School of Molecular and Life Science

Geographical and Temporal Changes of Reef Fish (Labridae) Assemblages: A Case Study of South Western Australia.

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Author's Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person, except where due acknowledgment has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

Animal Ethics: The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). The research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number #2014-050.

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Abstract

The main objective of this research was to assess the impact of recent sea surface temperature rise and heat wave disturbance on Labridae assemblages (a conspicuous and diverse family of reef fish) along the South-Western Australian (SWA) coastline between 2006 and 2015. Contemporary global trends of climate change have seen many marine ecosystems experience unprecedented temperature increase and habitat change. The frequency of marine disturbance events is predicted to increase with simultaneous increases in sea surface temperature. However, an understanding of how these disturbances will impact marine habitats and the organisms living within them remains, poorly understood for temperate marine assemblages. South-Western Australia has highly heterogeneous marine habitats with a large number of endemic species. South-Western Australia has recently been recognised as a marine warming hot spot with sea surface temperature and heat wave events predicted to increase in the future, greater than the global average. A marine heatwave in 2011 had broad impacts on the local marine assemblages in SWA.

Abundance data, habitat variables and Sea Temperature (ST) were analysed to determine if the documented changes in sea surface temperature were impacting the assemblage structure, composition and distribution of labrid fishes. Differences in the assemblage structure and distribution of labrids were observed between 2006 and 2015. Warm water labrids were documented in all of the seven regions in 2015 and at locations and reefs where they were either not seen, or rarely seen in 2006. All labrids had increased in abundance, with the exception of three temperate species, two of which were large, slow growing species. Some warm-water labrids that were rarely observed in 2006, had become so pronounced and influential in their respective assemblages in 2015, that in a multivariate regression tree analysis, they were considered the top indicator for their assemblage. While the structure and composition of labrid assemblages changed significantly in all regions, the scale of change was larger in the northern, warmer regions than the cooler regions, with the changes in the marine assemblages mostly being explained by increased ST, physical reef structure and change in kelp cover.

The length frequency distributions and biomass were assessed by climatic affiliation and trophic function to determine if labrids are changing their distributional ranges and successfully establishing outside their previous ranges. It was clear that there was a distinct poleward movement of labrids, with species being observed in areas in 2015 where they were not present in 2006. Many of the warm-water labrids also showed signs of successful establishment, with juvenile, mature female and mature male individuals all being present. The presence of multiple generations of warm-water species suggests that the species are recruiting successfully into regions in 2015 where they did not survive in 2006. Biomass also increased for most species of labrids with the exception of *A. gouldii* and *B. frenchii*. Taken together, the trends seen in this study indicate that these two species are likely decreasing in numbers due to climate change and fishing pressure. Lastly, we have seen the inundation of a new functional group of warm-water grazing herbivores (scarine labrids, or parrotfishes) in the northern warmer regions. Following disturbance caused by climate change, these scarine labrids have shown the capacity to maintain an altered habitat structure and could continue to influence the SWA coastline if they are able to migrate further south.

The data presented in this study supports the pattern of marine assemblages and habitat changing due to increased ST. It also shows that species are moving and establishing poleward, beyond their 2006 ranges. The most significant changes were in the warmer- northern regions of SWA. However, there was still a significant change in the cooler temperate waters. The changes in the SWA labrid population demonstrate their potential as valuable indicator group for the marine assemblage. Through this study on the family Labridae, I have generated a current picture of the SWA marine assemblages and in doing so have created a platform to launch further research to understand the processes and interactions driving change, and to model the impacts of climate change in SWA.

Authors Contributions

Chapter 2. In review. Please see Appendix C for signed author contribution statement

Chapter 2: Parker, J., Saunders, B., Bennett, S., DiBattista, J., Shalders, T., Harvey, E. 2018. A decade of change: Shifts in Labridae geographical distribution along a unique and dynamic coastline. Submitted to the Journal of Diversity and Distributions.

Author contribution: JP wrote and edited the manuscript, analysed and executed the data analysis and the development of figures and tables. JP, ES, BS and SB designed the study. EH and BS contributed to the manuscript, developed concepts and figures, secured funding and provided guidance. BS and SB contributed to raw data analysis. All co-authors reviewed and commented on the manuscript.

Chapter 3. Un-submitted Thesis Chapter

Chapter 3: The successful recruitment and establishment of range-shifting warm-water Labridae in temperate South Western Australia.

Author contribution: JP wrote and edited the manuscript, analysed and executed the data analysis, figures and tables. JP, ES, BS and SB designed the study. EH and BS reviewed and edited the chapter, helped with figure synthesis and provided guidance. BS and SB contributed to raw data analysis. All Supervisors reviewed and commented on the Chapter.

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Table of Contents

List of Figures

List of Tables

List of Abbreviations

BRUV-Baited Remote Underwater stereo-Video

DLI- Dufrêne and Legendre Index

DOV- Diver Operated stereo-Video

GRS- Great Southern Reef

LC- Leeuwin Current

MRT- Multivariate Regression Tree

nMDS- Non-metric Multidimensional scaling

PERMANOVA- Permutational Multivariate Analysis of Variance

ROV- Remote Operated Vehicles

ST- Sea Temperature

SST- Sea Surface Temperature

SWA- South Western Australia

WA- Western Australia

Chapter 1 General Introduction

Photograph: A curious *Achoerodus gouldii* off of Bremer Bay, Western Australia

1.1 Introduction

1.1.1 Trends of changing environment

Global climate change has been considered as one of the most important contemporary drivers of marine ecosystem structure (Seabra et al. 2015). Over recent years, gradual ocean warming has been driving many changes in the chemical and physical properties of marine environments (Poloczanska et al. 2016; Stuart-Smith, Edgar & Bates, 2015). The increase in sea surface temperatures has contributed to an erosion of resilience in marine habitats as key processes are modified, including trophic interactions and recruitment (Bennett et al. 2015b; Duffy et al. 2016; Zarnetske, Skelly & Urban, 2012). Sea temperature and habitat change may ultimately change the structure and functioning of established ecosystems into new novel ones, where historically different species interact (Bennett et al. 2015b; Wernberg et al. 2010; Wernberg et al. 2016). Documenting changes in our marine environments and interpreting these in regards to species distributions, habitat use, diet and reproductive biology of marine species occupying those habitats, is crucial for understanding and managing the future of our marine ecosystems and any potential threats and impacts.

1.1.2 Range shifts

Changes in the distribution and range of marine taxa have been recorded across the globe (Perry et al. 2005; Poloczanska et al. 2013; Verges et al. 2014). Changes in the range of many species, due to increases in sea temperature (ST), have already been recorded for corals (Yamano et al. 2011) and canopy forming macroalgae (Bennett et al. 2015b) that are critical for ecosystem function. The geographic distribution of marine fish is influenced by their tolerance to environmental variables, biotic and abiotic habitat changes, anthropogenic processes, sea surface temperature or a combination of these. Long term exposure to these environmental changes can lead to range expansion of warm-water species at the cooler edge of their range, or cool-water-species range retraction at their warm edge (Sorte et al. 2010).

1.1.3 Western Australia marine habitat

In comparison to other areas around the globe, the coastal marine environment of WA has been described as an ancient, oligotrophic seascape that has over the past 40 million years, via the Leeuwin Current (LC), experienced warm waters flowing poleward (Langlois et al. 2012b; McGowran et al. 1997). The LC elevates water temperatures during the winter and is responsible for the distribution of benthic marine larvae southward along the coast (Cure, 2016; Harvey et al. 2013; Kendrick et al. 2009). Although the geological and oceanographic history of WA has been temporarily stable, geographically WA has a highly heterogeneous coastline with a plethora of marine habitats driven by the gradual North-South gradient in temperature which support tropical coral reefs in the north and temperate algal and seagrass beds in the south (Langlois et al. 2012b). This diversity of habitats creates opportunities for specialisation, resulting in high numbers of marine endemics being recorded in WA, which is recognised as the second richest multi-taxon system in the world (Cheung et al. 2012; Fox & Beckley, 2005). The Southern coastline of WA is part of the Great Southern Reef (GSR), which is a biodiversity hotspot for many taxa and provides substantial socio-economic value to the surrounding communities that depend on this reef system (Bennett et al. 2016).

1.1.4 Recent climatic trends in WA

Similar to the rest of the world, South-Western Australia (SWA) has undergone a gradual increase in ocean temperature (Bennett et al. 2016; Cure et al. 2018; Wernberg et al. 2016). South Western Australia has also recently experienced a large marine heat wave in 2011 (Pearce and Feng, 2013). The heat wave equated to a century’s worth of warming over the space of 10 weeks, driving ST up 2-4 °C and resulting in altered species interactions and loss of macro-algae canopy (Bennett et al. 2015b; Cure et al. 2018; Wernberg et al. 2013).

Marine fish assemblages and the marine environment form a complex, interconnected relationship with one being dependent on the other (Micheil & Halpern, 2005). Recent anthropogenic environmental change however, has resulted in this relationship to become unbalanced in many areas of the marine world. Due to this change, an understanding of how the structural components of the marine habitat influences fish assemblages over temporal and spatial scales is crucial for managing marine habitats and taxa (Harvey et al. 2013). While marine habitat change on marine assemblages has been looked at on smaller spatial scales, recent studies have promoted the need to study marine fish assemblage response to changing environmental variables over large spatial scales (Booth, Bond & Macreadie, 2011; Harvey et al. 2013; Hiddink & Hofstede, 2008; Nye et al. 2009; Perry et al. 2005; Verge´s et al. 2014).

1.1.5 Labridae

Labridae are one of the most abundant and diverse families of reef fish in Australia. In SWA alone there are over 90 species associated with cool-water rocky reefs (Morton, Platell & Gladstone, 2008). Labrids are mostly benthic invertivores, but they fulfil many functional roles, from abundant and large mobile predators which reduce prey numbers and modify rocky reef assemblages, through to herbivorous species that can control algal growth on coral reefs (Lek et al. 2011; Morton, Platell & Gladstone, 2008). Additionally, labrids include many socially, economically and environmentally important species (Bellwood, 1994; Coulson et al. 2009; Cure et al. 2015).

1.1.6 Ecology of cool-water labrids

Cool-water labrids in SWA are for the most part, endemic to either WA or Australia (Hutchins, 2001), and have a large range of sizes representing several functional groups. Cool water labrids in SWA include large, long lived species such as the western blue groper (*Achoerodus gouldii*) and the western foxfish (*Bodianus frenchii*), which can live up to 75 and 80 years respectfully (Bryars et al. 2012; Coleman et al. 2011; Cossington et al. 2010). Similarly, most Labridae are hermaphrodites, starting out as females and changing sex to males with many, species having markedly different appearances between female and male (Lek, et al., 2012; Colman, et al., 2011). Temperate Labridae can have a highly plastic diet, changing as they grow, with species such as *Ophthalmolepis lineolatus* predating on small epifauna on Macrophytes. Other large species such as *A.gouldii*, consume large invertebrates over many years in its home range (Lek, et al., 2012). Temperate Labridae have relatively small home ranges compared to warm-water labrids (Bryars, et al., 2012), and when combined with a slow turnover rate they are exceptionally vulnerable to fishing pressure and changing environment (Bryars, et al., 2012; Cossington, et al., 2011; Coleman, et al., 2011).

1.1.7 Ecology of warm-water labrids

When compared to cool-water labrids, their warm-water counterparts are more diverse in function (Bellwood, 1994). Like cool-water labrids, most warm-water labrids have a very plastic diet. But, they also include Scarine labrids (Parrotfish) some of which are corallivores, and others are functionally herbivorous scrapers or excavators. Recent literature suggests that while many Scarine labrids function as herbivores, they are in fact microphages, which take energy from the consumption of epilithic microbial films (Clements & Choat, 2017). Most tropical species are highly associated with shallow reef systems between 1m and 10m deep (Bellwood, 1994), with most warm-water labrid species having high recruitment compared to their colder water relatives (Cossington et al. 2010; Parmesan, 2006). In combination with their increased spawning potential in warm-water, tropical labrids may have a better tolerance and adaptability to changing environmental variables than cooler water labrids (Domeier & Colin, 1997).

1.1.8 Labridae in the South west of Western Australia

Changes in the distribution of labrids in response to climate change have already been reported in SWA. An unusually high abundance of juvenile *Choerdon rubescens* (baldchin groper) was recorded in 2013, as a result of increased recruitment, following the 2011 marine heatwave (Cure et al. 2015). *Scarus ghobban* (a tropical labrid species) was observed in high abundances at the warm edge of the temperate SWA region. *Scarus ghobban* have had profound impacts, playing a pivotal role in maintaining turf algae dominance in habitat where canopy algae has declined (Bennett et al. 2015b). These members of the Labridae family have shown the capacity to shift their range southward, suggesting that other labrids may have a similar capacity to move and impact ecosystems (Bennett et al. 2015b; Cure et al. 2015).

1.2 Need for further research

Given the recent unprecedented changes experienced by marine ecosystems globally due to climate change, understanding of temporal variability of marine communities is crucial and is an area that is currently understudied (Barrett et al. 2007). Knowledge of temporal variability of marine communities is especially lacking for temperate reef assemblages, which are relatively understudied compared to tropical reef assemblages. In my conceptual model for my thesis (Figure 1:1), I identify the need for research into the composition of the SWA labrid assemblage which is addressed in Chapter 2. Further research is particularly needed to inform the management of SWA, which not only makes up part of the economically important Great Southern Reef, but also has a host of endemic species. In my conceptual model (Figure 1:1) I emphasise that the environment in which this unique marine assemblage occurs is further predicted to change relatively quickly compared to warm-water habitats, due to the east-west orientation of the southern coastline of WA (Wernberg et al. 2016). Despite being one of the most diverse and conspicuous families of marine fish in WA, there is very little quantitative data on the length, abundance and distributions of labrids from south-Western Australia’s shallow reefs. However, while there is a lack of data in SWA, many studies have highlighted the potential use of Labridae as a valuable indicator family for observing the impacts of climate change on marine ecosystems (Cure et al. 2015; Cure et al. 2018; Perry et al. 2005; Verges et al. 2014). Furthermore, labrids have been shown to be an effective surrogate for sub-tropical fish assemblage patterns on reefs in eastern Australia (Malcom & Smith. 2010).

While relatively large sized members of the Labridae family have been found to change their distributions (Cure, 2016), the species most likely to change their distributions and establish successfully are small, fast growing species, which makes up the majority of SWA labrid assemblage (Feary et al. 2014; Perry et al. 2005). In my conceptual model (Figure 1:1) I also identify the importance of investigating species length frequency distributions and life history traits, which I address in Chapter 3. To date, no studies have investigated changes in the geographical distribution or size-frequency distributions of the entire SWA labrid assemblage. In addition, fishing pressure historically has been demonstrated to negatively impact the abundances of some labrid species such as the western blue groper (*Achoerodus gouldii*) and baldchin groper (*Choerodon rubescens*) (Coulson et al. 2009; Johnson, 1982; Ottaway et al., 1987). Recent trends for recreational fishing effort have shown a 15% decrease, but fishing pressure on many labrids has increased, while catch rate for some species such as the western foxfish (*Bodianus frenchii*), has increased almost 50% (Ryan et al. 2013; Ryan et al. 2017). Some labrids may be especially vulnerable to fishing, and evidence of fishing pressure might be apparent in their length frequency distributions.

1.3 Why I conducted this study

South-Western Australian marine assemblages and habitat are changing, and with the predicted increase in disturbance events and ST increase, they are likely to keep changing (Cheung et al. 2012). The geographical layout and location of the SWA coastline is important and ideal for this study, as it has an almost linear decrease in mean ST (Figure App A:1), and a north-south, then west to east orientation. Its marine ecosystems and assemblages are predicted to change relatively rapidly due to its orientation and relatively isolated heterogeneous habitat (Figure 1:1). The orientation will result in limited areas for cool-water species to seek refuge from changing temperatures, potentially leading to extirpation or extinction (Bennett et al. 2016; Wernberg et al. 2016). Broad-scale surveys of SWA were conducted in 2006 (Saunders et al. 2014) prior to the 2011 marine heatwave event. Replication of the 2006 study in 2015 provides an unprecedented opportunity to compare marine assemblages over a large geographic and temporal scale to observe changes over the temporal and geographic scales. I chose the family Labridae as they are a diverse and abundant family that have been used around the globe for climate change studies. They are also functionally diverse, covering many different feeding groups and ecological roles. Additionally, members of the Labridae family have already been found to be influenced along SWA (Bennett et al. 2015b; Cure et al. 2015; Cure et al. 2018). In-depth data on whole family response to climate change in SWA is lacking, especially for a family as functionally diverse and economically and socially important as Labridae. This evidence makes Labridae the ideal family to evaluate how a decade of gradual ocean warming, disturbance events and habitat change has impacted SWA marine species.

The overarching objective of this thesis is to determine how labrids assemblages have changed in response to recent climatic trends over the past 10 years on SWA's temperate reefs (Figure 1:1). I specifically focus on labrid assemblage composition, the species that are most characteristic of those assemblages and how recent climate change has impacted these assemblages (Figure 1:1). I investigate species range shifts along the SWA coastline and whether the patterns in length frequency distributions provide evidence of successful establishment, and finally assess the biomass and functional diversity of shifting species (Figure 1:1).

1.4 Thesis Layout

1.4.1 Thesis map

This thesis is presented in two data chapters (Chapter 2 and Chapter 3), both of which have been written as manuscripts for publication. The implications of the main findings of the two data chapters are synthesised into a general discussion in Chapter 4. As the main data chapters have been prepared for submission, there may be some repetition at the start of each chapter.

1.4.2 Chapter 2

Motivation: Previous studies have found that select members of the Labridae family are influenced by changing environmental variables, however little research has been done on the whole labrid assemblage along the heterogeneous SWA coastline (Figure 1:1). The temperature gradient along the SWA coast makes it ideal for investigating labrid assemblage change over a large geographical area, due to warming temperature trends (Figure 1:1).

In Chapter 2 I present data collected from diver operated stereo-video surveys (DOVs), which were used to record the densities of labrid assemblages in 2015 and compare them to a previous survey of the same design from 2006. I investigate whether there are changes in the labrid assemblage composition and whether the changes (if any) observed in warmer water areas of SWA are of a greater magnitude than for cooler water assemblages. I identify the environmental variables that best explain the patterns in the labrid assemblages and I identify the species that are most indicative of the labrid assemblages at each region and how they define their communities.

