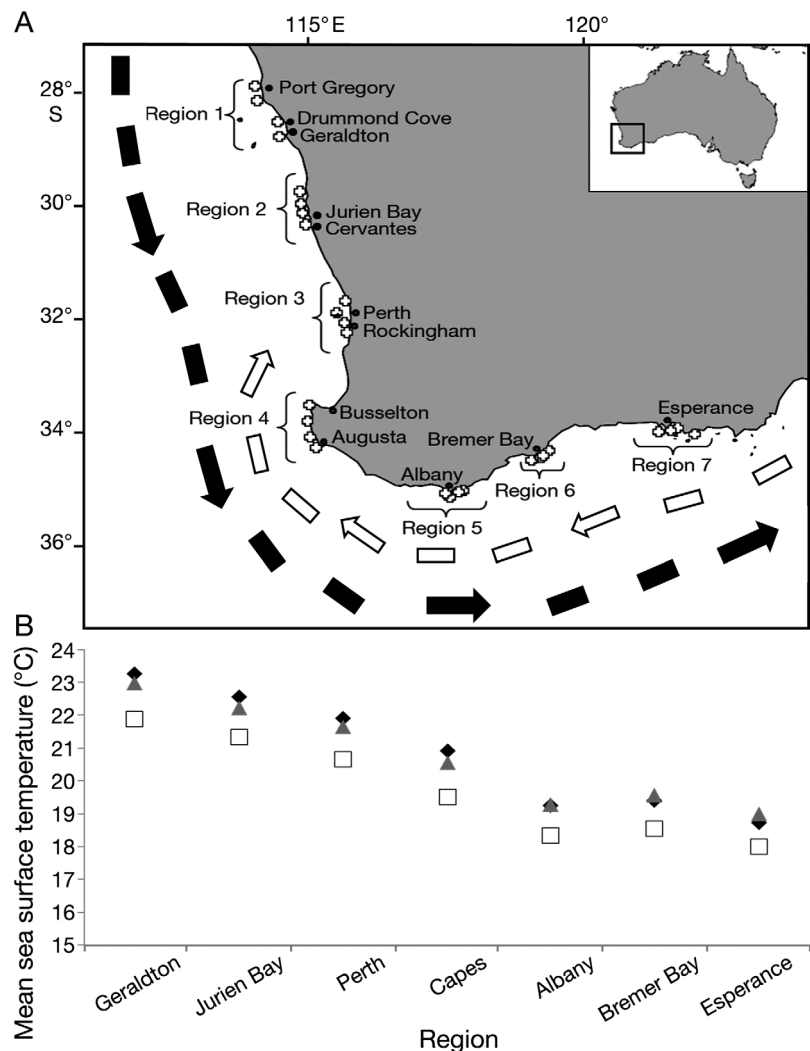


Fig. 1. (A) Map of the 7 geographical regions surveyed and the 4 locations (shown by the white crosses) nested within each. Leeuwin Current is depicted by the black lines and arrows and the Capes Current is indicated by the white lines and arrows. The 7 geographical regions that were surveyed from northernmost to southern and around to easternmost were (1) Geraldton, (2) Jurien Bay, (3) Perth, (4) South-West Capes, (5) Albany, (6) Bremer Bay and (7) Esperance. (B) The yearly sea surface temperature of the 7 study regions including the initial 2006 study (white squares), the marine heatwave in 2011 (black diamonds) and the most current survey in 2015 (grey triangles)

comprising Geraldton, Jurien Bay, Perth, the Capes, Albany, Bremer Bay and Esperance. The surveys were conducted in a hierarchical design which consisted of 7 distinct regions, with 4 locations in each region, 4 sites in each location and 12 belt transects of 5 × 25 m in each site. This resulted in 7 regions, 28 locations, 112 sites and 1344 replicate transects spanning 10° of longitude and 7° of latitude. The distances between the different survey hierarchies differed, following the method of Saunders et al. (2014).

## 2.2. Survey method

Diver operated stereo-video systems (stereo DOVs) were used to record the fish and marine habitat in the survey areas. Two SCUBA divers swam the stereo DOVs along 5 × 25 m belt transects. To reduce temporal variation, the surveys were completed at similar times in 2005–2005 and 2014–2015. Stereo-DOVs were initially described and developed by Harvey & Shortis (1995) and were used to increase precision and accuracy of species length and distance estimates in comparison to SCUBA diver underwater visual census (UVC) (Harvey et al. 2004, Goetze et al. 2019).

The surveys completed in 2005–2006 (Saunders et al. 2014) were recorded using a stereo-video system comprising 2 Sony TRV 900 digital video cameras. In the 2014–2015 surveys, the cameras were Sony HDR CX700, which recorded at a higher resolution (1920 × 1080 pixels at 50 frames per second [FPS] rather than 720 × 560 pixels at 25 FPS). The higher camera resolution captured by the systems used in 2014–2015 potentially resulted in smaller fish (less than 20 mm) being detected, but this will not have affected counts of labrids due to their larger size and conspicuousness. Both sets of cameras were securely mounted 70 cm apart, with the cameras tilted inwardly at 8° to optimise the area available for stereo-video analysis (Harvey et al. 2010, Saunders et al. 2014). Before and after each survey trip, calibration of the stereo-video systems were completed using the Vision Measurement System software package for the surveys completed in 2005–2006 (Robson et al. 2006) and CAL (Seager 2014) for the 2014–2015 surveys, allowing highly accurate calculation of the transect dimensions and fish length (Harvey et al. 2010).

## 2.3. Image analysis

Labridae length data from the 2005–2006 footage were quantified using the Vision Measurement System software package (Robson et al. 2006). The 2014–2015 videos were analysed using the software package Event-Measure (Stereo) (www.seagis.com. au). Although 2 different software programs were used, both used a similar workflow and algorithms, allowing an image analyst to identify labrids to the lowest taxonomic group possible and make length and distance measurements. Fish were measured for fork length (end of the snout to the middle of the fork caudal fin). Rules were integrated in the software that prevented fish that were more than 7 m from the camera or 2.5 m from the centre of the transect line from being measured or counted. If fish were within transects, but could not be measured due to an obstruction in the field of view of one camera, or if the fish was not on the right angle to be measured, they were still counted for abundance.

## 2.4. Sea surface temperature

Mean sea surface temperature was calculated for each survey site using NOAA Optimum Interpolation sea surface temperature (https://www.ncdc.noaa. gov, accessed 6 October 2015). Optimum Interpolation sea surface temperature combines *in situ* observations and satellite data to produce a 1° grid of latitude and longitude. The maximum temperatures for each month of 2006, 2011 (the year of the marine heatwave) and 2015 were averaged and the average maximum temperature was plotted on a scatter graph (Fig. 1). During the 2005–2006 survey, temperatures ranged from 22°C to 18°C from north to south in the survey area and from 23°C to 19°C in 2014–2015 over the same distribution (Fig. 1).