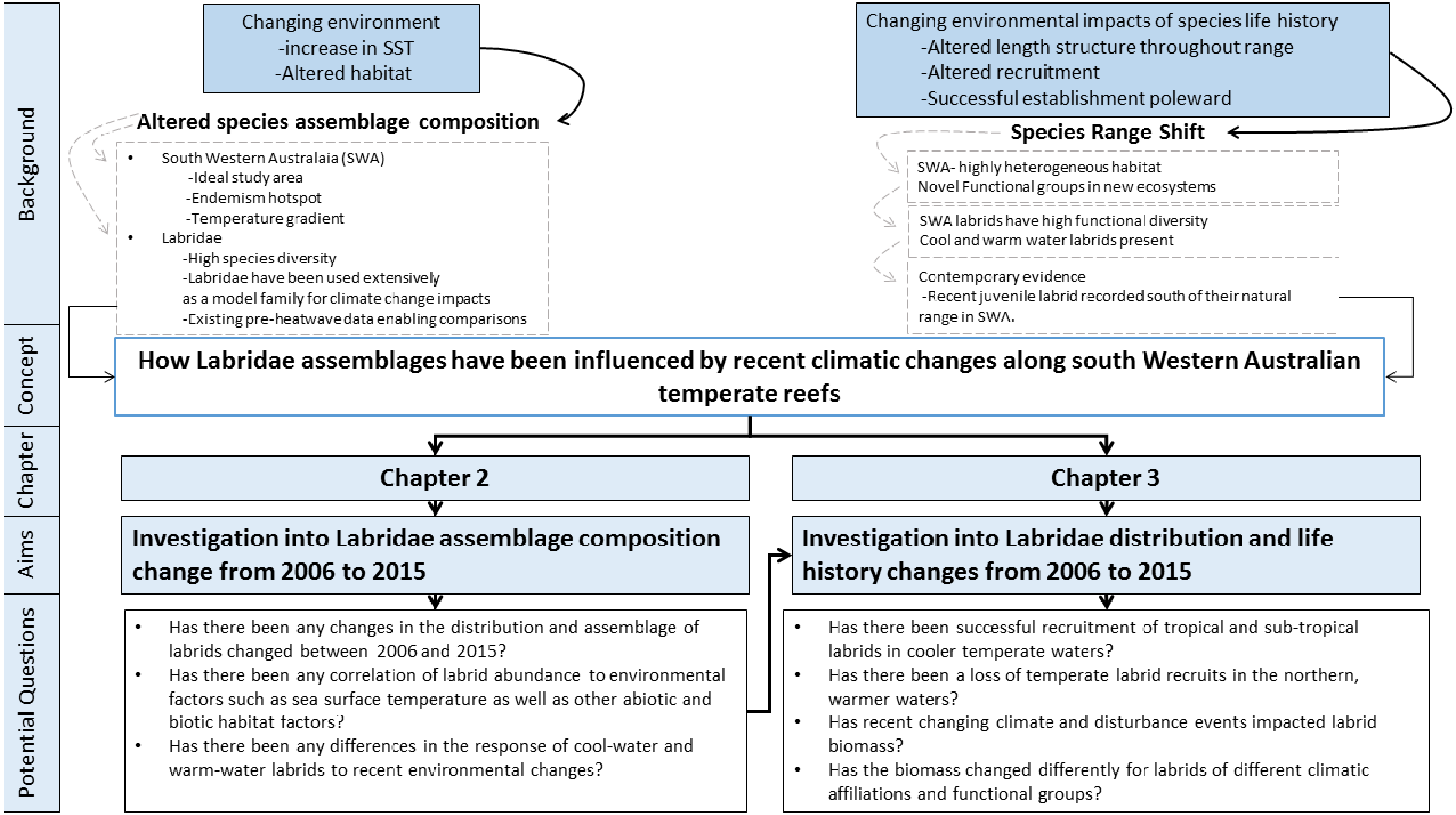
1.4.3 Chapter 3

Motivation: Successful establishment of tropical vagrants have been reported in numerous locations both globally and locally, with studies also recording successful establishment in SWA (Figure 1:1). A few of these species include members from the Labridae family, but no study has looked at the whole assemblage, which includes many small, fast growing species that are more likely to change their distribution successfully, compared to the more commonly studied larger, slow growing species.

In Chapter 3 I analyse the length-frequency structure of the labrids by region, specifically looking at how these have changed from 2006 to 2015. I also look at the proportion of recruits, specifically to identify if representatives of all size classes are present in 2015 in areas where species were not present in 2006. Such patterns would indicate successful establishment. Finally I assess changes in the biomass of tropical, sub-tropical and temperate affiliated labrids between the years 2006 to 2015.

1.4.4 Study area

The study area is south-Western Australia, from Port-Gregory in the north, around the south-west capes region, east to the Recherché archipelago. The study area is further described in the methods of each Chapter.



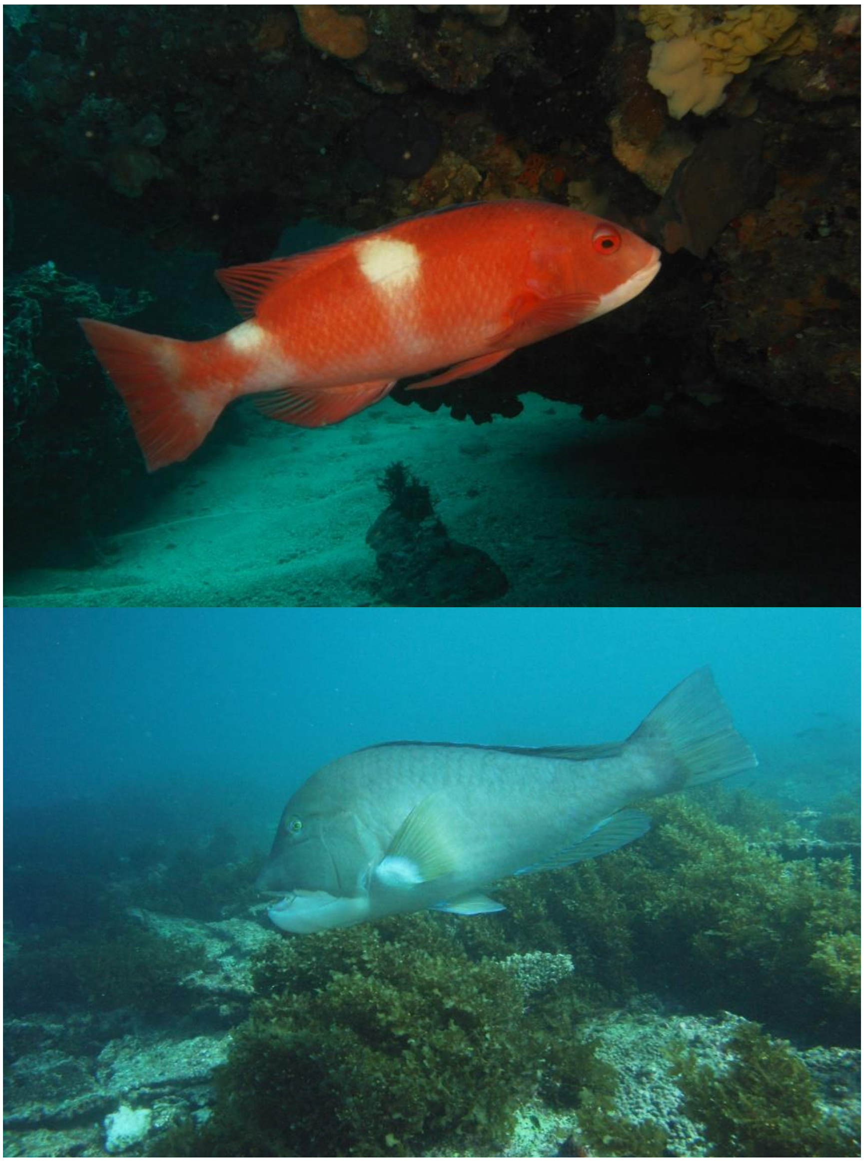
- Has there been any changes in the distribution and assemblage of labrids changed between 2006 and 2015?
- Has there been any correlation of labrid abundance to environmental factors such as sea surface temperature as well as other abiotic and biotic habitat factors?
- Has there been any differences in the response of cool-water and warm-water labrids to recent environmental changes?

- Has there been successful recruitment of tropical and sub-tropical labrids in cooler temperate waters?
- Has there been a loss of temperate labrid recruits in the northern, warmer waters?
- Has recent changing climate and disturbance events impacted labrid biomass?
- Has the biomass changed differently for labrids of different climatic affiliations and functional groups?

Figure 1:1 Conceptual flow diagram summarising the general structure of this thesis and its relative background.

Chapter 2

A decade of change: Shifts in Labridae geographical distribution along a unique and dynamic coastline.



Photograph: Top: *Bodianus frenchii*, Bottom: *Choerodon rubescens*

2.1 Abstract

Aim: Compare the distribution and composition of temperate Labridae (wrasse) assemblages on shallow water coastal reefs between 2006 and 2015, after a decade characterized by gradual ocean warming and severe heat wave disturbance events in South Western Australia.

Location: South-Western Australia from Port Gregory to the Recherché Archipelago.

Methods: Surveys of Labridae fishes were conducted in 2006 and repeated in 2015 across 112 reefs spanning 2000 km of coastline, using diver operated stereo-video systems (stereo-DOVs). We used a hierarchical design with seven regions, four locations in each region, four reef sites in each location and 12 transects in each site.

Results: We found a significant increase in tropical and sub-tropical labrid species in 2015 that were rarely observed in 2006. Three temperate species declined in abundance, which tended to be large slow growing fish, whereas 22 labrid species increased in abundance. There was also a discernible poleward shift in many of the most abundant and characteristic species from 2006 to 2015. The labrid community composition was explained predominantly by sea temperature (ST), physical reef structure and kelp (*Ecklonia radiata*) cover.

Main conclusion: Our study reveals that labrid assemblages associated with the shallow water temperate reefs of South-Western Australia have undergone rapid changes across large geographic distances (almost 2000km); with warm-temperate waters showing the strongest change. However, cool temperate waters on the south coast also showed significant changes in the composition of the labrid assemblages. Previous studies report that this area has remained stable in the face of changing climate. In 2006 across the entire geographic range, the labrid assemblage was largely comprised of temperate species, whereas in 2015 the northern regions were dominated by tropical and sub-tropical labrids.

Key words: Assemblage shifts, Climate change, Endemic fish, Labridae, Marine, Sea surface temperature, South-Western Australia

2.2 Introduction

The geographical distribution and structure of marine fish assemblages are influenced by a range of processes, including abiotic environmental niches (e.g. temperature), habitat availability, anthropogenic pressure (e.g. fishing pressure), or a combination of these factors (Bennett et al. 2015a; Galaiduk et al. 2013; Holbrook et al. 1997; Wendelaar Bonga, 1997). These processes are dynamic across both space and time, providing an opportunity to quantify their role in structuring marine fish assemblages (Booth et al. 2011).

Temperate reef ecosystems sit at the interface of several vectors of rapid global change, making them important environments to quantify the response of biotic communities (Bennett et al. 2016). Climate driven species redistribution, for example, can lead to increased diversity and abundance of tropical species (i.e. tropicalisation) on temperate reef ecosystems, while at the same time, driving the poleward retreat of temperate species (Bennett et al. 2015b; Cheung et al. 2012; Day et al. 2018; Verge´s et al. 2014). This can have important implications for the function of temperate reef ecosystems (Bennett et al. 2015b; Wernberg et al. 2016). Similarly, the proximity of temperate reefs to urbanized coastal areas can put heavy pressure on critical habitats through impacts such as eutrophication (Connell & Russell, 2009). Fish and invertebrate assemblages can also be impacted by habitat loss and fishing pressure, leading to a loss of lower-level interactions and trophic cascades (Ling et al. 2009; Pace et al. 1999; Shears & Babcock, 2002). Understanding how benthic habitat, fish assemblage distribution and habitat use vary across space and time is critical to the spatial management of reef fishes (Gorospe et al., 2018). Benchmarking marine assemblages is important (Dayton et al., 2000), as is re-visiting these benchmarks periodically to gauge changes in marine assemblages over time.

Western Australia (WA) has had an isolated and stable geological history, largely free from mass extinctions and glaciation events throughout the Cenozoic era (66.4 MYA to the present; (Langlois et al. 2012b; Molony et al. 2011; Phillips, 2001)). The coastal marine environment of WA has been described as an ancient oligotrophic seascape, which over the past 40 million years has experienced warm poleward flowing water via the Leeuwin Current (LC) (McGowran et al. 1997). Western Australia is recognised as the second richest multi-taxon centre of endemism in the world, with a variety of marine habitats that contribute to these high rates of endemism (Cheung et al. 2012; Fox & Beckley, 2005).

Tropicalisation of marine communities has been reported in various locations around the world (for example; Perry et al. 2005; Verge´s et al. 2014). South-Western Australia (SWA) has experienced a gradual increase in ocean temperatures, up to two times faster than the global average (Lough & Hobday 2011; Pearce & Feng, 2007). This is exacerbated by the LC, a poleward flowing boundary current along Western Australia’s coastline, resulting in an ocean warming hotspot (Cheung et al. 2012; Kendrick et al. 2009; Vergés et al. 2014). In 2011, a marine heatwave caused an unprecedented range contraction of kelp forests (*Ecklonia radiata*) and the tropicalisation of marine fish, seagrass and invertebrate assemblages across hundreds of kilometers of coastline (Bennett et al. 2015b; Cure et al. 2015; Day et al. 2018; Wernberg et al. 2016; Shalders et al. 2018). In 2015, the kelp canopy along parts of the SWA coastline had still not recovered from the 2011 heatwave event (Bennett et al. 2015b; Wernberg et al. 2016). An increase in the abundance of tropical herbivores (fish families Labridae, Kyphosidae and Siganidae), were also found to be contributing to the maintenance of the canopy free habitats and promoting an alternate turf-dominated state in the northern (warm) limits of the temperate reef distribution in the region (Bennett et al. 2015b; Wernberg et al. 2016).

Previous surveys of shallow water reef fish assemblages from temperate SWA have recorded 128 species of fish from 16 families between Port Gregory in the mid-west to Esperance in the southeast of Western Australia (Hutchins, 2001). Of these, 63 species were endemic to Australia and 20 of these were only observed in Western Australia. Across this region, labrids are a conspicuous family of fish and included 36 species, or 28% of all the fish species counted in Hutchin’s surveys (2001). Of these 36 species, 17 were endemic to Australia, and 8 were Western Australian endemics. To date, reported changes in fish distributions have focused on the west coast of SWA (Tuya, Wernberg & Thomsen, 2009; Wernberg et al., 2013). However, the southern coast of WA provides critical habitat for many reef fishes including 16 labrids which are Western Australian or Australian endemics (Hutchins, 2001). It is important that surveys focusing on the status of reef fish assemblages along the Western Australian coast also incorporate the south coast which is often neglected by researchers (Bennett et al. 2016) due to connectivity (Condie et al. 2005) and fisheries being managed by one agency (Gaughan, D.J. and Santoro, K. (eds) 2018).

The family Labridae (i.e. wrasses) is one of the most speciose families of reef fish, representing a broad range of trophic niches that is not seen in other families (Parenti & Randall, 2000; Westneat & Alfaro, 2005). In SWA, this family includes many commercially important species such as baldchin groper (*Choerodon rubescens*), western foxfish (*Bodianus frenchii*) and western blue groper (*Achoerodus gouldii*) (Coulson et al. 2009; Cure et al. 2015). This group also includes important herbivores and habitat modifiers (Choat et al. 2012; Bennett et al. 2015b). Labrids in SWA have diverse geographies and thermal affinities, whereby almost half of the species are endemic (Hutchins, 2001) and span narrow ranges, while others span broad cosmopolitan distributions across ocean basins. Moreover, they are associated with a wide range of habitats and functional groups, some filling narrow niches, whilst others are generalists. Other conspicuous families such as temperate Pomacentridae have been used effectively as indicators to assess climate mediated changes and ST increase in SWA (Shalders et al., 2018). However, this family is relatively small in SWA compared to Labridae and does not cover as many functional groups. Additionally, Wrasse are often large and a highly conspicuous family. These fish are therefore relatively easy to survey in comparison to some other families such as the small and cryptic Gobiidae and Blenniidae, which, while functionally important (Brandl et al., 2018), are difficult to survey with most video techniques (Thacker, 2008; Thacker & Roje, 2012).

Wrasses have been impacted by ocean warming in both the northern (Bianchi, 2007; Kruschel, Zubak, & Schultz, 2012) and southern hemispheres (Cure et al., 2015). There is also evidence that single species of Labridae are highly sensitive to SST change (Cure et al., 2015) and also are influenced by physical habitat structure (Hutchins, 2001; Tuya, Wernberg & Thomsen, 2009). Furthermore, labrids have been shown to be an effective surrogate for sub-tropical fish assemblage patterns on reefs in eastern Australia (Malcom & Smith. 2010). However, to date most studies have focused on a subset of species (for example Tuya, Wernberg & Thomsen, 2009) and have not examined broad spatio-temporal changes in the full assemblage (Hutchins, 2001; Tuya, Wernberg & Thomsen, 2009). Given their diverse thermal affinities, functional roles and trophic levels, labrids present an ideal model group to evaluate how climatic change may impact fish assemblages on temperate reefs. Also, examining this group along a coastline that has been characterised by environmental stability over evolutionary timescales, but which has experienced a decade of unprecedented and dynamic change, allows a rare opportunity to examine the response of species within leading, central and trailing edge populations of their distribution.

The aims of the study are: (1) to determine if the labrid distribution and assemblage composition has changed between 2006 and 2015, (2) to identify correlations between Labridae assemblage composition and enviromental factors such as ST and reef structure, including coral and macroalgae presence and (3) to identify any differences in the response of cool-water and warm-water labrids to recent environmental changes.

2.3 Methods

2.3.1 Study design

The study took place in SWA covering 2000 km of coastline, across 7 degrees of latitude and 10 degrees of longitude, from Port Gregory to the Recherché Archipelago (Figure.2:1). Seven regions were surveyed, including Geraldton (28.7774° S, 114.6150° E), Jurien Bay (30.2970° S, 115.0420° E), Perth (31.9505° S, 115.8605° E), the Capes (34.2256° S, 115.0609° E), Albany (35.0275° S, 117.8840° E), Bremer Bay (34.3940° S, 119.3760° E) and Esperance (33.8608° S, 121.8896° E. Each region was surveyed with diver operated stereo-video systems (stereo-DOVs) between December 2014 and July 2015. Surveys replicated those conducted by Saunders et al. (2014) between November 2005 and June 2006. To minimise temporal variability, surveys were conducted at similar times of year in 2014/15 and 2005/06. The surveys were conducted in a hierarchical design, with 7 regions, 4 locations in each region, 4 sites in each location and 12 replicate transects in each site, generating a total of 1344 transects for each time period. Each transect was 25 meters long by 5 meters wide and located haphazardly at each reef site. Within each site, shallow, complex rocky reef systems between 4 m and 12 m in depth were targeted. Regions were separated by hundreds of kilometers, Locations were separated by tens of kilometers, Sites were separated by hundreds of meters and Transects were separated by at least 10 meters, following the method of Saunders et al. (2014).

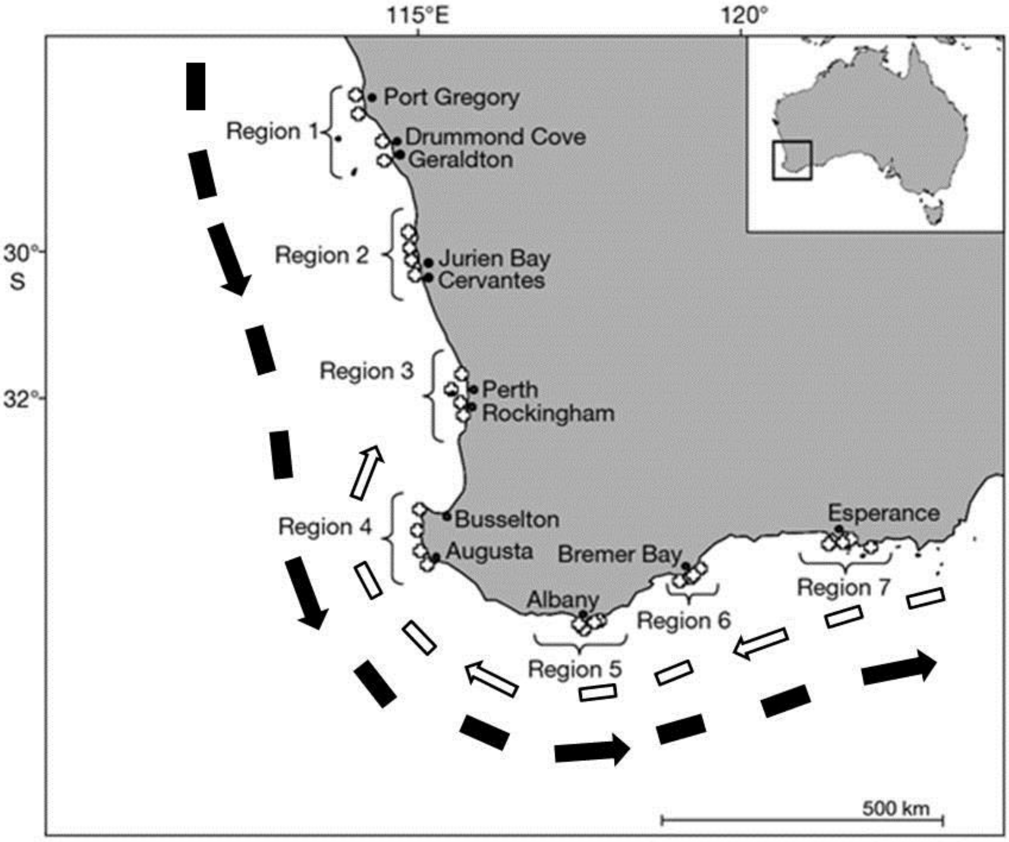


Figure 2:1: Survey area illustrating the seven geographical regions surveyed. Within each region four locations are also illustrated. Leeuwin Current is depicted by the black lines and the Capes Current is indicated by the white lines. The seven geographical regions that were surveyed north-west to south-east were: **1 Geraldton**, **2 Jurien Bay**, **3 Perth**, **4 South-western Capes**, **5 Albany**, **6 Bremer Bay** and **7 Esperance** (Saunders et al. 2014).