## 2.5. Statistical analysis

### 2.5.1. Individual length

Length–frequency analyses were undertaken for 8 species (*Achoerodus gouldii*, *Bodianus frenchii*, *Coris auricularis*, *Choerodon rubescens*, *Notolabrus parilus*, *Ophthalmolepis lineolatus*, *Scarus ghobban* and *Thalassoma lunare*). These species were selected based on the number of length recordings per species, the importance of the species in previous statistical analysis indicated by Dufrêne-Legendre index values (Parker et al. 2019), and the presence of appropriate supporting literature to identify the species' growth and life-history stages. These species were then graphically represented by length–frequency

histograms comparing 2005–2006 to 2014–2015 for each region (see Fig. S1 in the Supplement at www. int-res.com/articles/suppl/m667p161_supp.pdf). Most labrids are protogynous hermaphrodites; therefore, each graph includes lines indicating size at maturity to female and size at change to male. These sizes were estimated based on a number of sources (Ackerman 2004, Coulson et al. 2009, Cossington et al. 2010, Lek et al. 2012, Taylor & Choat 2014, Cure et al. 2015). All statistical analysis was conducted in Primer 7 and Primer 6 (Clarke & Gorley 2005, 2015) or RStudio (Version 1.1.453, R Core Team 2014).

Histograms were used to test for differences in the shapes of individual species' length–frequency distributions. This method was then also applied to the whole assemblage, with all labrid lengths being aggregated into equal-sized bins of 100 mm. A data matrix was created with the length bins as variables, and each measured fish as a sample, and this used to construct a Manhattan distance resemblance matrix. A 2-factor PERMANOVA was performed on the resemblance matrix to determine if there was a change ($\alpha = 0.05$) in species' length distributions between year (fixed factor, 2 levels) and region (fixed factor, 7 levels) (Table S2). Kolmogorov-Smirnov tests were used to compare the shapes of length–frequency distributions between years in each region.

### 2.5.2. Length–climate association

The Labridae assemblage across SWA contains species representing 3 climatic affiliations: tropical, subtropical and temperate (Table S1). In order to detect changes for labrids within each of these climatic affiliations, length data were grouped by temperate, sub-tropical or tropical climate affiliations. These lengths were then organised into length bins, pooled at the region level, displayed and analysed as above to further explore the trends in length frequencies for different climatic affiliations.

### 2.5.3. Biomass climate association

Biomass (weight in grams) values for individual labrids were calculated from their fork length measurement (Kulbicki et al. 1993, Taylor & Willis 1998). The equation Weight = $a$ × Length (mm)$^b$ was used, with the appropriate values for $a$ and $b$ being sourced from relevant published articles (Taylor & Willis 1998, Kulbicki et al. 2005) or FishBase (Froese & Pauly 2018). For the individuals that were not measured, but that were counted inside the transect area, we multiplied the number counted by the mean weight of the same species that occurred at that site. If that was not possible, we used the same method, but used the average at a greater replication level (location).

Species biomasses were summed into the 3 climate affiliations at the location level and mean biomass data for each climate affiliation represented graphically at the region level. A 2-factor PERMANOVA on region and year was run to determine if there were any changes in mean biomass (Table 1).

### 2.5.4. Biomass trophic level

To enable a finer-scale understanding of the changing biomass of the labrid assemblage, labrids within each climate affiliation described above were further split into 5 trophic groups: herbivores, generalist carnivores, omnivores, large invertivores and small invertivores (Table S1). This finer scale will help determine the impacts of recent climate change on Labridae feeding guilds and potential interactions between them. Functional groups were assigned to all labrid species except *Suezichthys cyanolaemus*, *Eupetrichthys angustipes*, *Thalassoma septemfasciatum*, *Halichoeres brownfieldi* and *Pseudojuloides elongatus* due to lack of published information on their diet. The mean trophic biomass was then presented graphically with the 5 trophic categories assigned within cli-

Table 1. Results of PERMANOVA tests for labrid biomass of the 3 different climate affiliations (temperate, sub-tropical and tropical). **Bold** p-values indicate significant results (p < 0.05)

| Source | df | SS | Pseudo-$F$ | p(perm) | Unique perms |
|---|---|---|---|---|---|
| Tropical | | | | | |
| Year | 1,42 | 22173 | 14.017 | **<0.001** | 9949 |
| Region | 6,42 | 24399 | 2.571 | **0.016** | 9943 |
| Year × region | 6,42 | 13587 | 1.432 | 0.191 | 9944 |
| Sub-tropical | | | | | |
| Year | 1,42 | 6922.3 | 22.797 | **<0.001** | 9936 |
| Region | 6,42 | 9101 | 4.995 | **<0.001** | 9940 |
| Year × region | 6,42 | 1301.4 | 0.714 | 0.707 | 9940 |
| Temperate | | | | | |
| Year | 1,42 | 707.95 | 0.702 | 0.543 | 9959 |
| Region | 6,42 | 71542 | 11.832 | **<0.001** | 9920 |
| Year × region | 6,42 | 6021.6 | 0.996 | 0.461 | 9928 |

mate associations and by year. A 2-factor PERM-ANOVA (year and region) was performed as described above (Table 2).

Where the PERMANOVA tests indicated statistically significant, or close to significant ($\alpha$ = 0.05), dif-ferences for factors of year or the interaction of year × region, Kolmogorov-Smirnov tests were run to identify the specific regions where particular species biomass had changed over time; this was then indicated on the figures.

Table 2. Results of PERMANOVA tests of labrid biomass of the 3 climate-affiliated categories split into a further 5 trophic classifications (herbivores, large invertivores omnivores, generalist carnivores and small invertivores) over the 7 regions sampled encompassing both years. **Bold** p-values indicate significant results (p < 0.05)

| Source | df | SS | Pseudo-$F$ | p(perm) | Unique perms |
|---|---|---|---|---|---|
| Tropical generalist carnivores | | | | | |
| Year | 1,42 | 6942.1 | 17.066 | **<0.001** | 9945 |
| Region | 6,42 | 13757 | 5.635 | **<0.001** | 9941 |
| Year × region | 6,42 | 13757 | 5.635 | **<0.001** | 9943 |
| Tropical herbivores | | | | | |
| Year | 1,42 | 3825.2 | 3.854 | **0.047** | 9949 |
| Region | 6,42 | 22346 | 3.752 | **0.004** | 9953 |
| Year × region | 6,42 | 4563 | 0.766 | 0.61 | 9951 |
| Tropical small invertivores | | | | | |
| Year | 1,42 | 10246 | 8.769 | **0.002** | 9946 |
| Region | 6,42 | 12523 | 1.786 | 0.088 | 9934 |
| Year × region | 6,42 | 6356.1 | 0.907 | 0.519 | 9930 |
| Sub-tropical generalist carnivores | | | | | |
| Year | 1,42 | 8328.8 | 15.279 | **<0.001** | 9949 |
| Region | 6,42 | 12845 | 3.927 | **<0.001** | 9936 |
| Year × region | 6,42 | 12845 | 3. 927 | **<0.001** | 9934 |
| Sub-tropical large invertivores | | | | | |
| Year | 1,42 | 5795.1 | 7.2828 | **0.005** | 9943 |
| Region | 6,42 | 59803 | 12.526 | **<0.001** | 9944 |
| Year × region | 6,42 | 8135.1 | 1.7039 | 0.099 | 9933 |
| Sub-tropical omnivores | | | | | |
| Year | 1,42 | 6969.4 | 16.771 | **<0.001** | 9948 |
| Region | 6,42 | 12294 | 4.931 | **<0.001** | 9935 |
| Year × region | 6,42 | 1967.2 | 0.789 | 0.6565 | 9935 |
| Sub-tropical small invertivores | | | | | |
| Year | 1,42 | 356.8 | 0.315 | 0.736 | 9957 |
| Region | 6,42 | 61052 | 8.975 | **<0.001** | 9932 |
| Year × region | 6,42 | 3184.9 | 0.468 | 0.929 | 9938 |
| Temperate generalist carnivores | | | | | |
| Year | 1,42 | 111.23 | 1 | 0.432 | 3060 |
| Region | 6,42 | 667.4 | 1 | 0.412 | 320 |
| Year × region | 6,42 | 667.4 | 1 | 0.497 | 9870 |
| Temperate large invertivores | | | | | |
| Year | 1,42 | 327.1 | 0.221 | 0.846 | 9947 |
| Region | 6,42 | 74404 | 8.385 | **<0.001** | 9934 |
| Year × region | 6,42 | 7512.8 | 0.847 | 0.58 | 9938 |
| Temperate omnivores | | | | | |
| Year | 1,42 | 452.74 | 0.611 | 0.6 | 9941 |
| Region | 6,42 | 72017 | 16.186 | **<0.001** | 9910 |
| Year × region | 6,42 | 5372.7 | 1.2075 | 0.27 | 9910 |
| Temperate small invertivores | | | | | |
| Year | 1,42 | 9275.8 | 6.619 | **0.009** | 9941 |
| Region | 6,42 | 23062 | 2.743 | **0.013** | 9938 |
| Year × region | 6,42 | 9510.4 | 1.131 | 0.357 | 9944 |

## 3. RESULTS

### 3.1. Labrid length analysis

The length–frequency of most species changed from 2005–2006 to 2014–2015, with more individual fish across a wider range of sizes in 2014–2015 compared to 2005–2006 with the frequency of larger individuals that were recorded also increasing over the sampling times. There was a difference in the mean size of species based upon their climate affiliation ($F_{2,12514}$ = 618.3, p < 0.001). Temperate species grew largest (max. length <1000 mm, mean ± SD = 223 ± 147 mm), but also included many small-bodied individuals (Fig. 2). In comparison, tropical species had no large individuals over 700 mm (Fig. 2), but an overall similar mean length to temperate species (mean ± SD = 222 ± 89 mm). Sub-tropical fishes consisted of smaller individuals (mean ± SD = 148 ± 81 mm), with over 75% around 1–200 mm and none measured over 500 mm (Fig. 2).

The length–frequency distributions of tropical labrids displayed significant differences between years (Fig. 2, Table S2). In 2005–2006, tropical-associated labrids were only present in the 3 northern most regions (regions 1, 2 and 3; Fig. 2), with the length–frequency distribution skewed heavily toward smaller size classes (rarely reaching 200 mm in fork length). Conversely, in 2014–2015, tropical labrids were observed in all regions. *Anampses geographicus*, *Labroides dimidiatus* and *Thalassoma septemfasciatum*, for example, were observed in the south coast regions 5, 6 and 7 in 2014–2015, and displayed more individuals and
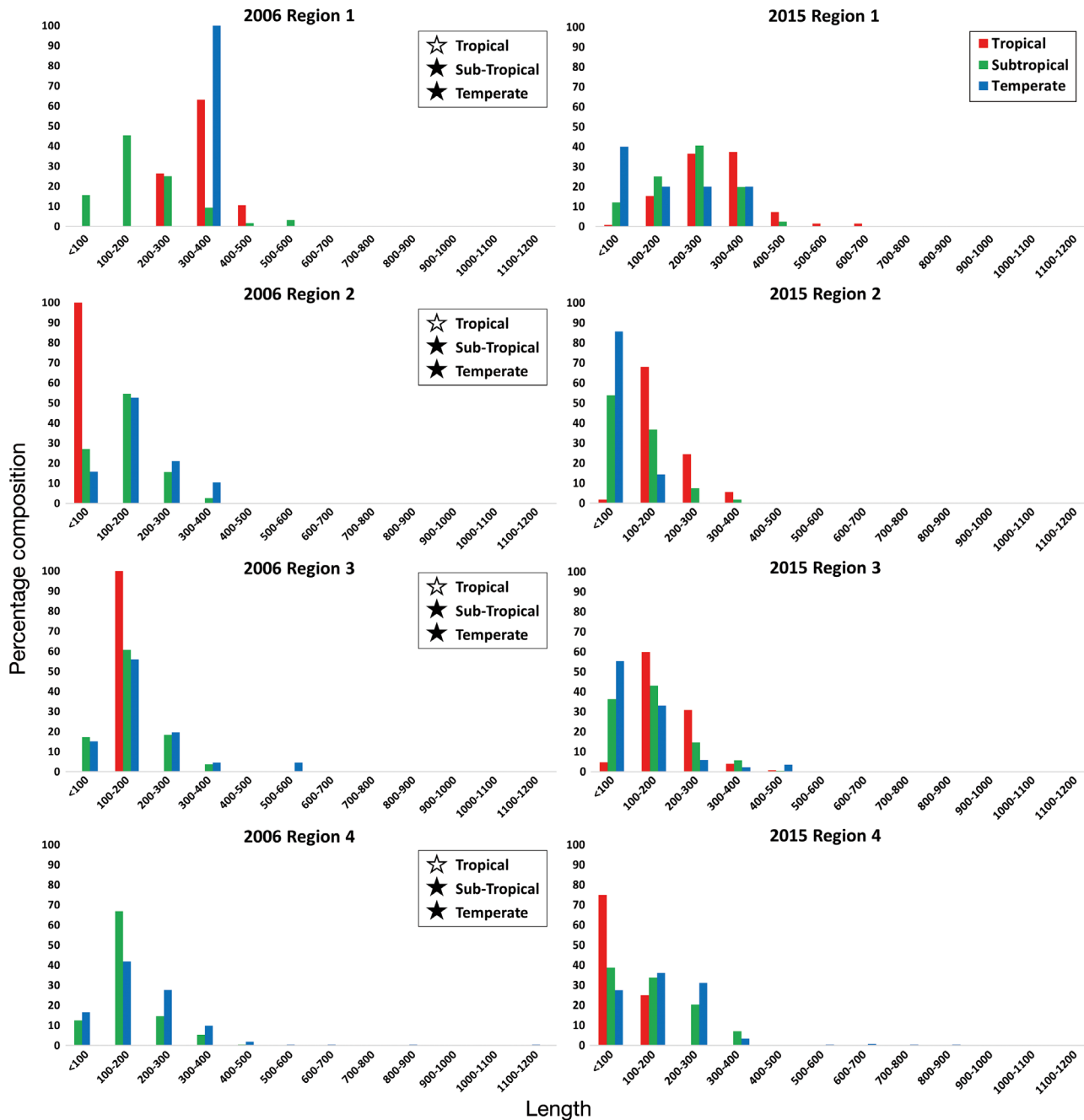
Fig. 2. (Above and following page). Length−frequency analysis of labrids. Left column represents the 2005−2006 data and the right the 2014−2015 data. Regions 1 to 7 are from warm to cool, north to southeast geographically. A black star indicates a statistically significant difference between years, white stars indicating no significant difference (Kolmogorov-Smirnov test, p < 0.05)

a greater number of size classes throughout the whole study area (Fig. 2).

Sub-tropical species were persistent in all regions for both 2005−2006 and 2014−2015. The length−frequency distributions of sub-tropical labrids were found to differ significantly by year, region and year × region (Table S2). This can be observed in their differ-ent length−frequency distributions between years in

all regions (Fig. 2), with the length distributions of sub-tropical fish comprised mostly of small individuals (<30 cm) in 2005−2006. In comparison, there was an increase in the ratio of larger-sized individuals by 2014−2015.