2.3.2 Survey Method

In order to record the marine biota and habitat, stereo-DOVs were maneuvered by SCUBA divers along transects. Stereo-DOVs were developed and described by Harvey and Shortis (1995) to eliminate diver identification bias and increase the accuracy and precision of length and distance estimates (Harvey et al. 2004).

In 2006 the stereo-video system utilised two Sony TRV 900 digital video cameras (Saunders et al. 2014), whereas in the 2015 two Sony CX700 video cameras were used. Both sets of cameras were housed in underwater housings. The cameras were then securely mounted 70 cm apart and the cameras were inwardly converged at 8 degrees to maximize the area available for stereo-video measurement (Saunders et al. 2014). Before and after each field trip the stereo-video systems were calibrated using the Vision Measurement System software package for the 2006 surveys (Robson et al. 2006) and CAL software (Seager, 2014) for the 2015 survey, which enabled the accurate calculation of transect dimensions. Two different systems were used because of changing camera models over the ten-year period between surveys. The higher camera resolution associated with the systems used in 14/15 may have resulted in smaller fish (less than 20 mm) being detected, but will not have impacted on counts of larger conspicuous labrids.

2.3.3 Image analysis

2.3.3.1 Abundance quantification

Fish counts from the 2006 footage were analysed using the Vision Measurement System software package (Robson et al. 2006), while the 2015 videos were analysed using the software package Event-Measure (Stereo) (www.seagis.com.au). Both of these packages, although different, allowed an image analyst to identify only Labrids (including subfamily Scarinae) to the lowest taxonomic group (see below). Rules were established within the software which prevented fish that were more than 7 m from the camera or 2.5 m from the centre of the transect line from being counted or measured. Fishes only seen on one camera due to the obstruction of the field of view by substrate or algae were still counted if analysts were confident that the fish was within the transect boundaries.

2.3.3.2 Habitat Analysis

In addition to fish abundance, benthic habitat was also measured and analysed from the stereo-DOV video footage. Habitat was analysed using a Visual Basic program in Microsoft Excel modified from Holmes’s (2005) original design. During each transect, five frames were chosen that were equally spaced. Within each frame we assessed the presence of habitat variables including Reef cover, Reef height, steepness of the sea bed (gentle slope, steep slope), Vertical wall, Overhanging wall, Overhead reef/ cave, Ecklonia cover, Non-Ecklonia canopy cover, Hard coral cover, Foliose presence, Combined turf and seagrass presence. These variables were given a value from 0 to six, with 0 meaning that the variable was not present and six meaning that the habitat was made up of 100% of that variable. These values were then used for geographical analysis and compiled to formulate a measurement at the reef site level, resulting in 60 measurements per 1500m^2 (Saunders et al., 2014).

2.3.3.3 Sea Surface Temperature

The mean ST was determined for each site at the time of each survey using the NOAA Optimum Interpolation sea surface temperature (OISST) (https://www.ncdc.noaa.gov, accessed 6 October 2015). OISST combines satellite data and *in situ* observations to produce a one degree grid. Monthly maximum temperatures were extracted from the corresponding survey areas from the SWA coast. These were then averaged over the year at each region, with 2006, 2011 (year of the biggest marine heat wave) and 2015 plotted to depict the correlation in temperature change over the study time. Furthermore, the minimum and maximum temperatures were averaged at the site level for both 2006 and 2015 for use in the MRT.

2.3.4 Statistical analysis

2.3.4.1 Assemblage

The raw transect assemblage data for the family Labridae was summed to site level (n=4 at each location). Assemblage data was then 4th root transformed to down-weight overly abundant species (Clarke and Gorley, 2015). Patterns in the data were illustrated by an unconstrained nMDS using a zero adjusted Bray-Curtis coefficient in PRIMER 6 on the centroids for each region by year (Clarke & Gorley, 2005). A Bray-Curtis coefficient was used to independently account for joint absences. This however, results in an undefined value when there is a sample with no individuals recorded. To avoid this issue, the zero-adjusted Bray-Curtis coefficient includes a dummy variable with a value of 1 in all samples (Clarke & Gorley, 2005). Using the PERMANOVA+ package in PRIMER 6 (Anderson et al. 2008), a three factor

PERMANOVA was run to determine if there was a significant difference in labrid assemblages among Year, Region and Location. The design included Year (fixed factor, two levels, 2006 and 2015), Region (fixed factor, seven levels) and Location (fixed factor, nested in region, four levels at each region).

Multivariate regression trees (MRT) were used to map the relationships between transformed (4th root) species and environmental data (De'ath, 2002) which included habitat and mean ST for each sampling year at each site. All environmental variables apart from Foliose presence (as it was very similar to turf algae presence (correlation =0.71)) were used in the MRT, with the MRT picking the optimum level of each variable that best explained the split in assemblage structure. The MRT for this study was used to observe how the nodes of the tree have changed from 2006 to 2015 and to identify the environmental drivers of labrid assemblages. The Dufrêne and Legendre index (DLI) was calculated for each species for each node of the tree (Dufrêne & Legendre, 1997). Each species was associated with a node or split in the tree where its maximum DLI value occurred (Clarke and Gorley, 2015). Higher values indicate that the species was more representative of the assemblage. The MRT and species assemblage was illustrated using the ‘Mvpart’ package (De’ath et al. 2005) in R Studio (R Core Team, 2015). The indicator species for the MRT were identified using the Mvpart and ‘Indicspecies Packages’ (De’ath et al. 2005; De Caceres & Jansen, 2016) in R; and were represented graphically. The assemblage DLI values were also represented in tabular format (Table App A: 2).

2.3.4.2 Abundance

To interpret changes in the distributions and abundances, the indicator species with the higher DLI values were explored graphically by plotting the mean abundance of each species for each reef site (1500 m^2) per location at each of the seven geographical regions.

2.4 Results

2.4.1 Geographical changes and patterns of labrid densities.

Across the 2,688 transects that were conducted in 05/06 and 14/15, a total of 17,615 individuals from 25 labrid species were recorded (Table App 2: A), with species richness and diversity higher in 2015 compared to 2006. In 2006, 4,798 individual labrid were recorded from 15 species versus 12,817 from 25 species in 2015. Of these ten newly observed species, six of these were warm temperate or tropical species (*Anampses melanurus*, *Chlorurus sordidus*, *Dotalabrus alleni*, *Scarus frenatus*, *Thalassoma lunare*, *Thalassoma lutescens (*Froese & Pauly 2010; Ackerman, 2004)). *Coris auricularis* was the most abundant species in both 2006 and 2015, with a total of 9,179 individuals present at 79% of sites. However, *Notolabrus parilus*, was more consistently observed in both sampling years than any other species and present at 92% of the sites, but only 2,141 individuals were recorded.

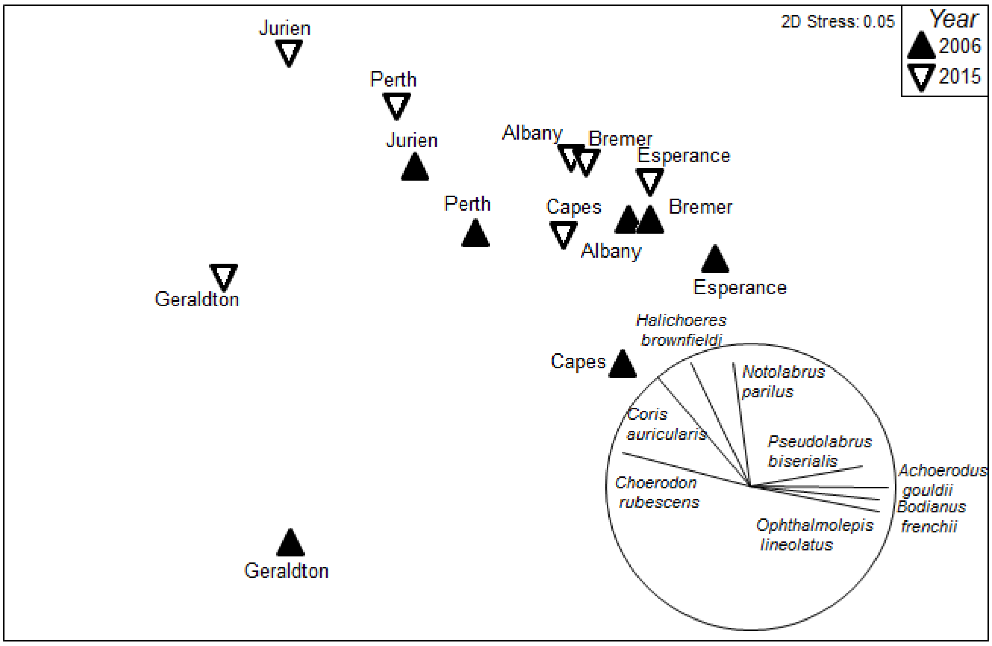


Figure 2:2: nMDS of the centroids of labrid assemblages for all seven regions (Geraldton, Jurien Bay, Perth, Capes, Albany, Bremer Bay and Esperance) in 2006 and 2015, with the most strongly correlated species overlaid as vectors. All differences between region and years were significant at α=0.05.

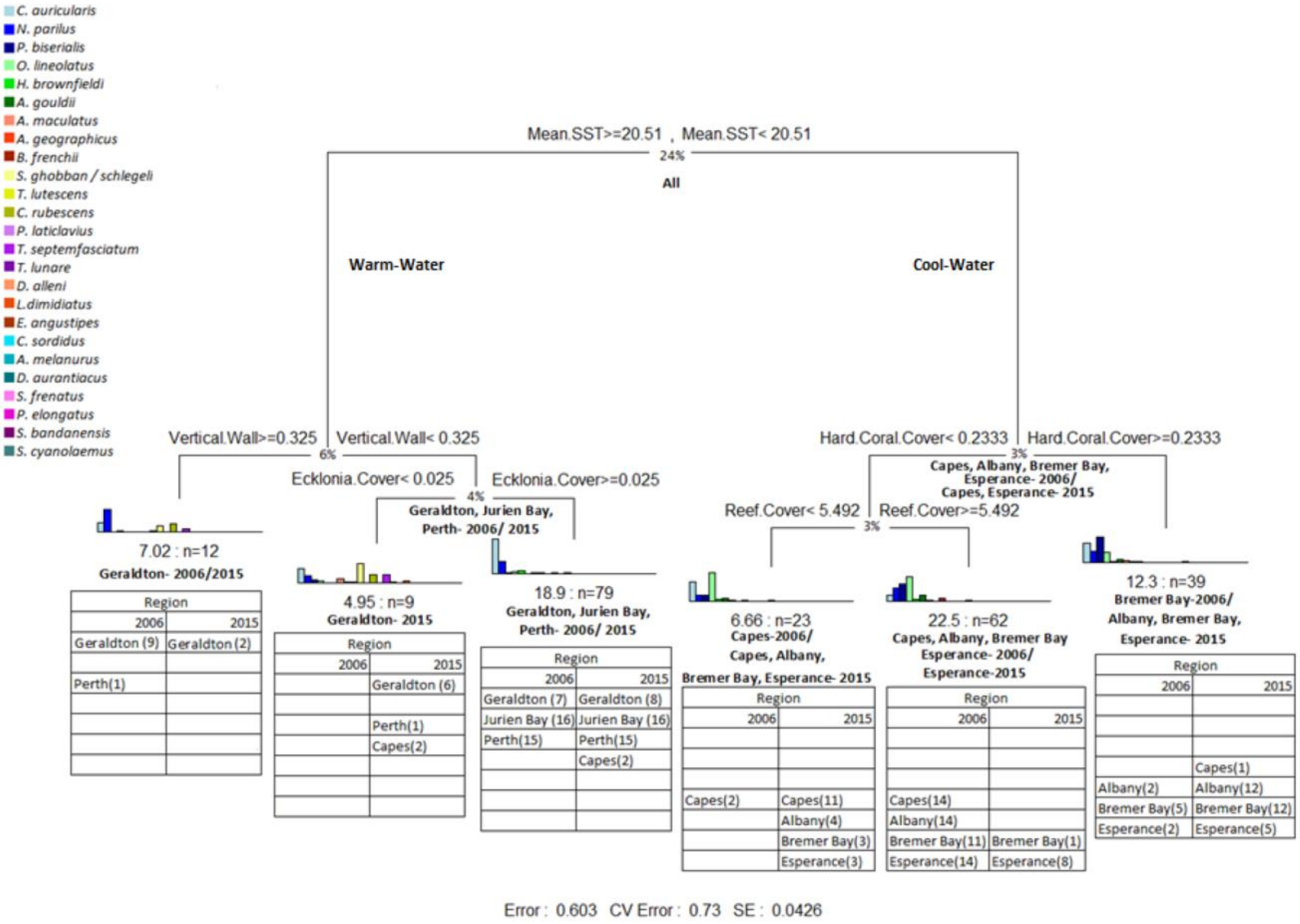
Sea temperature (ST) change was quantified between the 2006 and the 2015 surveys with approximately a 1 C° increase in ST from 2006 to 2015 across all regions with approximately a 4 C° temperature gradient descending from Geraldton to Esperance (Figure App A:1). Labrid assemblages changed between 2006 and 2015 across all regions, albeit with larger assemblage changes observed in the four warmer, western regions, than in the three cooler, southern regions (Figure 2:2). Importantly all Regions showed the same direction of shift, towards the top left of Figure 2:2. This regional difference in assemblage change between years was reflected by a significant interaction between Year, Region and Location on assemblage structure (Table 2:1). Further fine scale analysis by post hoc PERMANOVA test revealed that apart from 3 locations (two in Esperance and one in the Capes), all locations changed significantly from 2006 to 2015 (Table App A:1).

Table 2:1 Three factor PERMANOVA on the fourth root transformed densities of each labrid assemblage across the seven regions. year, region and location are fixed factors. Significant change (at α=0.05) were displayed in bold.

	df	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Year	1	20018	40.5760	**0.0001**	9953
Region	6	1.16E+05	39.1630	**0.0001**	9896
Location	3	3927.5	2.6537	**0.0005**	9935
YearxRegion	6	8327.2	2.8132	**0.0001**	9910
YearxLocation	3	3538.7	2.3910	**0.0030**	9925
RegionxLocation	18	26445	2.9780	**0.0001**	9862
YearxRegionxLocation	18	15100	1.7004	**0.0004**	9852
Res	168	82882			

The MRT identified 11 unique assemblages, including six terminal node assemblages (Figure 2:3). Mean ST from 2006 and 2015 explained the largest amount of variation (24%) in assemblage structure (Figure 2:3). This first split divides the labrid species into warm-water (left) and cool-water (right) assemblages. Within the warm-water assemblages, the secondary and tertiary splits divide assemblages by structural habitat characteristics of the reef, with large rocky formations and kelp (*Ecklonia radiata*) cover, explaining 6% and 3% of the variation in assemblage structure, respectively (Figure 2:3). Within the cool-water assemblages, the secondary and tertiary divisions were also driven by habitat characteristics of the reef, with the cover of hard temperate corals and rocky reef cover each explaining 3% of the variation.

Importantly, the second terminal node was the assemblage with the highest number of warm- affiliated species and was only observed in 2015, thereby representing a novel assemblage, not present in 2006. A similar pattern was observed in the cool-temperate portion of the tree. Most 2006 sites (83%) were found in the 5th terminal node, reflecting broad consistency between cool-water assemblages in 2006. In 2015, however, cool sites were split into nodes 4 and 6, while only a subset of the coolest (i.e. eastern-most) sites remained in the 5th node assemblage. This results in three separate cool-water assemblages in 2015, reflecting the multiple smaller assemblages in the warmer region.



Region	
2006	2015
Geraldton (9)	Geraldton (2)
Perth(1)	

Region	
2006	2015
	Geraldton (6)
	Perth(1)
	Capes(2)

Region	
2006	2015
Geraldton (7)	Geraldton (8)
Jurien Bay (16)	Jurien Bay (16)
Perth(15)	Perth(15)
	Capes(2)

Region	
2006	2015
Capes(2)	Capes(11)
	Albany(4)
	Bremer Bay(3)
	Esperance(3)

Region	
2006	2015
Capes(14)	
Albany(14)	
Bremer Bay(11)	Bremer Bay(1)
Esperance(14)	Esperance(8)

Region	
2006	2015
	Capes(1)
Albany(2)	Albany(12)
Bremer Bay(5)	Bremer Bay(12)
Esperance(2)	Esperance(5)

Figure 2:3 Multivariate regression tree analysis of the abundance of labrid species over the seven sampling regions of the southwest coast. The MRT is constrained by categorical benthic habitat, depth and longitude. At the centre of each split there is a value noting the percent of variation in the species abundance data explained by the split. Overall the tree explained a total of 40% of the variation in the transformed species abundance. Each split (node) is made up of both 2006 and 2015 assemblage data. The regions from each year that are encompassed by each terminal node are listed below them, followed in parentheses '()' by the number of sites from each region that are included in the node.