There were significant changes in temperate spe-cies size classes for both year and region (Table S2). While temperate species were present in all regions,
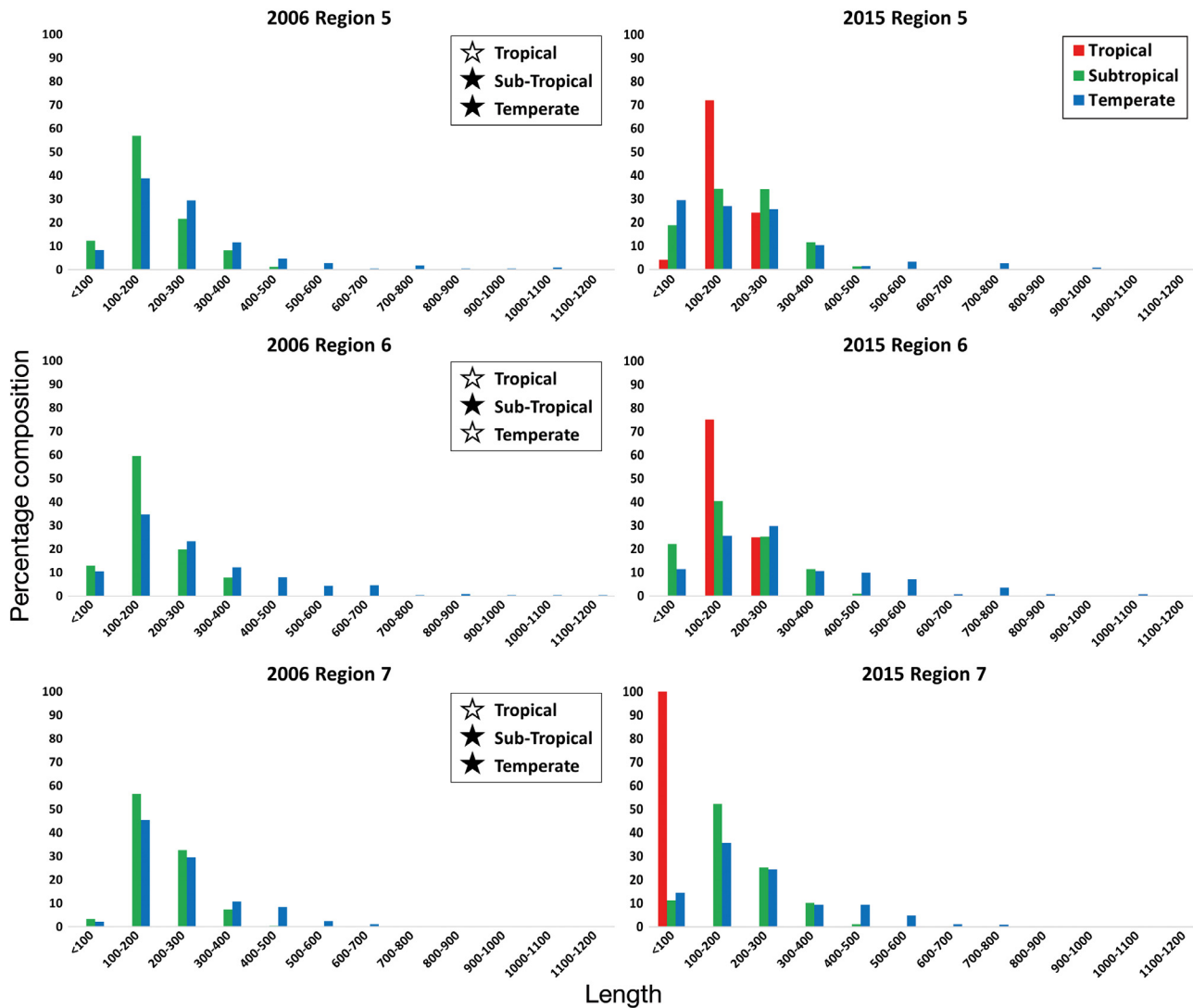
Fig. 2. (continued)

larger-bodied individuals were present in regions 4–7 in both 2005–2006 and 2014–2015 (Fig. 2). In general, there were more recruits and small-bodied temperate individuals (<100 mm) in 2014–2015, with the exception of region 6 (Fig. 2).

## 3.2. Individual species length distributions

Analysis of the individual species length distributions shows changes between 2005–2006 and 2014–2015 (Fig. S1). *Coris auricularis* accounted for 52 % of all (approximately 13 000) length measurements, and displayed a substantial increase in the number of length measurements for both juveniles and mature individuals. Overall, the large increase in juvenile *C. auricularis* individual lengths skewed the 2014–2015

length distributions heavily towards individuals under 200 mm, resulting in a significantly different length distribution in 2014–2015 in all regions when compared to 2005–2006 (Fig. S1C). Additionally, the tropical-associated species *Thalassoma lunare* (which were not observed in 2005–2006; Fig. S1H) and *Scarus ghobban* (which consisted of only a few observations in 2005–2006; Fig. S1G), showed a large increase in the numbers of juveniles and larger individuals at the northern, warmer regions (1 and 2) of this study in 2014–205. *Thalassoma lunare* were only observed in 2014–2015, and consisted of sexually mature females and males. For *Choerodon rubescens*, small juveniles were recorded further south in 2014–2015 (regions 3 and 4) compared to their 2005–2006 distributions, where they were not recorded south of region 2 (Fig. S1D).

Temperate labrids such as *Bodianus frenchii* (Fig. S1B) had significant changes in their length structure in the cooler regions (4, 6 and 7) between years (Table S2). *Bodianus frenchii* had fewer recruits in cooler water areas in 2014−2015, while larger sexually mature male and female individuals declined in warmer areas (Fig. S1B). Additionally, *Achoerodus gouldii* had fewer juveniles observed in regions 5 and 6, and its length structure showed a significant change in region 7, which had the lowest temperatures of the study area. For *Ophthalmolepis lineolatus*, significant changes in length−frequency distribution were observed (Table S2). In warmer waters, very few individuals were observed in 2014−2015 compared to 2005−2006. In regions 3 and 4, the distributions of *O. lineolatus* were dissimilar in shape in both 2005−2006 and 2014−2015, with *O. lineolatus* in region 4 in particular displaying a fuller, more complete size distribution in 2014−2015, driven by large numbers of fish in each size class in both years (Fig. S1F). Towards the cooler waters of regions 6 and 7, *O. lineolatus* length structure was composed predominantly of juveniles in 2005−2006, but these juveniles diminished in 2014−2015 as proportionally more adults were recorded.

### 3.3. Change in biomass with climatic affiliation

The biomass of all sub-tropical- and tropical-affiliated fish increased in each region from 2005−2006 to 2014−2015 (Fig. 3). The biomass of tropical labrids increased by a minimum of 3 kg up to 23 kg in the regions in which they were present in both 2005−2006 and 2014−2015 (Table 1, Fig. 3). Increases in biomass were particularly evident in the northern

regions 1, 2 and 3, where tropical species had a higher biomass than temperate species in 2014−2015. Sub-tropical fish biomass increased by a minimum of 5.5 kg to over 55 kg per region from 2004−2005 to 2014−2015, with sub-tropical species displaying a bimodal distribution in both 2005−2006 and 2014−2015 along SWA (Table 1, Fig. 3). This distribution shape was due to lower biomass in region 4 than in the neighbouring regions to the north and southeast. The biomass of temperate-affiliated labrids remained statistically stable over time, in contrast to tropical and sub-tropical labrid biomass. Importantly however, temperate species biomass did show a large decline in regions 5 and 6 of up to 18.5 kg and a corresponding increase in region 7 of 19 kg from 2005−2006 to 2014−2015 (Table 1, Fig. 3).

### 3.4. Trophic biomass

Each of the broad climatic affiliations were further broken down into 5 trophic groups (large invertivores, small invertivores, herbivores, generalist carnivores [invertivore and piscivore] and omnivores) to allow more detailed examination. For tropical labrids, there was a significant increase in small invertivores, generalist carnivores and herbivores (with large invertivores and omnivores not recorded for tropical-affiliated labrids) in 2015 compared to 2006 (Fig. 4). Herbivores dominated the biomass of tropical labrids and were predominantly present in the more northern regions (Fig. 4). No sub-tropical or temperate labrids were classified as herbivorous. Sub-tropical labrids were mainly omnivores and small invertivores in 2005−06. However, sub-tropical large invertivores increased their biomass signifi-
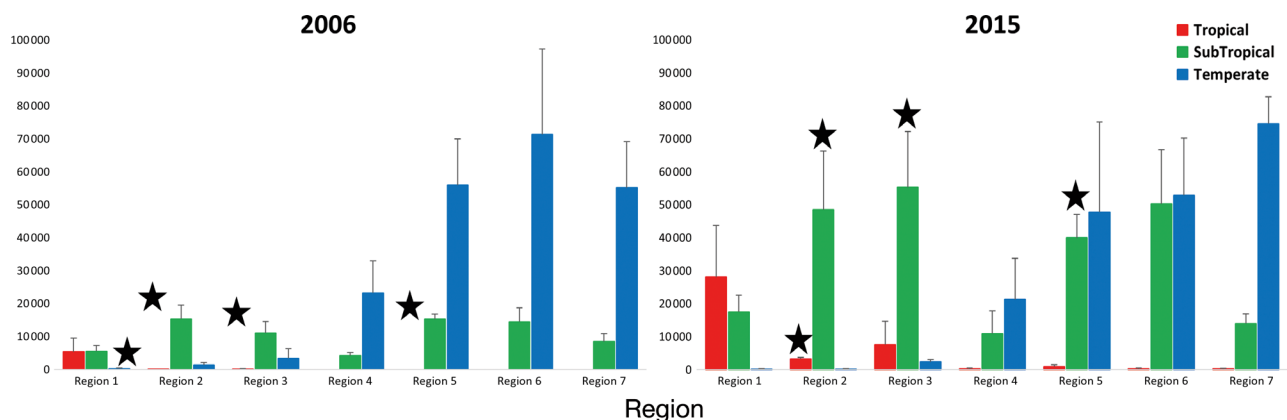


Fig. 3. Biomass of each climatically affiliated species over the study regions of 2005−2006 (left) and 2014−2015 (right). Standard error bars are depicted for each climate affiliation at each region. Black stars above certain regions and climate association indicate a significant difference in biomass (p < 0.05) from the pairwise test for climate association over year × region
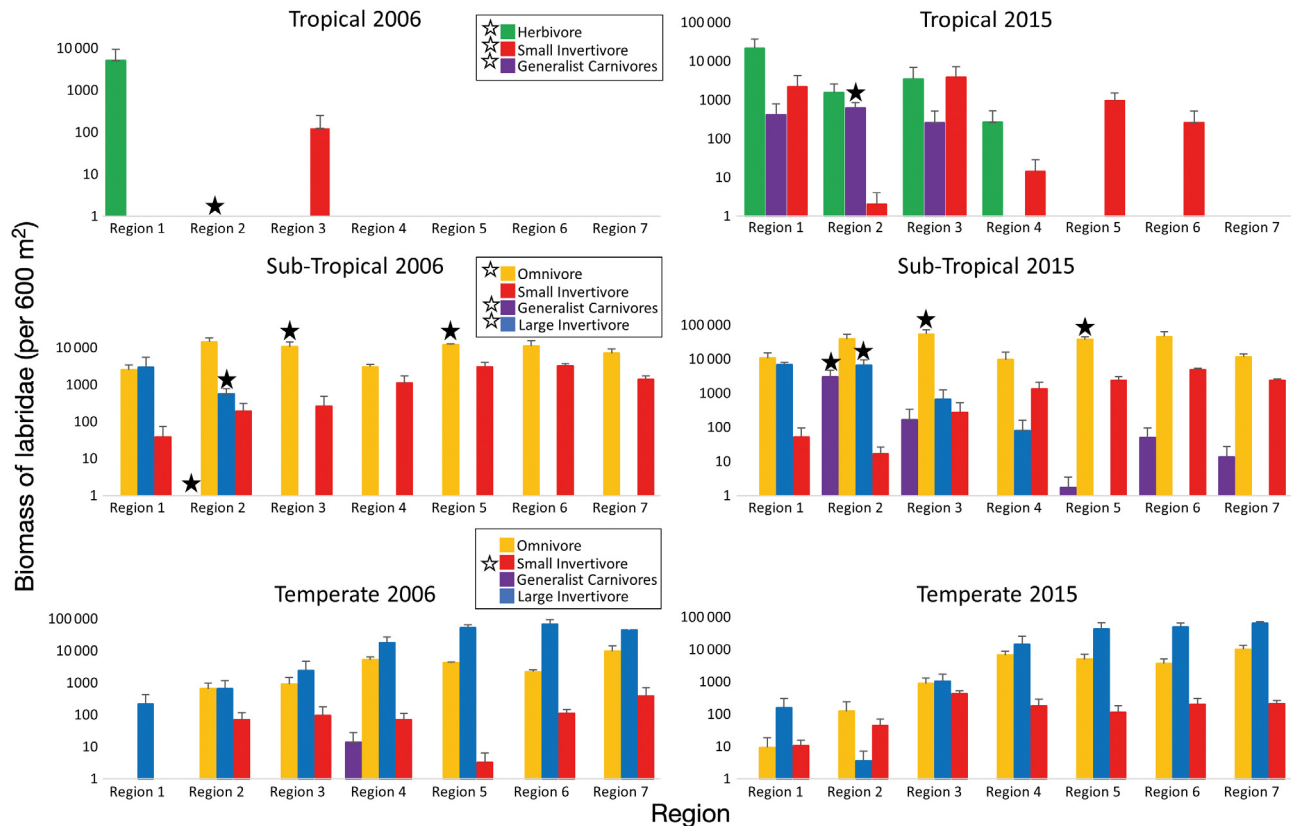
Fig. 4. Log-transformed biomass of the 5 different trophic levels of labrids. Each trophic biomass is associated with either tropical, sub-tropical or temperate climatic affiliations. A white star indicates a significant difference in biomass between years (PERMANOVA, p < 0.05). Standard error bars are depicted for each climate affiliation at each region. A black star indicates a significant pairwise test between year × region

cantly from 2005–2006 to 2014–2015, with a greater biomass present in the northern-most sites in 2014–2015 (Table 2, Fig. 4). The biomass of sub-tropical omnivores increased significantly over years and regions (Table 2). The bimodal distribution pattern of sub-tropical labrids (Fig. 3) appears to be driven by the distribution of biomass of sub-tropical omnivores, which was lower in region 4 than in the neighbouring regions (Fig. 4). The biomass of sub-tropical generalist carnivorous labrids also increased significantly, being very low or absent in 2005–2006, whereas in 2014–2015, greater biomass was recorded in region 2 (over 90 %) compared to the all other regions that year (Table 2, Fig. 4). Lastly, the biomass of temperate-affiliated fish was dominated by large invertivores and was generally consistent over time, displaying a 3 % decrease in biomass from 2005–2006 to 2014–2015 (Fig. 4). The exception was the biomass of temperate small invertivores, which significantly increased between years (Table 2). However, temperate small invertivores made up only a very small proportion of the temperate labrid biomass (Fig. 4).