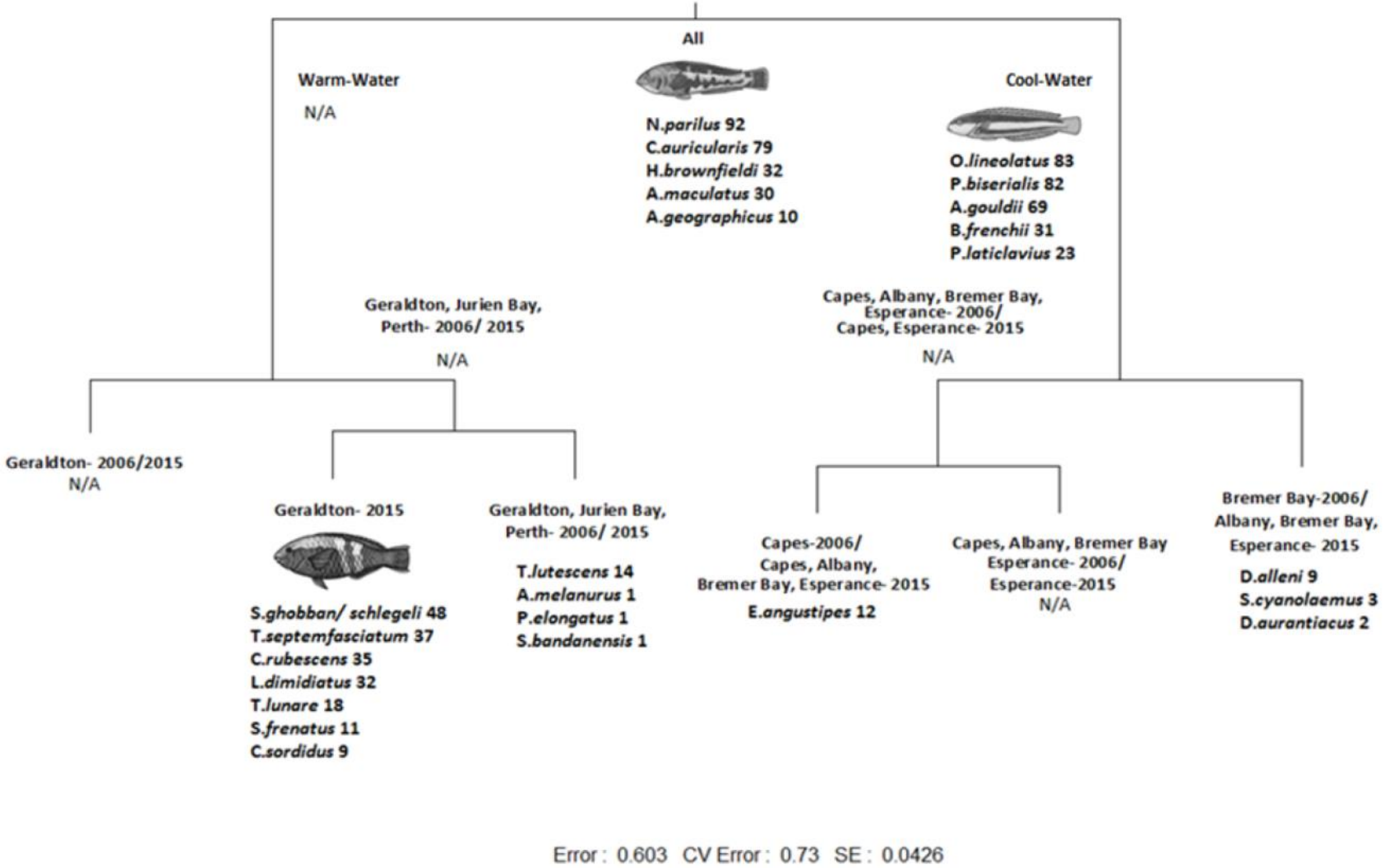


Figure 2:4 Multivariate regression tree analysis of the abundance of labrid species over the seven sampling regions along the southwest coast, depicting the indicator species identified for each terminal node. Each of the species is presented, followed by the Dufrêne and Legendre index (DLI) value. DLI and associated P values are summarized in Table App A:1.

Of the 25 species of labrid observed in this study, five species displayed DLI values > 50, making them 'highly-representative' of assemblage structure (Table App A:2). *Notolabrus parilus* and *Coris auricularis* were highly representative of all assemblages and were associated with the central root node of the MRT (Figure 2:4). *Ophthalmolepis lineolata*, *Pseudolabrus biserialis* and *Achoerodus gouldii* were highly representative of and associated with, the root-node of cool-water assemblages (Figure 2:4). Conversely, indicator species in warm-water sites were associated with terminal node assemblages. The key indicator species in the novel warm-water assemblages in 2015 (node 2) were *Scarus ghobban/schlegeli* and *Scarus frenatus*, three widespread parrotfish species that displayed low abundances in 2006, but were dominant species within the 2015 assemblage (Table App A:3). Similarly, the tropical species *Thalassoma lunare* and *Thalassoma lutescens* were not recorded in 2006, but were common at most warm-water sites (Geraldton, Jurien Bay and Perth) in 2015 (Figure App A:2). Moreover, the warm-water-affiliated tusk fish, *Choerodon rubescens*, was observed approximately 300 km further poleward in 2015 (region 4) than its most southern observation (region 3) in 2006. Of the 25 species of labrid that were observed, only three species (*A. gouldii*, *B. frenchii* and *Pictilabrus laticlavius*) declined in abundance between 2006 and 2015 (Figure App A:2). All three of these species are temperate indicator species, whereas no warm-water species declined over the same period.

2.5 Discussion

Species abundance and richness within labrid fish assemblages increased between 2006 and 2015 across 2000 km of temperate Australian coastline. Within this region the greatest changes were observed in warm-temperate habitats, in comparison to the cool-temperate habitats. This change was driven by an increased abundance of several warm-water affiliated species at the leading, poleward edge of their distribution, with no comparable decline of cool-water affiliated species from within the same assemblages. Changes within labrid assemblages were best explained by ST change and a loss of dominant habitat forming kelp forests, indicated by the primary and secondary splits in the MRT (Figure 2.3). These changes resulted in multiple, less diverse Labridae assemblages along the cooler end of this studies survey range.

2.5.1 Temperature change

One of the most prominent trends observed in our study was the increase in abundance and species richness of wrasses in warm-temperate environments. This pattern was consistent with observed temperature changes along the coastline over the past decade, whereby warm-temperate regions experienced an extreme marine heatwave in 2011, followed by several anomalously warm years in 2012 and 2013. Previous studies have shown that increased temperature promotes the dominance of warmer water species and is a driving factor for temperate marine species to move south towards the poles (Attrill & Power, 2002; Genner et al. 2004; Kirby et al. 2006; Pearce & Feng, 2013; Perry et al. 2005). This poses a severe risk to endemic species that already have their distributions restricted to a relatively small area. If they are continuously pushed towards the poles they could drastically decline in abundance either due the rapidly changing habitat of SWA or by running out of coastline to move into (Wernberg et al., 2011). Observed impacts to wrasse assemblage structure are consistent with previous studies that have demonstrated tropicalisation of fish assemblages following the heatwave (Day et al. 2018; Wernberg et al. 2016), with predicted marine tropicalisation along the WA coast by 2055 (Cheung et al. 2012) and observations of tropicalisation globally (Bennett et al.

2015b; Cure et al. 2015; Kumagai et al. 2018; Raitsos et al., 2010 Shalders et al. 2018; Vergés et al. 2014; Wernberg et al. 2016).

Moreover, the tropical species observed in SWA in 2015 appear to be well established. Recruitment pulses of warm-affiliated reef fishes were observed immediately following the heatwave (Cure et al. 2015), with these cohorts continuing to grow and persist on reefs, four years later (J. Parker, unpublished data). Warm, low variability (~ 4C° annual ST range) conditions facilitate the overwintering of warm-water affiliated species in SWA, likely attributing to the observed tropicalisation effect. *Thalassoma lunare and T. lutescens* species were observed in relatively high numbers in 2015 at three of the seven regions sampled, compared to the species being completely absent in 2006. This warmer, sub-tropical genus has increased its abundance along the coastline of SWA. Many of the individuals observed ranged from around 100 mm to 300 mm in length (J. Parker, unpublished data), with the larger, mature individuals potentially able to reproduce and generate successful progeny. These trends have also been observed in other families such as tropical members of Pomecentridae (*Abudefduf sexfasciatus* and *A. vaigiensis*) (Pearce et al., 2016). These tropical species were observed persisting over multiple years, south of their distributions and occurred at Rottnest Island (a location in this study where *T. lunare* was also observed), however breeding populations were not observed for *A. sexfasciatus* and *A. vaigiensis* (Pearce et al., 2016). This raises the question as to whether this is the same for tropical Labridae such as *T. lunare*.

Not all species that increased in abundance were strictly tropical. *Coris auricularis* is a cosmopolitan species throughout southern and western Australia, ranging from cool-temperate to tropical environments. *Coris auricularis* underwent the largest increase in abundance among the labrid species detected in this study and was an important indicator species for the entire survey area. In addition to its thermal plasticity, *C. auricularis* has high dietary plasticity, with different gut contents recorded throughout its distribution (Lek et al. 2011). Lek et al (2011) concluded that diet availability was not a limiting factor that restricted the range of this species. This plasticity may have enabled *C. auricularis* to adapt quickly to changing conditions along the coast and outcompete more spatially or functionally restricted species of labrids (also see Harvey et al. 2013).

The changes in species abundances emphasises the need for further study on species entire distributions, especially at the margins. Globally it has been observed that warming water increases larval survival at the cooler ends of a species distributions but, it is also detrimental at the warmer end of species ranges (Beaugrand et al., 2012; Cure et al., 2018; Ling et al., 2008; Poloczanska et al., 2016; Solmundsson et al., 2010). This study supports this, with warm-water species becoming more apparent at their cooler margins and moving poleward along the coast, while several cooler water species, declined in abundance at the warm edge of their distributions. The poleward redistribution of species in SWA, however, poses a significant risk, due to the steep temperature gradient and the orientation of the southern coastline. Sparse reef habitat poleward of southern Australia for species to move into and large horizontal distances between isotherms connecting shallow reef habitats, will make it difficult for species to keep pace with warming (Wernberg et al., 2011; Wernberg et al., 2016).

2.5.2 Decline in temperate water species

Labrid assemblages in the cooler temperate regions increased in abundance, but less than warm water regions. In contrast to warm-temperate regions, cool-temperate regions did not experience an extreme heatwave, but instead experienced a more gradual warming over the past decade. Three species were observed to decline between 2006 and 2015, each of which were temperate indicator species (*Pictilabrus laticlavius*, *A. gouldii* and *B. frenchii*). Both *A. gouldii* and *B. frenchii* have declined in the northern, warmer end of their surveyed range. While the exact cause of these species' declines remains unknown, fishing pressure may potentially contribute to the decrease of *B. frenchii* (western foxfish) and *A. gouldii* (western blue groper). Both of these species are susceptible to line and spearfishing (both from free divers and SCUBA divers in WA) (Cossington et al. 2010). Recent fisheries research surveys indicate that overall fishing effort has declined in SWA by almost 15% over 4 years (Ryan et al., 2013; Ryan et al., 2017). However, the catch rate for *B. frenchii* increased by 44% (increasing from 2135 to 3080 individuals caught) from 2011 to 2015 (Ryan et al., 2013; Ryan et al., 2017), indicating that fishing pressure could be having a negative impact on this species. Similarly, despite the general decrease in fishing effort, the catch rate of *A. gouldii* has marginally increased (Ryan et al., 2013; Ryan et al., 2017), indicating continuing fishing pressure on this species. Last et al. (2011) found that many large invertivores, including a very close relative to *A. gouldii*, the eastern blue groper (*Achoerodus viridis*), had experienced considerable range contractions due to the impact of overfishing. Additionally during the 1960’s, populations of *A. gouldii* decreased on the west coast of WA as a result of fishing, eventually resulting in a no take ban from 1973 to 1978 as a conservation measure but it is not known if this amount of time allowed the population to recover as their recovery capacity were not known at the time of the ban (Coulson et al. 2009; Johnson, 1982). These two examples above, highlight that long lived Labridae are vulnerable to overfishing. However, conservations methods such as no-take marine protected areas may have a high positive impact on blue groper as they have a relatively small home range (Bryars et al. 2012), and may be adequate to protect them and other long lived species of wrasse from continued fishing pressure.

A combination of continuing fishing effort and a changing climate may further reduce *A. gouldii* and *B. frenchii* populations, which could lead to localized extinction (Coleman et al. 2011). Rapidly changing environments have been shown to impact long-lived species more severely than fast growing, shorter-lived species (Perry *et al.*, 2005, Hiddink & Hofstede, 2008). This is supported by the results of this study with the two longest-lived species (*A. gouldii* and *B. frenchii*), declining compared to other shorter-lived species. However, a changing climate may not be detrimental to all fished species in the area. For example, *C. rubescens*, a commercially and recreationally fished species, has increased in abundance along the survey area (Cure et al. 2015). The third cool-affiliated species to decline (*P. laticlavius*) is not subject to fishing pressure. Possible drives could be increase in species invasions potentially from the warm-water species immigrating along the SWA coast and either predating on or competing with *P. laticlavius* (Moyle & Williams 1990). Other causes include *P. laticlavius* prey declining or a reduction in their preferred habitat. This is an important question that needs addressing for conservation strategies that aim to mitigate the impacts of climate change on declining temperate species. Indeed more research is required to determine the exact factors and/or causes for the decrease in abundance of *P. laticlavius*.

2.5.3 Habitat loss

The small kelp, *Ecklonia radiata*, is a dominant habitat forming macroalgal species on Australian temperate reefs (Bennett et al. 2016). Similar to other recent studies, we found that an extensive decline in the *E. radiata* canopy was a significant driver of wrasse assemblages in the northern most regions (Bennett et al. 2015; Wernberg et al. 2013; Wernberg et al. 2016). Local food webs in SWA are heavily dependent on the tissues of seagrasses, marine algae and the epifauna that live on them (Bruno & O'Conner, 2005; Lek et al. 2011; Steinberg et al. 1995). Declines in kelp, therefore would be expected to have flow on effects to Labridae species abundance and diversity (Lek et al., 2011), especially given the oligotrophic conditions of the LC and Cresswell Current (Harvey et al. 2013).

In this study, it was observed that the warmer herbivorous species such as *S. ghobban/schlegeli* have extended their range poleward into the now turf algae dominated habitats. Recent studies have shown that Scarine labrids (i.e. parrotfish) graze on the new turf algae and in the process, disturb or consume any potential macroalgae germlings (Bennett et al. 2015b), preventing the ecosystem from recovering to its hitherto kelp dominated state (Bennett et al. 2015b, Wernberg et al. 2016). Parrotfish are now the dominant labrid indicator species in the more northern, macroalgae reduced habitats, demonstrating the impact that these species can have on marine ecosystems and their assemblages.

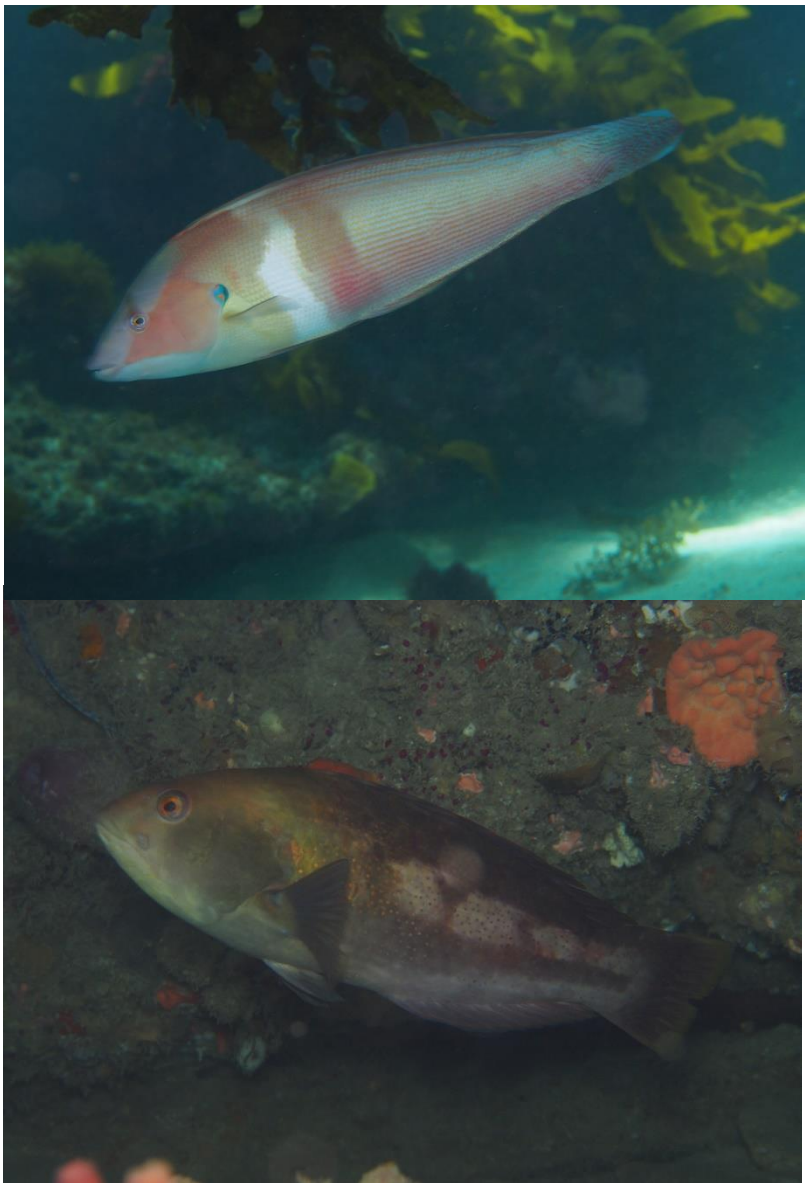
Wernberg et al (2013) found that only eight months after a marine heatwave event in 2011, marine assemblages had significantly changed in the mid-west coast of SWA, but not in the south-west. Our study has found that a significant change in the marine assemblage persists, in the mid-west, four years after this same heatwave and can now also be observed in the south-west fish assemblages too. Labrid assemblages on the cooler south coast, now reflect assemblages more typical of warmer habitats. This was clearly demonstrated by the grouping of the 2015 data into many smaller assemblages, a trait of warm-water ecosystems (Ebeling & Hixon, 1991), in comparison to a single more homogenous assemblage during 2006.

2.5.4 Recommendations and conclusion

Labrid assemblages are currently undergoing change at a rapid rate over a large geographical scale. This study shows that the largest changes have occurred in the warm-temperate west coast of SWA, but that cooler-temperate sites are also experiencing significant change. Identification of the warm-water species moving poleward into cooler waters identifies the areas where potential altered species-habitat interactions may occur. The apparent decline of large bodied cool-water indicator species suggests these species may be vulnerable to further warming and or fishing pressure and should, therefore be a management and conservation priority. Furthermore, the persistence of habitat change after the 2011 marine heatwave highlights the importance of continued monitoring as a precursor of the future trends in SWA. The changes observed in the northern, warmer regions, provide an insight to the possible trajectory of fish assemblages in the cooler temperate regions over the coming decades. Such projections are cause for serious concern, as the southern coastline of Australia is particularly sensitive to warming, due to the stable climatic conditions' species have adapted to over evolutionary time, the orientation of the coastline and lack of adjacent cool-water refuges for species to move into.

Australia's temperate reefs (i.e. the Great Southern Reef) are an economically important ecosystem (Bennett et al. 2016), where labrids are a dominant component of the fish assemblage. We have shown that the distribution, abundance and composition of labrids are changing in response to increased temperatures. Further research on the changes in labrid assemblages should focus on targeting a wider depth range to investigate the possibility of depth refugia (Booth et al. 2011; Langlois et al. 2012a; Wernberg et al. 2011a). This may be especially important for *B. frenchii*, which is a shallow representative of its closer foxfish relatives, which are associated with rocky reefs and kelp forests and can occur up to 340m in depth (Cossington et al. 2010; Gomon, 2001; Kuiter, 1993). In addition, future research could investigate the speed, extent and temporal persistence of changes to fish assemblages in SWA. South-Western Australia's marine environment oscillates between cooler El niño and warmer La niña driven climate cycles (c.f warm El Niño cycles in many tropical regions). Further research to understand the permanency of the ecosystem change over multi-year climatic cycles and to determine whether change is unidirectional or can be reversed, would therefore, be highly valuable.

Chapter 3 The successful recruitment and establishment of range-shifting warm-water Labridae in temperate South Western Australia.



Photograph: Top male *Coris auricularis*- Bottom Male *Notolabrus parilus*

3.1 Introduction

Global climate change, particularly increasing sea temperature (ST), is considered to be one of the most important processes that will shape future marine ecosystems (Seabra et al. 2015). Increasing ST is predicted to have profound impacts on the marine environment including, but not limited to, the disruption of the Autumn and Spring cycle with these disruptions being far larger at the El Niño Sothern Oscillation (ENSO) (Poloczanska et al. 2016; Pörter et al. 2014), and can result in reduction in the body size of marine ectotherms (Foster et al. 2012) and changing marine species distributions (Stuart-Smith, Edgar & Bates, 2017). Increasing ST is thought to be one of the most important contemporary drivers of marine biodiversity, altering the abundance and distribution of marine life and potentially compromising the ecological roles that they provide (Galaiduk et al. 2017; Seabra et al. 2015; Stuart-Smith, Edgar & Bates, 2015). Globally, there has been an increasing trend of marine species shifting to higher latitudes as a result of changing habitat and rising ST (Cure, et al. 2018; Stuart-Smith, Edgar & Bates, 2015). The shift of species ranges into other habitats has the potential to radically change ecosystem functions and composition (Ling, et al. 2008; Stuart-Smith, Edgar & Bates, 2015). Information on marine assemblage composition, species size at maturity and how the changing environment can disrupt these, is essential for determining the potential impacts of recent climate change and warming ST on marine ecosystems and biodiversity (Steffen, et al. 2009, Cure, et al. 2018; Verges, et al. 2014; Poloczanska, et al. 2016; Stuart-Smith, Edgar & Bates, 2015).

3.1.1 Distribution of marine species

Defining a species range is notoriously difficult and it can have an array of implications in ecology (Parmesan, et al. 2005; Sorte, et al. 2010; Seabra, et al. 2015). Sorte et al. (2010, p304) defined a range shift as “the expansion, contraction, or both, of a species’ range whereby a species moves into a new, adjacent location”. Life history traits of individual species, such as growth rate, length at maturity and recruitment, vary across different areas of their range, implying that between, and even within species sub-populations the response to changing ecosystems is variable and plastic (Booth et al. 2011; Poloczanska et al. 2016).

Using only abundance data as a metric to investigate the ecological importance of changes in the distribution of fishes can be misleading, especially for species within a family that may differ in size by several orders of magnitudes (eg a small Western king wrasse of 15cm versus a blue groper of 1.6m in length). Only considering abundance data might lead to the conclusion that frequently occurring small species have a greater functional impact to marine ecosystems than a few larger organisms (Saint-Germain et al. 2007). As a unit of measurement, biomass provides greater insight into the ecological role that species play within an ecosystem (Saint-Germain et al. 2007). Changes in the biomass of a species at a site is linked to the availability of resources and the environmental conditions (Duffy et al. 2016) and is a strong indicator for food-web dynamics and community structure (Brown, 2004; Saint-Germain et al. 2007).

It is thought that higher biomass occurs in communities where species are able to effectively use a larger fraction of the resources present in the habitat, and consequently consumer biomass is controlled by producer biomass (Duffy et al. 2016; O’Connor et al 2009). Temperature has a fundamental control over an organism’s metabolism. When combined with other processes, such as available food, temperature provides a template for biomass production (Duffy et al. 2016). For marine species biomass an increase in temperature can cause a recurring pattern of biomass increasing for a short period of time as species metabolisms increase, followed by a corresponding crash in species biomass as food sources are exhausted, resulting in disrupted trophic linkages in food webs (Duffy et al. 2016; Bruno et al. 2015; Froster et al. 2012; Pörtner et al. 2014). Monitoring changes in biomass is important for predicting the impact of temperature on both marine species and the marine food webs species are present in (O’Connor et al 2009). Biomass can also be used to identify a species’ optimum distribution and it can be used to determine if a species occurring outside its natural range is adapting and using the new resources effectively (Duffy et al. 2016).

3.1.2 Changing ecosystems

Previous research describes 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 die out (Figueira & Booth, 2010; Smith et al. 2016). Recently, warm-water species have been documented recruiting successfully into cooler water ecosystems and over-wintering (surviving the colder winter temperatures) (Bennett et al. 2016; Cure et al. 2018; Smith et al. 2016; Verges et al. 2014). The successful recruitment of warm-water species is seen most often in areas of poleward currents (Cure, et al. 2018; Last, et al. 2011; Verges, et al. 2014). The successful transition of tropical recruits is predicted to become more common as global ST continues to rise and the frequency of disturbance events, such as marine heat waves, increases (Bennett et al. 2016; Cure et al. 2018; Figueira & Booth, 2010; Verges, et al 2014; Wernberg et al. 2016). Unlike some quantitative measures, length distributions can be used to show both the changes in a species abundance, and also its recruitment patterns and the life stages present in a habitat (Cure et al. 2018). Species length distributions can also be used to track cohorts of recruits over time, and help interpret whether juveniles settling into new areas are surviving in waters that are normally thermally limiting (Smith et al. 2016).

3.1.3 Successful establishment

The successful establishment of any species is dependent the ability to survive the physical and chemical changes in the new host habitat, reach maturity and be able to reproduce (Smith et al. 2016; Steffen et al. 2009). Length is important in order to determine successful establishment as it can be used to determine species size at maturity, from which it can be inferred whether the species is surviving over multiple years and if it is reproducing successfully (Smith et al. 2016; Sorte, Williams & Carlton, 2010; Steffen et al. 2009). In addition, the more morphologically distinct the vagrant species is, the more likely it will become successfully established (Smith et al. 2016; Sorte, Williams & Carlton, 2010), implying that vagrants of different functionalities to those species that currently reside in an area may be more likely to successfully establish. Successful establishment of tropical vagrants has been reported in numerous locations both globally (Feary et al. 2014; Figueira & Booth, 2010; Verge´s et al. 2014) and locally in south-Western Australia (SWA) (Bennett et al. 2015a; Bennett et al. 2016; Cure et al. 2018; Smith et al. 2016; Wernberg et al. 2016).

3.1.4 Western Australia

Western Australia’s 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 Western Australian coast (Fox & Beckley, 2005). Furthermore, Western Australia has a great variety of marine habitats which contribute to the high endemism (Fox & Beckley, 2005). The coastal marine system of Western Australia has been described as an old, oligotrophic seascape that has been climatically buffered (Langlois et al. 2012b). The coast of SWA has had a relatively geologically isolated and stable past compared to other areas around the world, being free from mass extinctions and glaciation events throughout the Cainozoic era (from 66.4 million years ago to the present) (Langlois et al. 2012b; Phillips, 2011). 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). The Western Australian coastline is highly variable, with a temperature gradient decreasing linearly southward and then eastward (Langlois et al. 2012b). However, if species are displaced towards the poles, they may be ill adapted to the rapidly changing environment of the SWA coastline (Perry et al. 2005). Species displacement in SWA poses a risk to the species diversity and to the abundance of endemic species, which can have wide reaching impacts, not only to ecosystems, but also to tourism and fisheries (Bennett et al. 2016; Cheung et al. 2012; Harvey et al. 2013; Wernberg et al. 2011a). In 2011 a marine heatwave caused a 2-4 °C increase in ST resulting in the equivalent of a century of warming over a period of three months, causing dynamic habitat change that the habitat is still yet to fully recover (Cure et al. 2018; Wernberg et al. 2016). This disturbance resulted in mass die-offs of marine species and the dynamic shift of temperate ecosystems to more tropical ones, pushing cool-water species further south towards the poles (Cure et al. 2015; Wernberg et al. 2016).

3.1.5 Labridae

The marine fish family Labridae are one of the most diverse, conspicuous and abundant families of rocky reef-associated fish in temperate Australia (Morton et al. 2008; Bray, 2017). The family is comprised of more than 80 genera and 680 species globally, almost half of which occur in Australian waters (Western Australian Museum, 2016). Labrids fulfil many functional roles, they can be abundant, large, mobile predators that play an ecosystem function in reducing prey numbers and modifying rocky reef assemblages, including the western blue and baldchin groper (*Achoerodus gouldii* and *Choerodon rubescens* respectively). Most labrids are classified as benthic invertivores, consuming a wide variety of invertebrates on temperate reefs (Lek et al. 2011; Morton, Platell & Gladstone, 2008b). Labrids also includes many commercially and environmentally important species (Bellwood, 1994; Bennett et al. 2015b; 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 (Atrill & Power, 2002; Bianchi, 2007; Kruschel et al. 2012) and in SWA (Bennett et al. 2015b; Chapter 2; Cure et al. 2018; Wernberg et al. 2016). Although the labrid family is one of the most diverse families in WA (Hutchins, 2001), there is little information on the ranges of distribution of species of labrids in SWA. However, this information is needed to help determine the impacts that gradual climatic change and disturbance events are having in the vulnerable SWA ecosystem (Cure et al. 2018).

3.1.6 Aims

The goal of this research was to understand the response of the SWA labrid populations to environmental changes. We used labrid length frequencies and biomass to determine how the distributions of labrids changed along SWA between 2006 and 2015. Due to an increase in ST we hypothesised that; (1) Labridae distributions moved further south; (2) length frequency structure changed for different Labridae species and functional groups;, (3) functional group biomass has changed by region.

3.2 Method

3.2.1 Site description

This study sampled complex, shallow, rocky reef systems from 4m to 12m in depth across 2000km of coastline from Port Gregory to Recherché Archipelago along the south west of Australia. A total of 7 regions were sampled which included Geraldton, Jurien Bay, Perth, the Capes, Albany, Bremer Bay and Esperance.

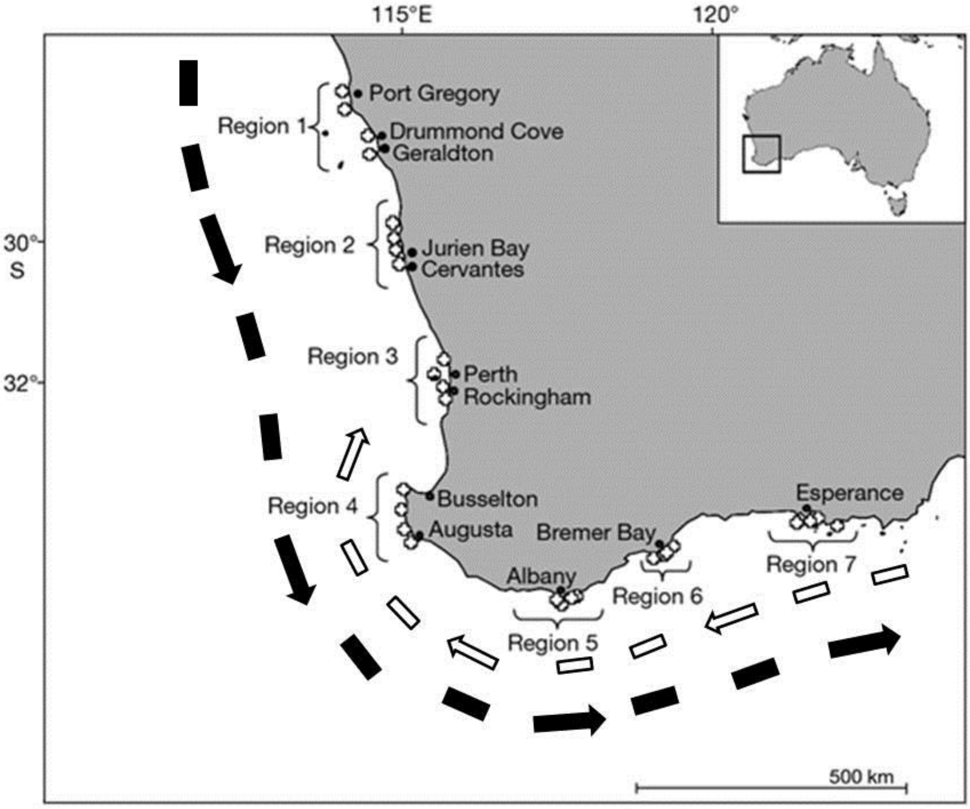


Figure 3:1: Depicts the 7 geographical regions surveyed and the 4 locations (shown by the white crosses) nested within each. Leeuwin Current is depicted by the black lines and the Capes Current is indicated by the white lines. The seven geographical regions that were surveyed from northernmost to southern and around to easternmost where: 1) Geraldton; 2) Jurien Bay; 3) Perth; 4) South-West Capes; 5) Albany; 6) Bremer Bay; and 7) Esperance.

3.2.2 Study design

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. The surveys were conducted in a hierarchical design which consisted of 7 distinct regions, 28 locations, 112 sites and 1344 replicate transects and spans 10 degrees of longitude and 7 degrees of latitude. The distances between the different survey hierarchies differed, following the method of Saunders et al. (2014).

3.2.3 Survey Method

Diver operated Stereo-videos systems (stereo DOVs) were used to record the marine habitat and fish in the survey areas. Two SCUBA divers swam the stereo DOVs along 25m by 5m belt transects. Stereo-DOVs were initially described and developed by Harvey and Shortis (1995) and were used to increase precision and accuracy of species length and distance estimates in comparison to SCUBA diver UVC (Harvey et al. 2004).

The surveys completed in 2005-2006 (Saunders et al. 2014), were recorded using a stereo video system comprised of two Sony TRV 900 digital video cameras. However, in the 2015 surveys the cameras were changed to use newer model (Sony CX700), video cameras which recorded at a higher resolution (1920 x 1080 at 50P rather than 720x560 at 25P). Both sets of cameras were securely mounted 70cm apart, with the cameras tilted inwardly at 8 degrees to optimise the area available for stereo-video analysis (Saunders et al. 2014). Before and after each survey trip, calibration of the stereo-video systems was done using the Vision Measurement System software package for the surveys completed in 2005-2006 (Robson et al. 2006) and CAL (Seager et al. 2014) for the 2015 surveys, allowing highly accurate calculation of the transect dimensions. The cameras recorded a very similar field of view with standardisation of the sampling area achieved through the measurement software. Over the two sampling times (2006 and 2015) two different camera systems were used due to improving technology. The higher camera resolution captured by the systems used in 14/15, potentially resulted in smaller fish (less than 20 mm) being detected, but this will not have impacted on counts of larger, conspicuous labrids.

3.2.4 Image analysis

Image analysis involved identification of fishes to the lowest taxonomic resolution possible. 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 7m from the camera or 2.5m from the centre of the transect line from being measured or counted. If fish were within transects but could not be measured due to obstruction of one camera, they were still counted for abundance.

3.2.5 Statistical analysis

3.2.5.1 Length - Individual

Length frequency analysis was undertaken for a select number of species (*Achoerodus gouldii, Bodianus frenchii, Coris auricularis, Choerdon rubescens, Notolabrus parilus, Ophthalmolepis lineolatus, Scarus ghobban* and *Thalassoma lunare*). These species were selected based on the number of length recordings, the importance of the species identified in Chapter 2 via DLI value and if there was appropriate supporting literature to identify the species growth and life history stages. These species were then graphically represented by length frequency histogram comparing 2006 to 2015 for each region. Most species were protogynous hermaphrodites. Each graph was overlaid with lines indicating size at maturity to female and size at change to male. For the species that were not protogynous hermaphrodites, one line was used to indicate the size at maturity. These sizes were estimated based on a number of sources (Ackerman, 2004; Cossington et al. 2010; Coulson et al. 2009; Cure et al. 2015; Lek et al. 2012; Taylor et al. 2014). All statistical analysis was conducted in Primer 7 or Primer 6 (Clarke & Gorley, 2005; Clarke & Gorley, 2015).

To test for differences in the shapes of length frequency distributions, frequency data were organised into length class bins. The length bins were devised by evenly dividing the subject species maximum length into 12 bins. When length bins were made for the whole assemblage, there were again 12 bins of 100mm intervals. Next a Manhattan distance resemblance matrix was constructed. A two factor PERMANOVA was performed on the resemblance matrix to determine if there was a change (α=0.05) in species length distributions between year (fixed factor, 2 levels) and region (fixed factor, 7 levels). Lastly, a Kolmogorov–Smirnov test was run where a significant interaction, or main test for difference between years was found. Kolmogorov–Smirnov tests were used to compare the shapes of length frequency distributions between years at each region.

3.2.5.2 Length - climate association

Labrid raw length data were grouped into temperate, sub-tropical and tropical climate affiliations (Table App B: 1). These lengths were then organised into bins, pooled at the region level, displayed and analysed as above.

3.2.5.3 Biomass climate association

Biomass (weight in grams) values for individual labrids were calculated from their fork length measurement (Kulbicki et al 1993; Taylor and 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 and Willis 1998) and Fishbase (Froese & Pauly 2010). Some labrids were unable to be measured due to either the heads or tails being obscured by structure, other fish, or the fish not being in a suitable position. If the fish could not be properly measured, the individual was counted and the distance to the fish measured. Furthermore, species with a low precision for their length measurement were rejected during quality control of the raw data. For the individuals that had no length measurements, but that were counted inside the transect area, we multiplied the number counted by the average weight of the same species that occurred in that site. If that was not possible we used the same method, but used the average at a greater replication level (location).

Species biomass was summed into the three climate affiliations at the location level (Table S3:1). Biomass was square root transformed and mean biomass data for each climate affiliation represented graphically. A two factor PERMANOVA on region and year was run to determine any changes in mean biomass.

3.2.5.4 Biomass Trophic level

To enable a finer scale understanding of the changing biomass of the labrid assemblage, labrids within each climate affiliation were further split into five rough trophic groups: Herbivores, Generalist Carnivores, Omnivores, Large Invertivores and Small Invertivores (Table App B: 1). Functional groups were assigned to all labrid species except *Suezichthys cyanolaemus, Eupetrichthys angustipes, Thalassoma septemfasciatum, Halichoeres brownfieldi* and *Pseudojuloides elongatus* as there was no conclusive literature found to define their diet. The mean trophic biomass was then presented graphically with the five trophic categories compared between climate associations and year. A two-factor PERMANOVA (year and region) was done as described above.

Where the PERMANOVA tests indicated statistically significant or close to significant ($\alpha = 0.05$) differences for Factors of year or the interaction of year x region, post-hoc pairwise tests were run to identify the specific regions where particular species biomass had changed over time, this was then indicated on the figures.

3.3 Results

3.3.1 Labrid length analysis

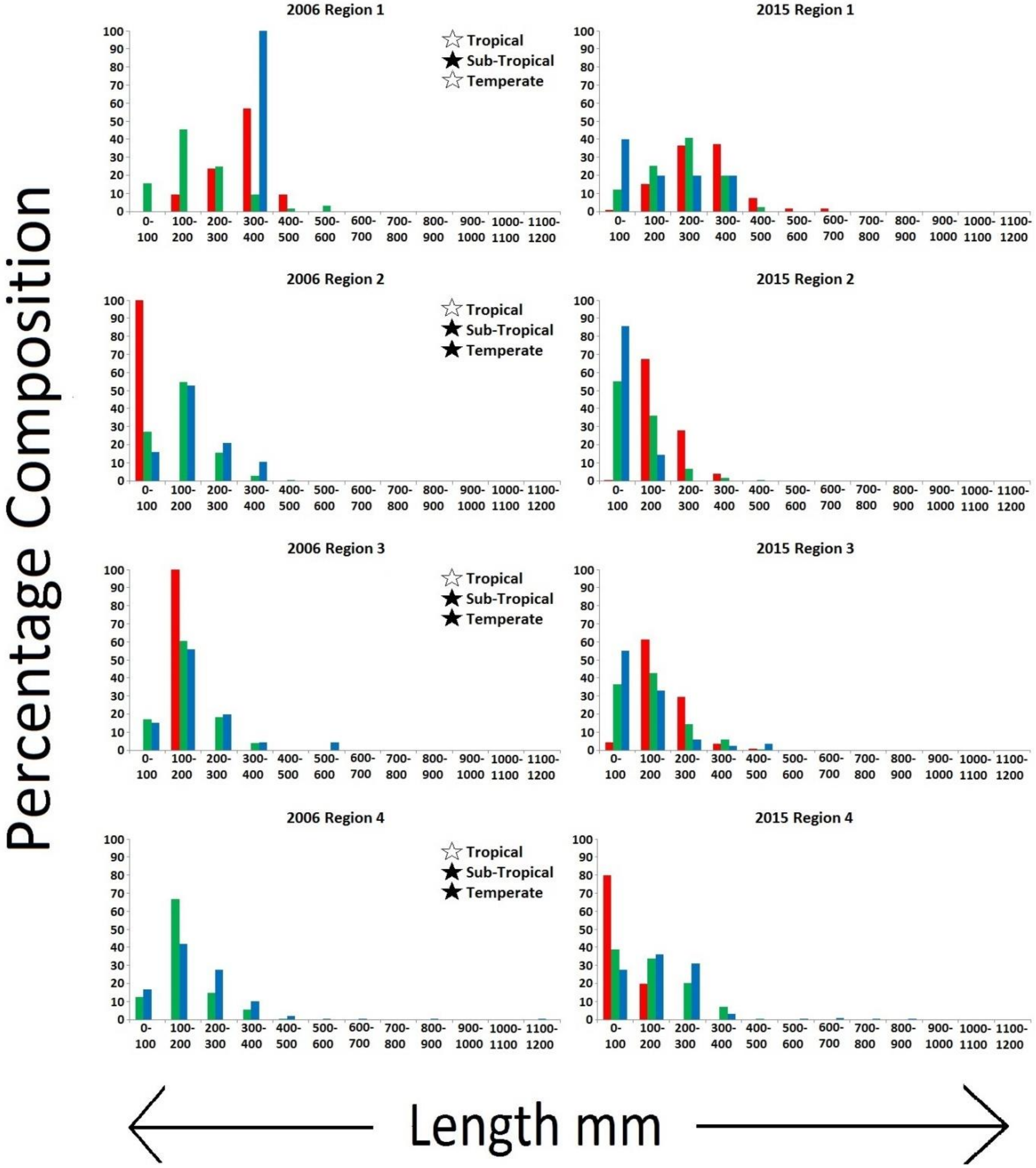
3.3.1.1 Climatic affiliation length distribution

The length frequency of most species changed from 2006 to 2015, both in terms of an increase in the number of individual lengths recorded and an increase in the size of individuals that were present. 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 < 1000mm, Temperate mean = 223mm ± 147 mm SD), but also included small bodied individuals (Figure 3:2). In comparison, tropical species had no very large individuals over 700mm (Figure 3:2), but an overall similar mean length (Tropical mean = 222mm ± 89mm SD) with few fishes measured over 500mm in fork length. Sub-tropical fishes consisted of smaller individuals with over 75% around 1-200mm and none measured over 500mm (Figure 3:2. Mean = 148, ± 81mm SD).