## 4. DISCUSSION

### 4.1. Naturalisation/establishing populations

Our study illustrates how tropicalisation is influencing length–frequency distributions and biomass of fishes in SWA. Between 2005–2006 and 2014–2015, the warming trend in ocean temperature has allowed new species to emigrate and expand their range (sensu Walther et al. 2009). Warm-water-affiliated fish have increased in biomass in SWA, with mature female and male stages of *Thalassoma lunare*, *Thalassoma lutescens*, *Scarus ghobban*, *Coris auricularis* and *Choerodon rubescens* recorded further poleward than their observed distributions in 2005–2006. The size distribution of sub-tropical species changed significantly in each region over the 10 yr period, resulting in a wider range of length frequencies for the group in 2014–2015 compared to 2005–2006. Such changes in length distributions suggest that that observed range-extending species do not just represent recruitment pulses that die off during the cooler winter temperatures, but are overwintering and es-

tablishing on temperate reefs. This study found evidence of multiple generations and fully grown individuals of *T. lunare*, *T. lutescens*, *S. ghobban*, *C. auricularis* and *C. rubescens* in many of the regions that they were not recorded in in 2005–2006, and these individuals are surviving to reproductive maturity. This would suggest that these fishes have successfully established further south of their previously recorded distributions (Smith et al. 2016). This observation is supported by previous reports of *C. rubescens* successfully establishing itself south of its previously recorded range from 2011 to 2013 (Cure et al. 2015, 2018).

One of the most important findings of this research is the increase in total biomass of tropical and subtropical fishes driven by an increase in both abundance and individual size of fishes. This pattern suggests that there have been increasingly favourable conditions for warm-water fish over the decade between surveys, assisting growth, reproduction and immigration into cooler ecosystems (Macpherson 2002, Hiddink & Hofstede 2008). While there has been a notable increase in the sizes of individual fish, the overall increase in the density of individuals is having an even greater impact, consistent with previous studies (O'Connor et al. 2009, Parker et al. 2019). In the more northern warmer-water fish assemblages, scraping herbivores drove the increase in biomass of tropical species, and this has been attributed to the maintenance of low biomass turf habitats, following kelp habitat loss in 2011 (Bennett et al. 2015a). Interestingly, although there was an increase in warm-water species, there was not a corresponding decline in temperate fish biomass.

## 4.2. Vulnerable temperate species

Unlike tropical and sub-tropical species, temperate labrids have remained relatively stable between 2005–2006 and 2014–2015 in terms of biomass and distribution. This contrasts to some degree with previous findings that temperate species have low resilience to changing conditions, such as temperature increases, in their relatively stable environments (Coleman et al. 2011, Bryars et al. 2012, Parker et al. 2019). Long-lived species such as *Achoerodus gouldii* and *Bodianus frenchii* are especially vulnerable to climate change (Coulson et al. 2009), including increasing ocean temperature and changing physical environment, due to them being secondary consumers (Thackeray et al. 2016), their long life cycles, large body size (Hiddink & Hofstede 2008) and rela-

tively small home ranges (Bryars et al. 2012), and the fact that they take longer to adapt to change due to their long generation times (Perry et al. 2005). However, the trend of the distribution of temperate species remaining stable in SWA is supported by similar observations in another family of long-lived, temperate fishes in SWA. The distribution of territorial temperate water damselfishes (Pomacentridae) has not changed over the same time period (Shalders et al. 2018). However, cool-water species are still at risk in SWA, as the orientation of the coastline does not allow species to move further south and take refuge from the increasing temperatures, which is further exacerbated by the warm poleward flowing Leeuwin Current, leading to an increased risk of rapid expiration or extinction (Bennett et al. 2016, Wernberg et al. 2016).

Large temperate invertivores are targeted by recreational and commercial fishing, which may explain some of the changes in their size distributions. Recent trends show a 15% drop in overall recreational fishing effort along SWA from 2013 to 2016 (Ryan et al. 2015, 2017). However, the successful catch rate of *B. frenchii* has increased by almost 50% and that of *A. gouldii* has also increased (Ryan et al. 2015, 2017). The increased catch rate of *A. gouldii* and *B. frenchii* relative to overall fishing effort could be due to an increase in their abundance; however, Parker et al. (2019) reported a decline in the abundance of these species. The length–frequency analysis for *A. gouldii* illustrated a clear reduction in the number of individuals over the size of 500–600 mm in 2014–2015. With the minimum catchable size limit for *A. gouldii* being 500 mm (Department of Primary Industries and Regional Development 2018), we suggest that the increased recreational catch reflects targeted fishing for these species. It is also probable that fishing pressure is contributing to a decline in the adult population. With large invertivores making up an important proportion of temperate-affiliated labrid biomass, there is a possibility that further pressures will lead to the loss of an important trophic group in SWA.

Some temperate species which are not targeted by commercial or recreational fishing, such as *O. lineolatus*, have exhibited a decline in the frequency of individuals within juvenile size classes along their distribution. In the northern, warmer regions, the decline of *O. lineolatus* could be, in part, due to warming and the associated reduction in canopy algae habitat, which they may use for protection and food, in terms of the invertebrates that live on the thallus of the algae. This loss of recruits also occurs

where there is a corresponding increase in subtropical- and tropical-affiliated labrid biomass. Many studies label labrids as invertivores, but multiple authors report that some species of labrid include fish in their diet (Ackerman, 2004, Lek et al. 2011, Holmes et al. 2012). As an example, when present in large numbers, *T. lunare* can drive a decline in juvenile fish abundance (Holmes et al. 2012). It is possible that an increasing abundance of *T. lunare*, or other functionally similar warm-water species, is driving a decrease in the frequency of juveniles of other species through direct predation in SWA. Another driver for the changes in *O. lineolatus* biomass in SWA assemblages may be direct competition from functionally similar species such as *C. auricularis*, which has a highly plastic diet and is capable of competing with *O. lineolatus* (Lek et al. 2011). Similarly, other tropical- and sub-tropical-affiliated piscivorous species (outside the scope of the present study) could potentially be contributing to the decline of temperate labrids; however, further study is needed to disentangle what is driving the change in temperate species length frequencies.

### 4.3. Distribution of tropical herbivores and their establishment

This study supports the results of a current growing body of literature that warm-water species are increasing their range further south along the SWA coastline (Bennett et al. 2015b, Wernberg et al. 2016, Cure et al. 2018). Many factors are responsible for the success of climatically tropical-affiliated herbivores such as *S. ghobban*. In SWA, warming ocean temperatures and the heatwave in 2011 drove the reduction of *Ecklonia radiata* kelp canopy cover in the north of the survey area and promoted the growth of turfing algae (which is a large component of the diet of *S. ghobban*), resulting in a regime shift, facilitating new fish species to permeate the ecosystem (Bennett et al. 2015b, Wernberg et al. 2016). Smith et al. (2016) observed that the most successful naturalisation occurred when a species was moving into a neighbouring unoccupied niche. This trend explains why *S. ghobban* has become a dominant labrid species, as they are immigrating from neighbouring ecosystems and are the only labrid herbivore observed to have established itself in SWA. Furthermore, *S. ghobban* are especially likely to thrive along the SWA coast, as there are no labrids and few other species that perform their ecological function as roving grazers. The increase in biomass of tropical-affil-

iated herbivores has the potential to introduce unprecedented top-down control of the algal canopy as they prevent re-establishment of the canopy by consuming macroalgae germlings as a by-product of feeding on turf algae (Bennett et al. 2015b). This potential shift away from algal canopy habitat can have negative consequences for the species that depend on it for food and shelter (Levin & Hay 1996, Bennett et al. 2015b, Cheminée et al. 2017).