The length frequency distributions of tropical labrids did not change significantly with the interaction of years and region, however there were differences between years (Figure 3:2, Table App B:2). In 2006 tropical associated labrids were only present in the three northern most regions (region 1, region 2 and region 3 (Figure 3:2)) with the length frequency distribution skewed heavily toward smaller size classes (rarely reaching 200mm in fork length). Conversely, in 2015, tropical labrids were observed in all regions with their length distributions demonstrating a more even, less skewed distribution with both smaller and larger individuals present (reaching 300mm in fork length throughout the study area) (Figure 3:2).

Sub-tropical species were persistent in all regions for both 2006 and 2015. The length frequency distributions of Sub-tropical labrids were found to differ significantly by year, region and year×region (Table App B:2), and can be observed in their different length frequency distributions between years at all regions (Figure 3:2), with more small bodied sub-tropical individuals in 2006, whereas in 2015, there was a relatively even distribution in sizes from 100mm to 400mm in fork length.

There was a significant change in temperate species size classes for both year and region (Table App B: 2). While temperate species were present in all regions, larger bodied individuals were present in regions 4-7 in both 2006 and 2015 (Figure 3:2). In general there more recruits and small bodied temperate individuals (0-100mm) in 2015, with the exception of regions 1 and 6 (Figure 3:2).


Percentage Composition
2006 Region 1
☆ Tropical
★ Sub-Tropical
☆ Temperate
2015 Region 1
2006 Region 2
☆ Tropical
★ Sub-Tropical
★ Temperate
2015 Region 2
2006 Region 3
☆ Tropical
★ Sub-Tropical
★ Temperate
2015 Region 3
2006 Region 4
☆ Tropical
★ Sub-Tropical
★ Temperate
2015 Region 4
0 10 20 30 40 50 60 70 80 90 100
0-100 100-200 200-300 300-400 400-500 500-600 600-700 700-800 800-900 900-1000 1000-1100 1100-1200
Length mm

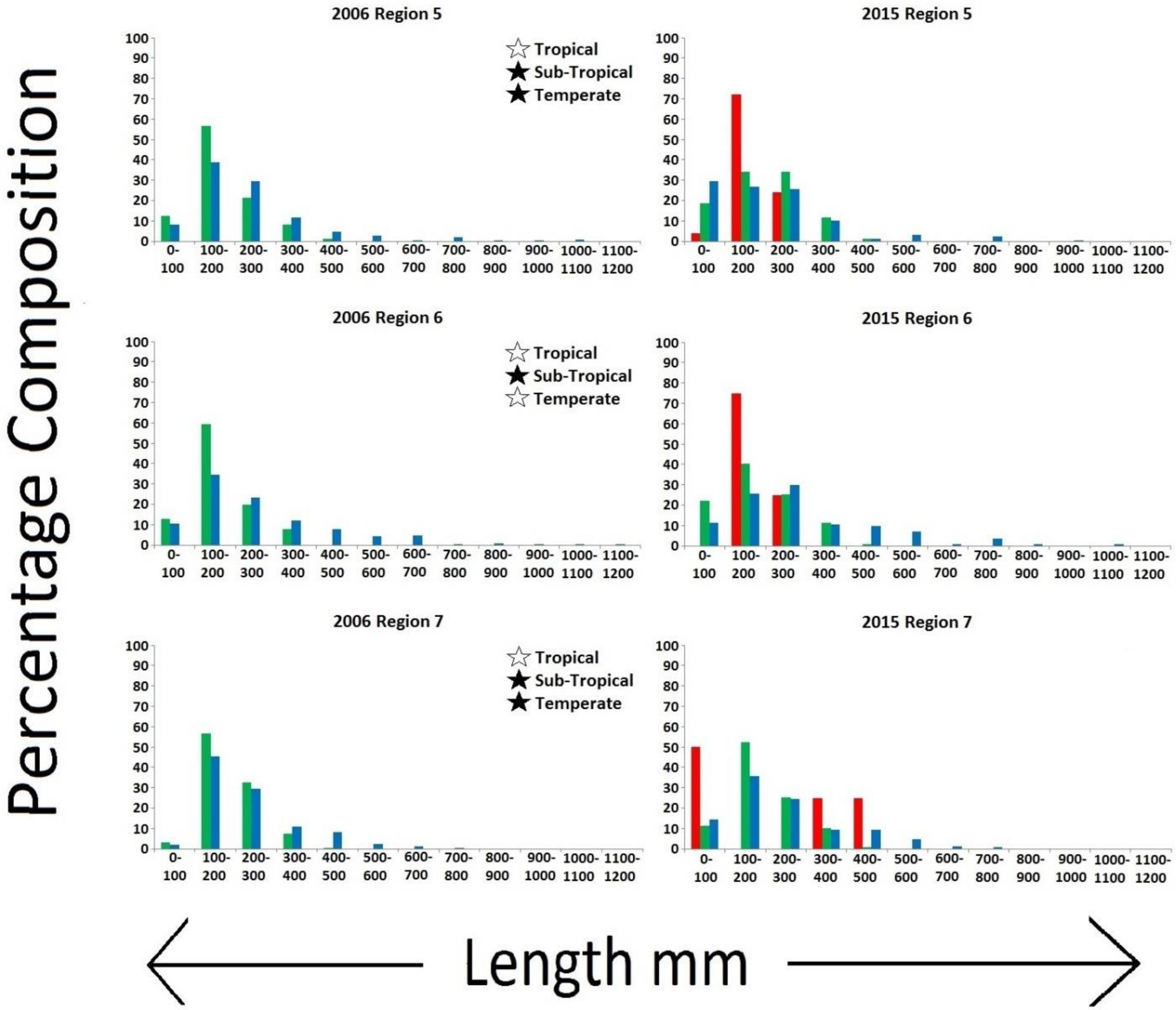


Figure 3:2: length frequency analysis of labrids with Temperate (blue), Sub-tropical (green) and Tropical (red) climate affiliations. Left column represents the 2006 data and the right the 2015 data. Regions 1 to 7 are from warm to cool, north to southeast geographically. Black star indicates statistically significant difference between years (Kolmogorov-Smirnov tests α=0.05).

3.3.1.2 Individual species length distributions

Analysis of the individual species length distributions shows changes between 2006 and 2015 (Appendix B.1). *C. auricularis* (which accounted for 52% of the almost 13,000 length measurements) displayed a substantial increase in the number of length measurements for both juveniles and mature individuals, resulting in a significantly different length distribution in 2015 in all regions when compared to 2006 (Appendix B.1C). Additionally, tropical associated species *Thalassoma lunare* (which was not observed in 2006 (Appendix B.1H)) and *Scarus ghobban* (which consisted of only a few observations in 2006 (Appendix B.1G)), showed a large increase in the numbers of juveniles and larger individuals at the northern (Geraldton, Jurien Bay), warmer regions of this study in 2015. However, only sexually mature females and male *T. lunare* were observed in 2015. *Choerodon rubescens* showed a converse trend, with small juveniles being recorded further south in 2015 (Perth and Capes regions), compared to their 2006 distributions where they were not recorded south of Jurien Bay (Appendix B.1D).

Some opposing trends were also evident, especially in the temperate labrids. *Bodianus frenchii* (Appendix B.1B), which had significant changes in their length structure in the cooler regions (4, 6 and 7) between years (Table App B:2). *Bodianus frenchii* had fewer recruits in cooler water areas in 2015, while larger sexually mature male and female individuals declined in warmer areas (Figure App B:1). Additionally, *A. gouldii* had fewer juveniles observed in region 5 and 6, and its length structure showed a significant change at region 7, which has the lowest temperatures of the study area. For *Ophthalmolepis lineolatus,* significant changes in length frequency distribution were observed (Table App B:1). In the warmer waters, very few individuals were observed in 2015 compared to 2006. At region 3 and region 4 the distributions of *O. lineolatus* were dissimilar in shape in both 2006 and 2015 with *O. lineolatus* at the Capes region in particular, displaying a fuller, more complete size distribution in 2015, driven by large numbers of fish in each size class in both years (Appendix B.1F). Towards the cooler waters of region 6 and region 7, a significant change in *O. lineolatus* length structure was observed, driven by the large juvenile cohort which was present in 2006 but had diminished in 2015.

3.3.2 Labrid biomass

3.3.2.1 Change in biomass with Climatic affiliation

The biomass of all sub-tropical and tropical affiliated species increased at each region from 2006 to 2015 (Figure 3:3). The biomass of tropical labrids increased almost 10-fold from 2006 to 2015 (Table 3:1 and Figure 3:3). Biomass increase was particularly evident in Geraldton, Jurien Bay and Perth where tropical species had a higher biomass than temperate species in 2015. In comparison, tropical species only outweighed temperate species in Geraldton in 2006. Sub-tropical species increased over 300%, with sub-tropical species displaying a binominal distribution in both 2006 and 2015 along SWA. A driver for the sub-tropical biomass pattern was due to lower biomass at the Capes region than at the regions to the north and south. The biomass of temperate affiliated species remained stable over time, in contrast to the significant increase in tropical and sub-tropical biomass.

Table 3:1 PERMANOVA tests for the biomass of labrid with the 3 different climate affiliations (Temperate, Sub-Tropical and Tropical) Bold P-Values indicate significant result (P-value < 0.05).

Tropical

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Year	1	40935	18.766	**0.0001**	9948
Region	6	26736	2.0428	**0.0132**	9911
YearxRegion	6	15144	1.1571	0.2955	9916
Residuals	42	91615			9916

Sub-Tropical

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Year	1	17763	21.161	**0.0001**	9951
Region	6	21814	4.3313	**0.0001**	9942
YearxRegion	6	5835.6	1.1587	0.2967	9914
Residuals	42	35255			

Temperate

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Year	1	1735.7	0.9841	0.4149	9941
Region	6	84277	7.9639	**0.0001**	9908
YearxRegion	6	10376	0.98053	0.4921	9883
Residuals	42	74077			

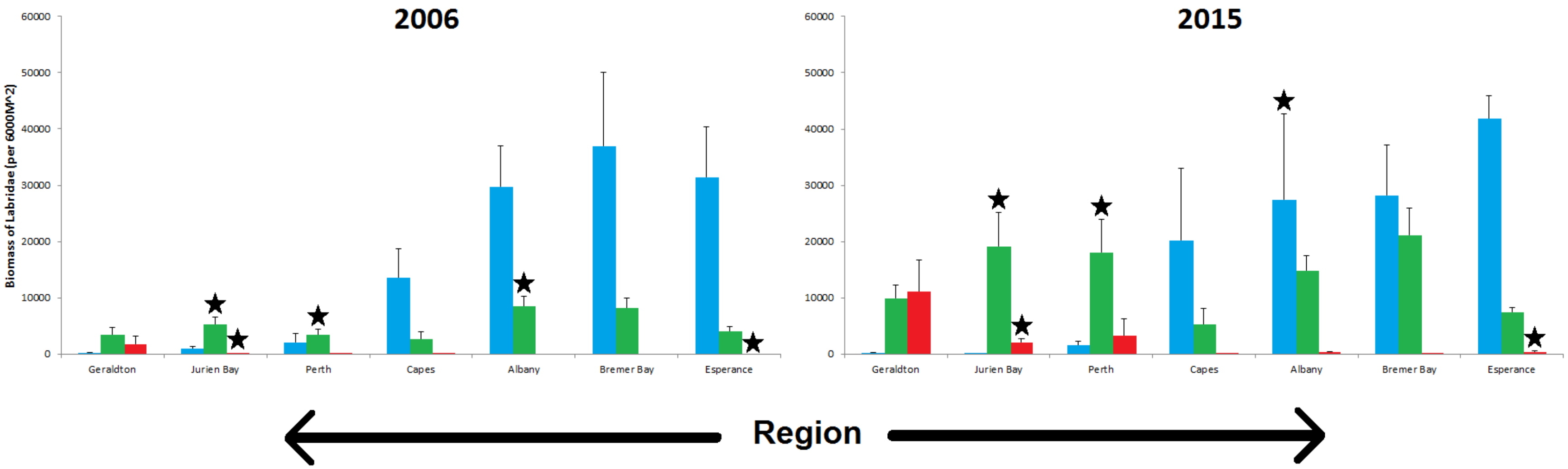


Figure 3:3: Shows two bar plots depicting the biomass of each climatically affiliated species over the study regions of 2006 (Left) and 2015 (Right). Temperate Data is shown in Blue; Sub-Tropical indicated by Green and Tropical species biomass is indicated in Red. . Black stars above certain regions and climate association biomass indicate a significant difference in biomass (P value< 0.05) from the pair wise test for climate association over year by region.

3.3.2.2 Trophic biomass

Each of the broad climatic affiliations were further broken down to five trophic factors (large invertivores, small invertivores, herbivores generalist carnivores and omnivores), to allow more detailed examination of these groups. For tropical labrids there was a significant increase in small invertivores, generalist carnivores and herbivores (with large invertivores and omnivores not recorded for tropical climatic affiliated labrids) over the two years (Figure 3:4). Herbivores dominated the biomass of tropical labrids and were predominantly present in the more northern regions (Figure 3:4). Herbivores were not observed for sub-tropical and temperate labrids. Sub-tropical labrids were mainly omnivores and small invertivores in 2006. However, sub- tropical large invertivores have increased their biomass significantly from 2006 to 2015 with much larger biomass present in the northern most sites in 2015 (Table 3:2 and Figure 3:4). The biomass of sub-tropical omnivores too, increased significantly over years (Table 3:2) at all regions (Figure 3:4). The binominal distribution pattern in sub-tropical labrids (Figure 3:3), is mainly due to the distribution of biomass of sub-tropical omnivores (Figure 3:4). The biomass of generalist carnivores for sub-tropical labrids also increased significantly, being very low or absent in 2006, whereas in 2015 greater biomass was recorded in the northern most regions (Table 3:2 and Figure 3:4). Lastly, the biomass of temperate affiliated species was dominated by large invertivores, but was generally consistent over time (Figure 3:4). The exception was the biomass of temperate small invertivores, which significantly increased between years (Table 3:2). However, temperate small invertivores made up only a very small proportion of the temperate labrid biomass (Figure 3:4).

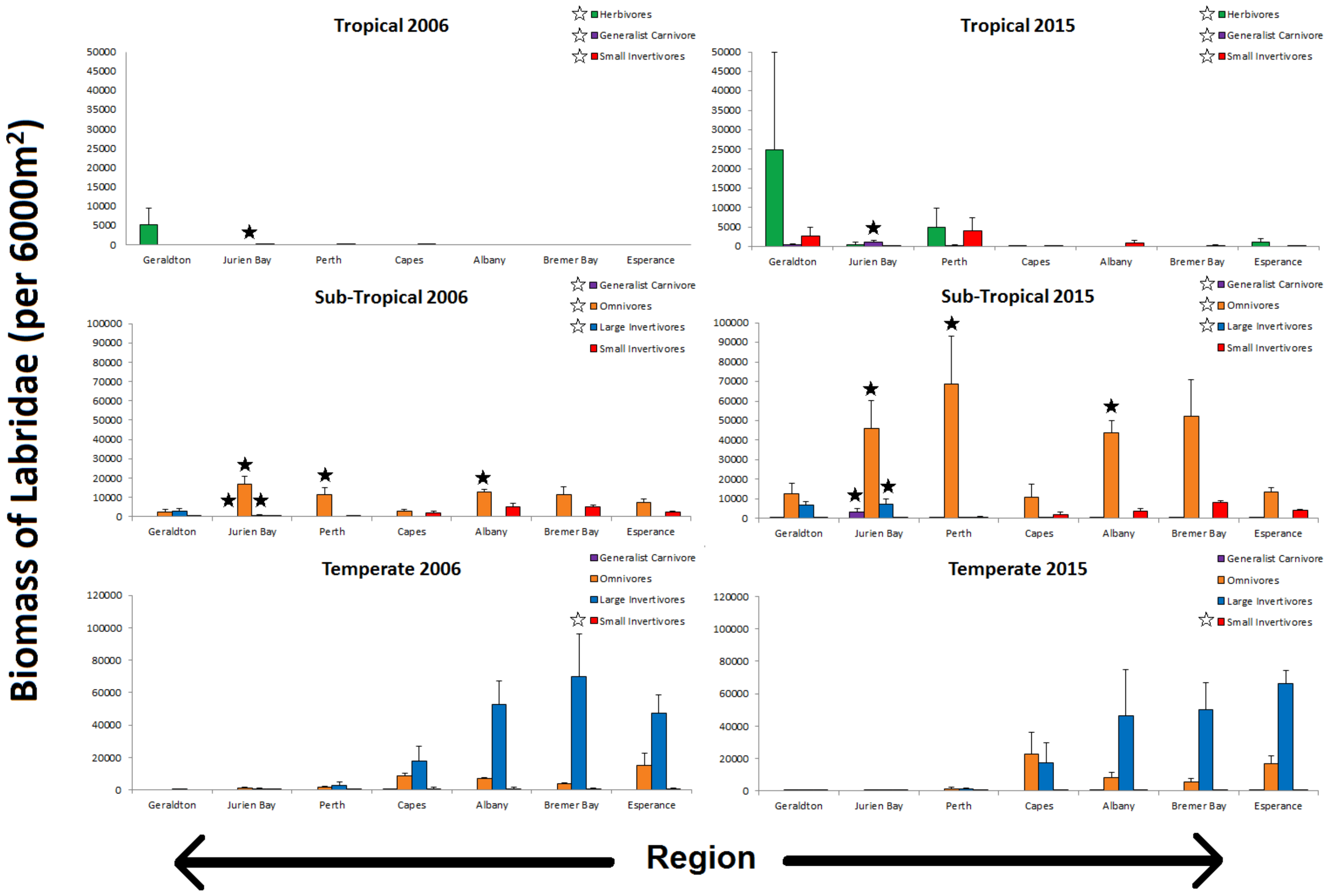


Figure 3:4: Biomass of the five different trophic levels of labrids. Each trophic biomass is associated with either Tropical, Sub-Tropical or Temperate climatic affiliations. The five tropic levels are Herbivores (🟩), Generalist Carnivores (🟪) Small Invertivores (🟥), Large Invertivores (🟦) and Omnivore (🟧). Where a PERMANOVA test was significant between years (α>0.05) a white star was used to indicate this on the figure. Where there was a significant Pairwise test between year × Region a black star was placed over that region and functional group.

Table 3:2 Results of PERMANOVA tests of the labrid biomass of the three climate affiliated categories split into a further five trophic classifications (Herbivores, Large invertivores Omnivores, Generalist Carnivores and Small Invertivores) over the seven regions sampled encompassing both years. Bold P-Values indicate significant result (P-value < 0.05).

Source	df	SS	Pseudo-F	P(perm)	Unique perms
Tropical Generalist Carnivore					
Year	1	5604.5	22.913	<**0.001**	9932
Region	6	9345.2	6.368	<**0.001**	9949
YearxRegion	6	9345.2	6.368	<**0.001**	9954
Res	42	10273			
Tropical Herbivores					
Year	1	6808.3	10.063	**0.002**	9931
Region	6	21557	5.311	<**0.001**	9941
YearxRegion	6	3988.7	0.983	0.449	9955
Res	42	28414			
Tropical Small Invertivores					
Year	1	14086	17.947	**0.001**	9932
Region	6	6023	1.279	0.27	9944
YearxRegion	6	4891.1	1.039	0.41	9940
Res	42	32965			
Sub-Tropical Generalist Carnivore					
Year	1	9257.8	23.865	<**0.001**	9930
Region	6	7125.8	3.062	**0.001**	9946
YearxRegion	6	7125.8	3.062	**0.001**	9952
Res	42	16293			
Sub-Tropical Large Invertivores					
Year	1	5433	10.808	**0.001**	9916
Region	6	40236	13.34	<**0.001**	9940
YearxRegion	6	4995.8	1.656	0.137	9934
Res	42	21113			
Sub-Tropical Omnivores					
Year	1	2549.8	27.456	<**0.001**	9931
Region	6	3639.4	6.532	<**0.001**	9944
YearxRegion	6	397.93	0.714	0.668	9945
Res	42	3900.5			
Sub-Tropical Small Invertivores					
Year	1	90.073	0.233	0.763	9948
Region	6	34321	14.783	<**0.001**	9940
YearxRegion	6	951.48	0.41	0.937	9927
Res	42	16252			

Source	df	SS	Pseudo-F	P(perm)	Unique perms
Temperate Generalist Carnivore					
Year	1	70.234	0.526	0.481	9905
Region	6	544.48	0.68	0.685	9929
YearxRegion	6	863.8	1.079	0.409	9932
Res	42	5604.2			
Temperate Large Invertivores					
Year	1	168.16	0.189	0.759	9914
Region	6	53006	9.949	**<0.001**	9930
YearxRegion	6	3795.7	0.712	0.669	9958
Res	42	37293			
Temperate Omnivores					
Year	1	293.93	0.918	0.39	9954
Region	6	46211	24.047	**<0.001**	9938
YearxRegion	6	5048.7	2.627	0.009	9948
Res	42	13452			
Temperate Small Invertivores					
Year	1	6975	10.211	**0.002**	9916
Region	6	11574	2.824	**0.02**	9936
YearxRegion	6	3721.7	0.908	0.507	9945
Res	42	28690			

3.4 Discussion

3.4.1 Naturalisation / establishing populations

The results found that tropicalisation not only affects the marine community structure in terms of abundance of organisms (Bennett et al. 2016; Wernberg et al. 2016), it also impacts length frequency and biomass. Tropical affiliated species have undergone a significant change in SWA. A range of warm-water species including the *Thalassoma* genus, *S. ghobban C. auricularis* and *C. rubescens* had juveniles, mature females and males present further south of their observed distributions in 2006. Sub-tropical species have changed significantly at each region over the 10 year sample time resulting in a more stable and even length frequency structure in 2015 compared to 2006. These patterns meet the assumptions of successful establishment (Smith et al 2016). Between 2006 and 2015 the warming trend in ST has allowed new species to emigrate and expand their range (*sensu* Walther et al. 2009). Tropical species in SWA that were rarely observed in 2006, appear to have established multiple generations of individuals, suggesting that they are able to survive the colder winter temperatures further south of their previous distribution. This pattern is supported by previous reports of *C. rubescens* successfully establishing itself south of its previously recorded range (Cure et al. 2015; Cure et al. 2018).

When biomass was taken into account, it was obvious that not only was the length frequency of tropical fish more even in 2015, but the biomass of tropical affiliated herbivores far outnumbered any other functional group in the northern areas. Tropical herbivores were dominated by the grazing parrot fish *S. ghobban* (Bellwood & Choat, 1990; Bennett et al. 2015b). The establishment of tropical grazers, a completely new functional group for SWA labrids, has been assisted by the rapid die off of canopy macroalgae and it being succeeded by turf algae, which is the primary food source of the tropical grazers (Bennett et al. 2015b). This trend could continue if changes in algae continue further down the coast. Biomass and number of length measurements can be used together to interpret patterns such as the decrease in sub-tropical labrid (which are dominated by sub-tropical omnivores) biomass at the Capes region. Here, the biomass and number of length measurements for *C. auricularis* is anomalously low. Although *C. auricularis* appears to be establishing along the whole SWA coastline, some unknown factors are keeping numbers low in the Capes region. These could include competition with other species, but it is likely that the environment at the Capes does not support them as well as the environments at other regions. Marine habitats in the Capes region are highly exposed and abundances of many fish species are lower than elsewhere along SWA shallow reefs (e.g. Saunders et al. 2014). Overall, the patterns observed in the study suggest that both tropical and sub-tropical affiliated labrids are becoming established further south of their endemic ranges, including the establishment of completely new functional groups.

3.4.2 Overall increase in biomass

One of the most important findings is the large increase in labrid biomass. Increasing temperature can lead to an increase in producer biomass and/or an increase in consumer biomass relative to producer biomass (O’Connor et al. 2009). The increase in biomass could also be driven by the increase in warm-water species immigrating into cooler ecosystems (Hiddink & Hofstede, 2008; Macpherson, 2002). The increase in species biomass observed in this study was due to a greater density of individuals and not an increase in individual size. This concept is supported by the increase in abundance patterns reported in Chapter 2 and further supported by previous research (O’Connor et al. 2009). Increase in species densities may indicate an increase in productivity and turnover in the system, as a result of decreased canopy cover (Steneck & Dethier 1994). Turfing algae, which has replaced canopy macroalgae in some areas, has a higher productivity and turnover in comparison to *Ecklonia radiata* kelp, which may allow more energy to enter the system, increasing its carrying capacity (Klumpp & McKinnon 1989; Steneck & Dethier 1994). However, increase in species densities and biomass might only be an initial trend, in response to an increase in primary productivity. Generally increases in species biomass, consumption and diversity eventually reach a limit and decline dramatically, potentially culminating in reduced population density in the long term, due to intraspecific competition (Bruno et al. 2015; O’Connor et al. 2009). Changing biomass is normally a dynamic process (O’Connor et al. 2009), stressing the need for further temporal replication of the survey. The vast increase in labrid biomass could have far reaching impacts on an environment that may not have the resources or processes to carry it. Consequences could include increasing competition for resources with other species (including non-labrids), altered spawning times and trophic mismatch (Bruno et al. 2015; O'Connor et al. 2009).

3.4.3 Vulnerable temperate species

Unlike the tropical and sub-tropical affiliations, temperate species have remained relatively stable between 2006 and 2015. Although they are not declining in biomass, temperate species have previously been found to have a reduced resilience to changing conditions in their relatively stable environments (Bryers et al. 2012; Coleman et al. 2011). Long lived species such as *A. gouldii* and *B. frenchii* are especially vulnerable to a changing environment and temperature increase, due to them being secondary consumers, their long life cycles, their relatively small home ranges and that they take significantly longer to adapt to change (Bryers et al. 2012; Coleman et al. 2011; Coulson et al. 2009; Hiddink & Hofstede, 2008; Perry et al. 2005; Thackeray et al. 2016). This idea is supported by similar observations in another family of long-lived, territorial, temperate damsel fishes in SWA, where the distribution of cooler water Pomacentridae has not changed over time (Shalders et al. 2018). Cool-water species are further 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, leading to potential rapid decline in their numbers and even lead to expiration or extinction (Bennett et al. 2016; Chapter 2; 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 recreational fishing effort along SWA from 2013 to 2016 (Ryan et al. 2013; Ryan et al. 2017). However, the catch rate of *B. frenchii* has increased almost 50% and *A. gouldii* has also increased despite the decline in fishing pressure (Ryan et al. 2013; Ryan et al. 2017). The increase catch rate of *A. gouldii* and *B. frenchii* could be due to increase in their abundance or more effective fishing equipment. However, Chapter 2 saw a decline in *A .gouldii* and *B. frenchii*. While the length frequency analysis for *A. gouldii* illustrated a clear drop in presence of individuals over the size of 500mm-600mm in 2015. With the minimum catchable size limit for *A. gouldii* being 500mm (Department of Primary Industries and Regional Development, 2018), it’s probable that fishing pressure is contributing to a decline in the adult population. With large invertivores making up an important portion of temperate affiliated labrid biomass, there is a possibility that further pressures will lead to a loss of an important trophic group in SWA. Loss of trophic groups could have important ramifications for ecosystem function and species interactions and calls for management for these valuable species which could include alleviating fishing pressure (Edwards & Richardson, 2004).

3.4.4 Distribution of tropical herbivores and their establishment

This study further supports the current growing body of literature that warm-water species are increasing their range further south along the SWA coastline (Bennett et al. 2015b; Bennett et al. 2016; Chapter 2; Cure et al. 2018; Wernberg et al. 2016). Many factors are responsible for the success of tropical, climatically affiliated herbivores like *S. ghobban*. In SWA warming ST and the heatwave in 2011 decimated *E. radiata* kelp in the north of the survey area and promoted the growth of turf alga (which is a large component of *S. ghobban’s* diet) which resulted in a regime shift, facilitating the species to permeate the new ecosystem (Bennett et al. 2015b; Wernberg et al. 2016). Chapter 2 found that *S. ghobban* had become so prevalent in the Geraldton region that it was a major indicator species of that assemblage. Smith et al. (2016) observed that the most successful naturalisation occurred when a species is moving into a neighbouring unoccupied niche. This trend explains why *Scarus ghobban* has become an important indicator 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 affiliated herbivores has the potential to introduce unprecedented top down control of the macroalgal canopy as they prevent re-establishment of canopy through the process of feeding on turf algae (Bennett et al. 2015b). This shift away from macroalgal canopy habitat can have negative consequences for the species that depend on it for food and shelter (Bennett et al. 2015b; Cheminee et al. 2017; Levin and Hay, 1996).

3.4.5 Consumption of juveniles by larger labrid species

Some temperate species, such as *O. lineolatus,* have seen a decline in juvenile size classes along their distribution. In the northern, warmer, regions the decline of *O. lineolatus* could be in part due to an increase in ST and the associated loss of macroalgae habitat that they may need for protection. This loss of recruits also occurs where there is a corresponding increase in sub-tropical and tropical affiliated labrid biomass. Many labrids have very flexible diets and some species can adapt their diet when in new environments (Lek et al. 2012). 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). The loss of *O. lineolatus* juveniles in the northern most study areas, matched up with a large increase in biomass of the tropical species *T. lunare,* a species that prey on fish as well as invertebrates (Ackerman, 2004, Holmes et al. 2012). When present in large numbers, *T. lunare* can drive a decline in juvenile abundance fishes (Holmes et al. 2012) and it is possible that *T. lunare* are driving a decrease in the frequency of juveniles of other species through direct predation.

While *T. lunare* have previously been reported to play an important function in consuming juvenile fishes, all omnivores recorded in this study have also been recorded consuming fish (Lek et al. 2011). One such species, *C. auricularis,* has seen dramatic increases in biomass in the southern, cooler regions between 2006 and 2015. *Coris auricularis* has a highly plastic diet and is capable of competing with *O. lineolatus* as they fulfil a similar functional role (Lek et al. 2011). In the cool Albany and Bremer Bay regions, *O. lineolatus* has a decrease in numbers in juvenile size classes, while these same regions have more *C. auricularis* juveniles, adult males and females. Juvenile *C. auricularis* may out-compete *O. lineolatus* with adult *C. auricularis* possibly including the juveniles of local temperate species such as *O. lineolatus* in their diet. The consumption of juvenile *O. lineolatus* by warm-water labrids may also explain why there are more *O. lineolatus* observed at the Capes (which is warmer than the Albany and Bremer Bay regions and so may be expected to have less *O. lineolatus* individuals present), as there is a smaller increase in biomass of *C. auricularis* at the Capes region compared to any other region.

If many species of labrids are in fact generalist carnivores or omnivores, the changing distributions in response to climate change could have a series of environmental impacts that have not yet been considered. Ruiz et al (1999) found that the wider impacts of range changes in fishes are especially severe for piscivorous fish as they predate the endemic species. If these immigrant warm-water predatory labrids are consuming other species, there is potential that they may remove an endemic key-stone species, which could have ecosystem-wide flow-on effects. Similarly, other tropical and sub-tropical affiliated piscivorous species (outside the scope of this study) could contribute to the decline of temperate labrids. Further research should target other warm-water families of warm-water piscivorous fish.

3.4.6 Great Southern reef

Temperate ecosystems are the most vulnerable to changing environments. In the case of the Great Southern Reef (GSR), this vulnerability is further exacerbated by the orientation of the Australian coastline in relation to the poles (Bennett et al. 2016; Stevens, 1989). The GSR has already seen changes in its marine assemblages (Bennett et al. 2016; Chapter 2; Shalders et al. 2018; Wernberg et al. 2016). The GSR has one most diverse and endemic rich assemblages in the world, generating $120 million dollars to the Australian economy in fisheries alone and $200 billion dollars in nutrient recycling services (Bennett et al. 2016). However, the increase in warm-water affiliated species biomass, newly emerging species functions, the decrease in endemic temperate species biomass and change in length structure, could put the unique values of GSR in jeopardy. In comparison to tropical reef systems, temperate reefs are highly understudied (Parsons et al. 2016; Truong et al. 2017). The lack of research on temperate reefs needs to change if management strategies are to be put in place to mitigate the recent species life history, biomass and habitat changes.

3.4.7 Conclusion and recommendations

This study examined whether labrid distributions, lengths and biomass changed along the SWA coastline in the ten years between 2006 and 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 cooler waters. The changes in length structure of large, slow growing temperate affiliated species indicate that fishing pressure is having an impact on target species in SWA, which could synergise with future climate change. The combined total labrid biomass has increased exponentially, which could cause radical change to habitat and food webs in the future. The decline of temperate juveniles could be due to them being consumed by highly adaptable immigrating warm-water predators, which could have a wide impact on temperate ecosystems. From this study it is certain that tropical labrids are becoming established in the warmer areas of SWA and that there is a change in the labrid assemblage along the whole SWA temperate reef system.

South-West Australia and the Great Southern Reef are an economically important and biologically significant area that is understudied. Ongoing replication of this research should be done to better understand the extent and rate of the changes to the SWA marine environment. Future study should also target a wider depth range to investigate the possibility of depth refugia in response to climate change (Booth et al. 2011; Langlois et al. 2012a; Wernberg et al. 2011a). Further research at deeper locations will be especially important for the larger species considered in this study including *B. frenchii*, which is a shallow living representative of its genus, with its relatives being found up to 340m in depth (Cossington et al. 2010; Gomon, 2001; Kuiter, 1993). Lastly, specific research should explore the diet of warmer water species to confirm that labrid species are consuming cool-water affiliated endemic species, which could have severe implications for the temperate marine assemblages of the GSR.

Chapter 4 General Discussion

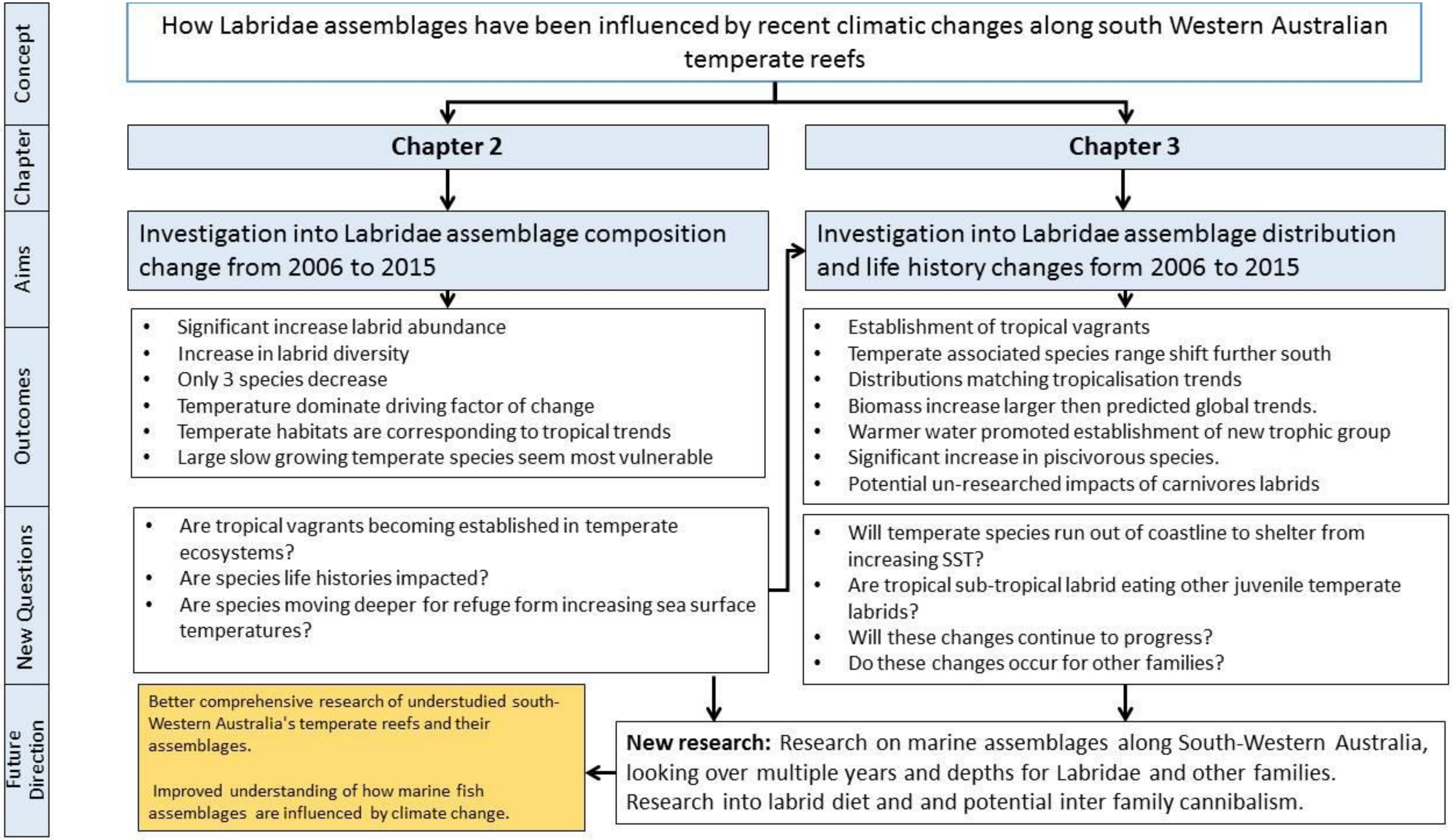
Photograph: Dr Benjamin Saunders preforming transects - South Western Australia

4.1 Summary of findings

This thesis aimed to determine the changes in labrid assemblages along South Western Australia (SWA) over 10 years between 2006 and 2015. The study I conducted demonstrated that labrid assemblages are changing along the whole SWA coast. Sea temperature and altered benthic habitats were the most important defining variables driving assemblage structure (Chapter 2 Figure 2:3). All of the regions sampled in SWA are experiencing influxes of warm-water species into temperate regions. It was also evident that ecosystems and assemblages in the cooler regions of the south coast, which were thought to be stable, are beginning to display characteristics more associated with warmer water regions. It was observed that labrid assemblage structure was breaking down from larger assemblages in 2006 into smaller, more specialised assemblages in 2015 (Figure 2:3). This change is in contrast to recent studies that found that the marine assemblages along the south coast past the Capes were relatively stable, despite the increasing ST (Shalders et al. 2018; Wernberg et al. 2013; Wernberg et al. 2016). I also observed declining abundances of large bodied temperate species, some of which are targeted by fishermen, but which also have an important social value for both fisheries and tourism. In the process of identifying the most representative species in the SWA marine assemblages, this study found that some of the most characteristic species were the new tropical species that were recorded in high numbers in 2015 (Figure 2:4). Furthermore, the trends observed in this study suggest that warm-water labrids may be an important indicator for future changes to marine ecosystems.