Many temperate ecosystems are vulnerable to warming. SWA makes up the western-most extent of the Great Southern Reef (GSR). The GSR is especially vulnerable due to the west–east orientation of the Australian coastline in relation to the poles (Stevens, 1989, Bennett et al. 2016). The GSR has already seen changes in its marine assemblages due to the 2011 marine heatwave, including mass canopy-forming algae die-offs and drastic changes in marine assemblage composition (Bennett et al. 2016, Wernberg et al. 2016, Shalders et al. 2018, Parker et al. 2019). The GSR has one of the most diverse and endemic assemblages in the world, generating AU\$120 million dollars to the Australian economy in fisheries alone and AU\$200 billion dollars in nutrient recycling services (Bennett et al. 2016). However, the increase in warm-water-affiliated species further south of their normal range, the increase in warm-water fish biomass, newly emerging species functions, the decrease in endemic temperate fish biomass and the change in length structure put the unique values of the GSR in jeopardy. In comparison to tropical reef systems, temperate reefs are highly understudied (Parsons et al. 2016, Truong et al. 2017), and as a result, our understanding of the consequences of changing ecosystem and species function is limited.

### 4.4. Conclusion

This study examined whether labrid distributions, lengths and biomass changed along the SWA coastline in the 10 yr between 2005–2006 and 2014–2015. Our results indicate that warm-water-affiliated species are becoming established in the northern-most survey regions, with some species establishing further south, in historically cooler waters. The changes in length structure of large, slow-growing temperate-affiliated species indicate that fishing pressure is potentially having an impact on target species in SWA, which could have negative synergistic effects with climate change. The combined total labrid biomass has increased dramatically, which could drive

wider change to habitat and food webs in the future. From this study it is apparent that tropical labrids are becoming established in the warming areas of SWA.

## LITERATURE CITED

Ackerman J (2004) Geographic variation in size at age of the coral reef fish, *Thalassoma lunare* (Family: Labridae): a contribution to life history theory. Honours thesis, James Cook University, Townsville

Audzijonyte A, Richards A, Stuart-Smith D, Pecl G and others (2020) Fish body sizes change with temperature but not all species shrink with warming. Nat Ecol Evol 4: 809–814

Bennett S, Wernberg T, Bettignies TD, Kendrick G and others (2015a) Canopy interactions and physical stress gradients in subtidal communities. Ecol Lett 18:677–686

Bennett S, Wernberg T, Harvey E, Santana-Garcon J, Saunders B (2015b) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecol Lett 18:714–723

Bennett S, Wernberg T, Connell S, Hobday A, Jonson C, Poloczanska E (2016) The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. Mar Freshw Res 67:47–56

Bianchi C (2007) Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia 580:7–21

Booth D, Bond N, Macreadie P (2011) Detecting range shifts among Australian fishes in response to climate change. Mar Freshw Res 62:1027–1042

Bray DJ (2017) Wrasses, Labridae. In: Fishes of Australia. http://fishesofaustralia.net.au/home/family/106 (accessed 2 January 2018)

Brown H, Gillooly F, Allen P, Savage M, West B (2004) Toward a metabolic theory of ecology. Ecology 85: 1771–1789

Bruno JF, Carr LA, O'Connor MI (2015) Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126–3140

Bryars S, Rogers P, Huveneers C, Payne N, Smith I, Mcdonald B (2012) Small home range in southern Australia's largest resident reef fish, the western blue groper (*Achoerodus gouldii*): implications for adequacy of no-take marine protected areas. Mar Freshw Res 63:552–563

Caputi N, Jackson G, Pearce A (2014) The marine heat wave off Western Australia during the summer of 2010/11 – 2 years on. Fisheries Research Report No. 250. Department of Fisheries, Perth

Cheminée A, Pastor J, Bianchimani O, Thiriet P and others (2017) Juvenile fish assemblages in temperate rocky reefs are shaped by the presence of macro-algae canopy and its three-dimensional structure. Nat Sci Rep 7:14638

Cheung W, Meeuwig J, Feng M, Harvey E and others (2012) Climate-change induced tropicalisation of marine communities in Western Australia. Mar Freshw Res 63: 415–427

Clarke K, Gorley R (2005) PRIMER: getting started with v6. PRIMER-E, Plymouth

Clarke K, Gorley R (2015) PRIMER v7: user manual/tutorial. PRIMER-E, Plymouth

Coleman F, Koenig C, Huntsman G, Musick J and others (2011) Long-lived reef fishes: the grouper–snapper complex. Fisheries 25:14–20

Cossington S, Hesp S, Hall N, Potter I (2010) Growth and reproductive biology of the foxfish *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. J Fish Biol 77:600–626

Coulson P, Hesp A, Hall N, Potter I (2009) The western blue groper (*Achoerodus gouldii*), a protogynous hermaphroditic labrid with exceptional longevity, late maturity, slow growth, and both late maturation and sex change. Fish Bull 107:57–75

Cure K, Hobbs J, Harvey E (2015) High recruitment associated with increased sea temperatures towards the southern range edge of a Western Australian endemic reef fish *Choerodon rubescens* (family Labridae). Environ Biol Fishes 98:1059–1067

Cure K, Hobbs J, Langlois T, Abdo D, Bennett S, Harvey E (2018) Distributional responses to marine heat waves: insights from length frequencies across the geographic range of the endemic reef fish *Choerodon rubescens.* J Mar Biol 165:1–14

Department of Primary Industries and Regional Development (2018) Recreational fishing guide 2017/18. Department of Fisheries, Perth

Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ (2016) Biodiversity enhances reef fish biomass and resistance to climate change. Proc Natl Acad Sci USA 113:6230–6235

Figueira W, Booth D (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Glob Change Biol 16:506–516

Forster J, Hirst A, Atkinson D (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proc Natl Acad Sci USA 109:19310–19314

Fox N, Beckley L (2005) Priority areas for conservation of Western Australian coastal fishes: a comparison of hotspot, biogeographical and complementarity approaches. Biol Conserv 125:399–410

Froese R, Pauly D (2018) FishBase. www.fishbase.org

Goetze J, Bond T, McLean D, Saunders B and others (2019) A field and video analysis guide for diver operated stereo-video. Methods Ecol Evol 10:1083–1090

Harvey E, Shortis M (1995) A system for stereo-video measurement of sub-tidal organisms. Mar Technol Soc J 29: 10–22

Harvey E, Fletcher D, Shortis MR, Kendrick GA (2004) A comparison of underwater visual distance estimates made by SCUBA divers and a stereo-video system: im-

plications for underwater visual census of reef fish abundance. Mar Freshw Res 55:573–580

Harvey E, Goetze J, McLaren B, Langlois T, Shortis M (2010) Influence of range, angle of view, image resolution and image compression on underwater stereo- video measurements: High-definition and broadcast-resolution video cameras compared. Mar Technol Soc J 44:75–85

Harvey ES, Cappo M, Kendrick GA, Mclean DL (2013) Coastal fish assemblages reflect geological and oceanographic gradients within an Australian zootone. PLOS ONE 8:e80955

Hiddink J, Hofstede RT (2008) Climate induced increases in species richness of marine fishes. Glob Change Biol 14: 453–460

Holmes T, Wilson S, Vanderklift M, Babcock R, Fraser M (2012) The role of *Thalassoma lunare* as a predator of juvenile fish on a sub-tropical coral reef. Coral Reefs 31: 1113–1123

Hutchins B (2001) Biodiversity of shallow reef fish assemblages in Western Australia using a rapid censusing technique. Rec West Aust Mus 20:247–270

Kordas RL, Harley CDG, O'Connor MI (2011) Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. J Exp Mar Biol Ecol 400:218–226

Kruschel C, Zubak I, Schultz S (2012) New records of the parrot fish, *Sparisoma cretense*, and the cleaver wrasse, *Xyrichtys novacula*, by visual census in the Southern Adriatic. Ann Ser Hist Nat 22:47–53

Kulbicki M, Mou Tham G, Thollot P, Wantiez L (1993) Length–weight relationships of fish from the lagoon of New Caledonia. Naga 16:26–30

Kulbicki M, Guillemot N, Amand M (2005) A general approach to length–weight relationships for New Caledonian lagoon fishes. Cybium 29:235–252

Langlois TJ, Radford BT, Niel KV, Meeuwig JJ and others (2012b) Consistent abundance distributions of marine fishes in an old, climatically buffered, infertile seascape. Glob Ecol Biogeogr 21:886–897

Last P, White W, Gledhill D, Hobday A, Brown R, Edgar G, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Glob Ecol Biogeogr 20: 58–72

Lek E, Fairclough D, Platell M, Clarke K, Tweedley J, Potter I (2011) To what extent are the dietary compositions of three abundant, co-occurring labrid species different and related to latitude, habitat, body size and season? J Fish Biol 78:1913–1943

Lek E, Fairclough D, Hall N, Hesp S, Potter I (2012) Do the maximum sizes, ages and patterns of growth of three reef-dwelling labrid species at two latitudes differ in a manner conforming to the metabolic theory of ecology? J Fish Biol 81:1936–1962

Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, Grenouillet G (2020) Species better track climate warming in the oceans than on land. Nat Ecol Evol 4: 1044–1059

Levin PS, Hay ME (1996) Responses of temperate reef fishes to alterations in algal structure and species composition. Mar Ecol Prog Ser 134:37–47

Ling SD, Johnson CR, Frusher SD, Ridgway KR (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Natl Acad Sci USA 106: 22341–22345

Macpherson E (2002) Large-scale species-richness gradients in the Atlantic Ocean. Proc R Soc B Biol Sci 269: 1715–1720

McGowran B, Li Q, Cann J, Padley D, Mckirdy D, Shafik S (1997) Biogeographic Impact of the Leeuwin Current in Southern Australia since the Late Middle Eocene. Palaeogeogr Palaeoclimatol Palaeoecol 136:19–40

Morton J, Gladstone W, Hughes J, Stewart J (2008a) Comparison of the life histories of three co-occurring wrasses (Teleostei: Labridae) in coastal waters of south-eastern Australia. Mar Freshw Res 59:560–574

Morton J, Platell M, Gladstone W (2008b) Differences in feeding ecology among three co-occurring species of wrasse (Teleostei: Labridae) on rocky reefs of temperate Australia. J Mar Biol 154:577–592

O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift Food web structure and metabolism. PLOS Biol 7:e1000178

Parker J, Saunders B, Bennett S, DiBattista J, Shalders T, Harvey E (2019) Shifts in Labridae geographical distribution along a unique and dynamic coastline. Divers Distrib 25:1787–1799

Parsons DF, Suthers IM, Cruz DO, Smith JA (2016) Effects of habitat on fish abundance and species composition on temperate rocky reefs. Mar Ecol Prog Ser 561:155–171

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Phillips J (2001) Marine macroalgal biodiversity hotspots: Why is there high species richness and endemism in southern Australian marine benthic flora? Biodivers Conserv 10:1555–1577

Poloczanska E, Brown C, Sydeman W, Kiessling W and others (2013) Global imprint of climate change on marine life. Nat Clim Chang 3:919–925

Poloczanska E, Burrows M, Brown C, Molinos JG and others (2016) Responses of marine organisms to climate change across oceans. J Mar Biol 3:1–21

Pörtner HO, Karl D, Boyd PW, Cheung W and others (2014) Ocean systems. In: Field CB, Barros VR, Dokken DJ, Mach KJ and others (eds) Climate change 2014: impacts, adaptation, and vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change. Cambridge University Press, Cambridge, p 411–484

Robson S, Shortis M, Woodhouse N (2006) Vision measurement system (VMS). Geometric Software, Coburg

Russ GR, Lou DC, Ferreira B (1996) Temporal tracking of a strong cohort in the population of a coral reef fish, the coral trout, (*Plectropomus leopardus*) Serranidae: Epinephelinae, in the central Great Barrier Reef, Australia. Can J Fish Aquat Sci 53:2745–2751

Ryan K, Hall N, Lai E, Smallwood C, Taylor S, Wise B (2015) State-wide survey of boat-based recreational fishing in Western Australia 2013/14. Fisheries Research Report No. 268. Department of Fisheries, Perth

Ryan K, Hall N, Lai E, Smallwood C, Taylor S, Wise B (2017) Statewide survey of boat-based recreational fishing in Western Australia 2015/16. Fisheries Research Report No. 287. Department of Primary Industries and Regional Development, Perth

Saunders BJ, Harvey ES, Kendrick GA (2014) Factors influencing distribution and habitat associations in an endemic group of temperate Western Australian reef

fishes over a latitudinal gradient. Mar Ecol Prog Ser 517:193–208

Seabra R, Wethey D, Santos A, Lima F (2015) Understanding complex biogeographic responses to climate change. Sci Rep 5:12930

Seager J (2014) SeaGIS. www.seagis.com.au

Shalders T, Saunders B, Bennett S, Parker J, Harvey E (2018) Potential climate-mediated changes to the distribution and density of pomacentrid reef fishes in south-western Australia. Mar Ecol Prog Ser 604:223–235

Smith SM, Fox RJ, Donelson JM, Head ML, Booth DJ (2016) Predicting range-shift success potential for tropical marine fishes using external morphology. Biol Lett 12:20160505

Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. Glob Ecol Biogeogr J Macroecol 19:303–316

Stevens G (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240–256

Stuart-Smith RD, Edgar GJ, Bates AE (2017) Thermal limits to the geographic distributions of shallow-water marine species. Nat Ecol Evol 1:1846–1852

Taylor BM, Choat JH (2014) Comparative demography of commercially important parrotfish species from Micronesia. J Fish Biol 84:383–402

Taylor RB, Willis TJ (1998) Relationships amongst length, weight and growth of north-eastern New Zealand reef fishes. Mar Freshw Res 49:255–260

Thackeray SJ, Henrys PA, Hemming D, Bell JR and others (2016) Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245

Truong L, Suthers I, Cruz D, Smith J (2017) Plankton supports the majority of fish biomass on temperate rocky reefs. J Mar Biol 164:1–12

Vergés A, Steinberg P, Hay M, Poore A and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B Biol Sci 281:20140846

Walther GR, Roques A, Hulme PE, Sykes MT and others (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Wernberg T, Russell B, Moore P, Ling S and others (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. J Exp Mar Biol Ecol 400:7–16

Wernberg T, Bennett S, Babcock R, Bettignies T and others (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–172

Western Australian Museum (2018) Wrasses. Australian Museum, Sydney. https://australianmuseum.net.au/wrasses (accessed 3 June 2018)