Chapter 2 raised some questions as to whether the changes in distribution and abundance represented successful establishment (revised conceptual flow diagram, Figure 4:1). Chapter 3 addressed these questions, and identified that some warm-water affiliated species are becoming established south of their normal distribution. It also confirmed that life history stages of species have been impacted differently by climate change, with juvenile stages becoming more prevalent in comparison to later stages. Biomass increased for most labrids between 2006 and 2015, but the increase occurred at different scales for different climatically affiliated species (Chapter 3 Figure 3:3). The source of the increase in biomass was not due to an increase in body size, but an increase in juvenile presence. The increase in juveniles was most notable in the warmer northern waters. The data also supports trends of tropicalisation reported in previous research, with local species moving from their centre of distributions towards the pole along SWA and establishing successfully in new areas (Cheung et al. 2012; Cure et al. 2018; Wernberg et al. 2013). The species that were most successful were the groups of species that were the most functionally different to the local established species (Smith et al. 2016). Although the biomass of large bodied temperate species stayed relatively stable there were fewer big individuals of these species in 2015, which is a possible result of fishing, as abundances of large bodied labrids sharply declined at the legal catch size. One possible unexpected interpretation of the results is that some of the warmer species moving into cooler water areas may actually be consuming juveniles of resident species in order to maintain their biomass (Ackerman, 2004; Lek et al. 2011; Holmes et al. 2012). Chapter 3 also generated future questions (outlined in Figure 4:1) that will be important for future management of SWA marine ecosystems.

With increases in ST and heat wave events in SWA predicted to be double the global average in the near future, this study supports the growing literature that suggests the current SWA marine assemblages are at risk of permanently changing (*sensu* Wernberg et al. 2016). Additionally, in SWA once a species moves past the Capes region they can no longer move further towards the pole, and in order continue to move to cooler waters (Bennett et al.2016; Wernberg et al. 2011b). Instead they are restricted to following the temperature gradient (Figure App A: 1) east along the coastline, towards the Great Australian Bight. However, options of refuge for cool-water species are limited, and in the future the SWA coastline will increase in temperature relatively rapidly, further limiting refuge areas. Therefore, a cool-water species' only option may be to retreat into deeper water habitats to escape increasing ST, otherwise they risk extinction. The removal of species from marine assemblages could have substantial economic ramifications for tourism and recreational fishers, as the species that tended to be most at risk from climate change were those routinely targeted by recreational or commercial fisheries. With the prediction that SWA will continue to change rapidly this study's findings highlight the need for more research and for rapid adaptive management in order to manage the changes that labrids are already experiencing.



How Labridae assemblages have been influenced by recent climatic changes along south Western Australian temperate reefs

Investigation into Labridae assemblage composition change from 2006 to 2015

- Significant increase labrid abundance
- Increase in labrid diversity
- Only 3 species decrease
- Temperature dominate driving factor of change
- Temperate habitats are corresponding to tropical trends
- Large slow growing temperate species seem most vulnerable

- Are tropical vagrants becoming established in temperate ecosystems?
- Are species life histories impacted?
- Are species moving deeper for refuge form increasing sea surface temperatures?

Investigation into Labridae assemblage distribution and life history changes form 2006 to 2015

- Establishment of tropical vagrants
- Temperate associated species range shift further south
- Distributions matching tropicalisation trends
- Biomass increase larger then predicted global trends.
- Warmer water promoted establishment of new trophic group
- Significant increase in piscivorous species.
- Potential un-researched impacts of carnivores labrids

- Will temperate species run out of coastline to shelter from increasing SST?
- Are tropical sub-tropical labrid eating other juvenile temperate labrids?
- Will these changes continue to progress?
- Do these changes occur for other families?

New research: Research on marine assemblages along South-Western Australia, looking over multiple years and depths for Labridae and other families. Research into labrid diet and and potential inter family cannibalism.

Better comprehensive research of understudied south-Western Australia's temperate reefs and their assemblages.

Improved understanding of how marine fish assemblages are influenced by climate change.

Figure 4:1 Updated flow diagram detailing the outcomes and the future research possibilities identified in this study.

4.2 Limitations of the thesis

With the projected increase in ST, disturbance events and the uncertainty of their impacts on labrid assemblages, more research will be critical to inform future management. A key limitation of this study is the lack of temporal replication. Further replication was not logistically feasible due to the time constraints of a Master's thesis, both in the context of collecting and analysing the resulting imagery. Further temporal replication will assist with modelling future trends that will inform the management of potential impacts (Patil, Peng & Leek, 2016). Future sampling could also target years of the El Niño and La Niña cycles to further progress our understanding of how SWA marine assemblages are changing over time (Wernberg et al. 2016). South Western Australia has a high frequency of endemic species and the unique marine ecosystem itself is predicted to change relatively rapidly, further highlighting the need for ongoing repeated monitoring studies in order to identify the rates of these change as soon as possible.

4.3 Future implications for assemblages in SWA-

4.3.1 Labrid assemblage competition

The increase in abundance and biomass of warm-water labrids will increase direct competition with their cooler water family members. However, because warm-water labrids have been recorded to have high feeding rates and plastic diets, they may be able to easily out compete resident cooler water species (Bennett et al. 2015b; Lek et al. 2011). With the predicted rapid increase in sea surface temperature we could see SWA labrid assemblages become fully dominated by warm-water labrids and a resulting decline in temperate endemic species The results of Chapter 2 and 3 showed a similar pattern were the increase warm-water species *C. auricularis* coincided with a decrease in the cooler water species *O. lineolatus*. These two species might be competing with each other for food resources, leading to the decline of *O. lineolatus* (Lek et al. 2011). In addition, many other labrids have also been found to include fish in their diets (Lek et al. 2011), such as *T. lunare* which are a predator of juvenile fish (Holmes et al. 2012). *Coris auricularis* could further contribute to the declines in temperate species by consuming their juveniles. If warm-water piscivorous labrids are consuming temperate species then the monitoring and research of the potential impact that these species could inflict on SWA should be of key importance.

4.3.2 Implications for other families of marine species

This thesis only targeted species from the family Labridae however; there are further implications for other species. The large increase in *Scarus* abundance and diversity observed in the data could lead to continued prevention of macroalgae canopy recovery in SWA’s northern more regions (Bennett et al. 2015b). Furthermore, endemic species of macroalgae further along the SWA coastline are at risk of the synergistic impacts. Further ST increase, turf algae dominance and the feeding pressure of herbivorous labrids consuming the macroalgae recruits as a by-product of feeding on the turf algae, would drive a region wide habitat shift, and loss of endemic diversity. The overall increase in labrid biomass may lead to a density dependent resource limitation in the marine habitats of SWA, precipitating higher competition between species (O’Conner et al. 2009; Sánchez Lizaso et al. 2000). Changes in distribution and tropicalisation have been reported in other families, such as pomacentrid fishes (Shalders et al. 2018), corals (Verges et al. 2014; Hughes et al. 2010; Yamano et al. 2011), invertebrates (Caputi et al. 2016) and macroalgae (Bennett et al. 2015a; Verges et al. 2014; Wernberg et al. 2016). The changes in distributions and tropicalisation observed in other species, combined with the findings in my thesis, indicate that the whole marine assemblage of SWA is undergoing significant changes and emphasises that SWA’s marine assemblages need further targeted future research, especially if new, warm-water species are predating upon and outcompeting local cool-water species.

4.4 Future implications- management

4.4.1 Predicted continued climate change

This study has observed how 10 years of climate change can impact labrid assemblages. Climate change and ST is projected to continue to increase over the next four decades (Chueng et al. 2012), and also implies that the changes seen in this study will likely continue, with some models predicting the continued warming will lead to complete habitat change and species diversity crashes (Bruno et al. 2015; O'Connor et al. 2009). Additionally, the evidence provided by this study demonstrates the shift of the cool-water ecosystems towards warm-water ecosystems, posing a problem for cool-water species which, due the SWA coastline, are unable to move further south to cooler waters. The inability of cool-water species to move further south in SWA leaves these species with the options of trying to take refuge in deeper water, adaptation, or extinction (Smith et al. 2016). The orientation that SWA has to the South Pole and the relative long-term stability of its environment, makes it especially susceptible to rapid change. Continuous monitoring is essential; to gauge the rate of this change, and the results should be incorporated into adaptive management practices, such as revising marine sanctuaries with the changing species distributions and habitat rehabilitation.

4.4.2 Evidence of impact on fisheries important, long-lived species

The impacts of climate change on the SWA coastline identified in this study also have economic ramifications. I documented a decrease in the abundance of the important recreationally fished temperate species *A. gouldii* and *B. frenchii*. Such a decline is also supported by recent and historical scientific and anecdotal evidence (Gaynor et al. 2008; Gaynor, 2014; Johnson, 1982; Ottaway et al. 1987). These declines show evidence of the effects of fishing pressure; in the case of the *A. gouldii* population, they were found to have declined in numbers at 500mm, which is their catch size threshold (Department of Primary Industries and Regional Development, 2018). Furthermore, the *B. frenchii* population is potentially even more at risk, as over the four years from 2013 - 2016 recreational fishing effort for *B. frenchii* species increased by 44% (Ryan et al. 2013; Ryan et al. 2017). Coupled with the exceptionally long life span of *B. frenchii* (Cossington et al. 2010) the decline in numbers seen in this study indicate that *B. frenchii* is particularly sensitive and at risk from fishing. The decrease in these species will lead to a loss of socio-economic value for recreational fishers and divers.

Alternatively, an increase in value for fishers may be gained by targeting warm-water species such as *C. rubescens* and other similar warm-water species, that could potentially extend their distribution into the areas where cooler water target species are diminishing. A change in management to shift the proportion of fishing effort away from sensitive cooler water species and toward warmer water species, might mitigate the effects of fishing on these vulnerable species. Additionally, education efforts could target key areas such as recreational fishing sectors. The essential message for management agencies and public alike is that the future of climate change on SWA is highly uncertain. It may also be necessary for resource managers to establish preventative measures such as full protection for both *B.frenchii* and *A. gouldii*. While full protection may be unpopular with fishers, such strong measures may be necessary to protect our iconic and vulnerable labrid species (Coleman, et al. 2011; Last, et al. 2011).

4.5 Future research

4.5.1 Depth

An area of research that this study did not consider is different ocean depths. An understanding of labrid connectivity across a range of depths will better disentangle how marine species adapt with changing climate by either moving towards cooler waters or deeper to escape rising temperatures (Booth et al. 2011; Wernberg et al. 2011a). Species adaptation to changes is principally important in SWA as the orientation of the coastline with the South Pole means that species are limited in their ability to move south. However, labrids have been found to inhabit deeper waters than those sampled in this study (Cossington et al. 2010). Sampling depth could be incorporated to further data set replication at each site via use of DOVs or BRUVs (baited remote underwater stereo-video) to sample deeper water assemblages. Other methods could also include Remote Operated underwater Vehicles (ROVs) for deeper waters. The ROVs are able to collect similar transect and density data to DOVs but do not require divers for their operation.

4.5.2 Other families

As this study observed profound changes to the diverse labrid assemblages and distributions, broadening the focus of research to other families will assist in determining whether the changes seen in the plastic labrid assemblage are reflected in the other families present in SWA. Addressing this gap in the knowledge would allow a broader understanding of the whole assemblage health of SWA and help identify the species most at risk. Researching other marine families is especially important for species that have multiple stressors on them, such as those that are targeted by recreational and commercial fisheries, as these are the species most at risk of expiration or extinction (Coleman et al. 2011). Additionally, looking at the whole marine assemblage will give a baseline of species for further research to build on in SWA.

4.5.1 Study over whole species ranges

The constant shifting of labrid species ranges needs to be monitored, to further understand the impact that climate change and increasing ST are having on labrid distributions. This study targets a specific geographical area and not the whole of species distributions. To achieve better understanding of how the changing environment is impacting species ranges, studies should specifically target species distributions. Emphasis should be put on the species range ends where changes will be most obvious, as increased temperature negatively impacts growth and reproduction at the range ends (Cure et al. 2018; Smith et al. 2016). The testing of thermal tolerance limits would also be beneficial to answering how the changing environment is impacting species ranges. Testing thermal tolerance limits could be set up in a controlled laboratory environment, targeting the thermal tolerances of select species and measure stress, hormonal change and reproductive capacity at different temperatures (Donelson et al. 2014; Trip et al. 2016). This area of research could be further advanced by DNA sampling and analysis along the target species distribution, to determine if species that are present in different temperature brackets are becoming distinct populations. This testing will provide an understanding of the genetic connectivity relationship between the original source population and range shifting labrids, and if they are establishing to create distinct populations.

4.5.2 Ecological impacts of species distributions changing

The implication that warm-water labrid species may have been wrongly assumed to be invertivores and instead are potentially consuming other, cool-water fish species, could have a range of negative impacts (Bruno and O’Conner, 2005; Lek et al. 2012; Smith et al. 2016). Better understanding of labrid diet is an urgent issue that requires targeted research, as species that include other fish in their diet have been found to have the largest impact of any functional group when entering new ecosystems, due to their ability to consume important endemic species (Bruno and O’Conner, 2005; Lek et al. 2012). To address the lack of knowledge of SWA labrid diets, gut contents analysis should be carried out on species such as *C. auricularis* and *Thallasoma* spp. that have been observed to consume fish and have moved southward on the SWA coastline. Gut contents analysis should include samples along species entire range and could specifically compare the gut contents of the source population, with the individuals outside their normal distribution, and would also disentangle whether these species are adapting to consume local cool-water species (*sensu* Chapter 3). Gut contents analysis could be accomplished by eDNA using PCR-based molecular analysis of stomach contents and it has the benefit of being able to identify species DNA fragments hours after the prey has been consumed (Leray et al. 2015; Thomsen & Willerslev, 2015). If gut contents research was undertaken it could provide an explanation of why some temperate species are declining.

4.6 Conclusion

South Western Australia is one of the world’s most diverse marine habitats, yet there is relatively little data on this temperate marine ecosystem. This study has focused on rectifying this gap in current knowledge by targeting one of the SWA’s most abundant and diverse families over 10 years of climate change, to determine how labrid assemblages have been impacted from 2006 to 2015. This study found a significant, radical change in labrid assemblages along SWA’s shallow reefs from 2006 to 2015. These changes include the inundation of tropical species into regions they were previously absent. This study also found that species and habitat changed on different scales, with warmer temperate habitats and assemblages changing more than cooler ones. The changes in the southern more regions of the study area challenge the previous finding that the southern-most areas of SWA are unaffected by increasing ST. Instead it was found that larger, 2006 cool-water assemblages were breaking down into smaller, more specialised assemblages in 2015, which is a prominent warm- water characteristic (Ebeling & Hixon, 1991).

The results of this thesis provide future directions to better study temperate reef assemblages over long time periods and over large geographical areas. This study focused on one diverse and highly plastic family of reef fish and it makes a substantial contribution to understanding the processes of change in marine ecosystems in temperate Western Australia. Future research efforts should focus on the whole marine assemblages over multiple habitat types, not just shallow reef systems. Advancing our research and understanding of SWA marine assemblages will potentially allow us to use targeted management programs to increase resilience of SWA marine systems. My study adds to evidence that South Western Australia’s unique marine environment is under threat, and these trends will continue into the future. However, with the right research and adaptive management the impacts of recent climate change can be monitored, and resilience to future changing conditions promoted.

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Appendix A Chapter 2

Appendix A contains tables and figures in support of Chapter 2.

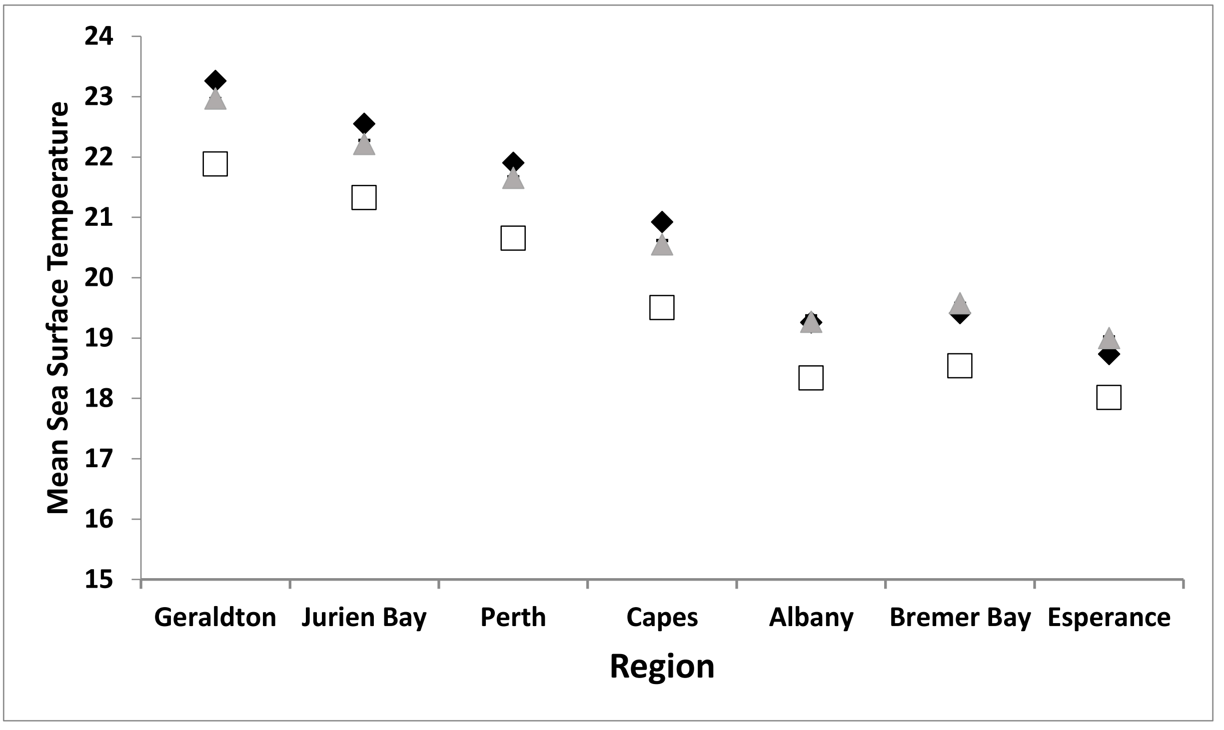


Figure App A: 1 Mean yearly sea surface temperature of the seven survey regions with linear trend line overlayed from the initial 2006 study (White Squares), during the marine heatwave in 2011 (Black Diamonds) and the current recent survey in 2015 (Grey Triangles).

Table App A: 1 Results of post-hoc PERMANOVA test of the different labrid assemblages for the interaction of year by location, grouped into the seven sampling regions. The significant differences (α=0.05) are indicated in bold.

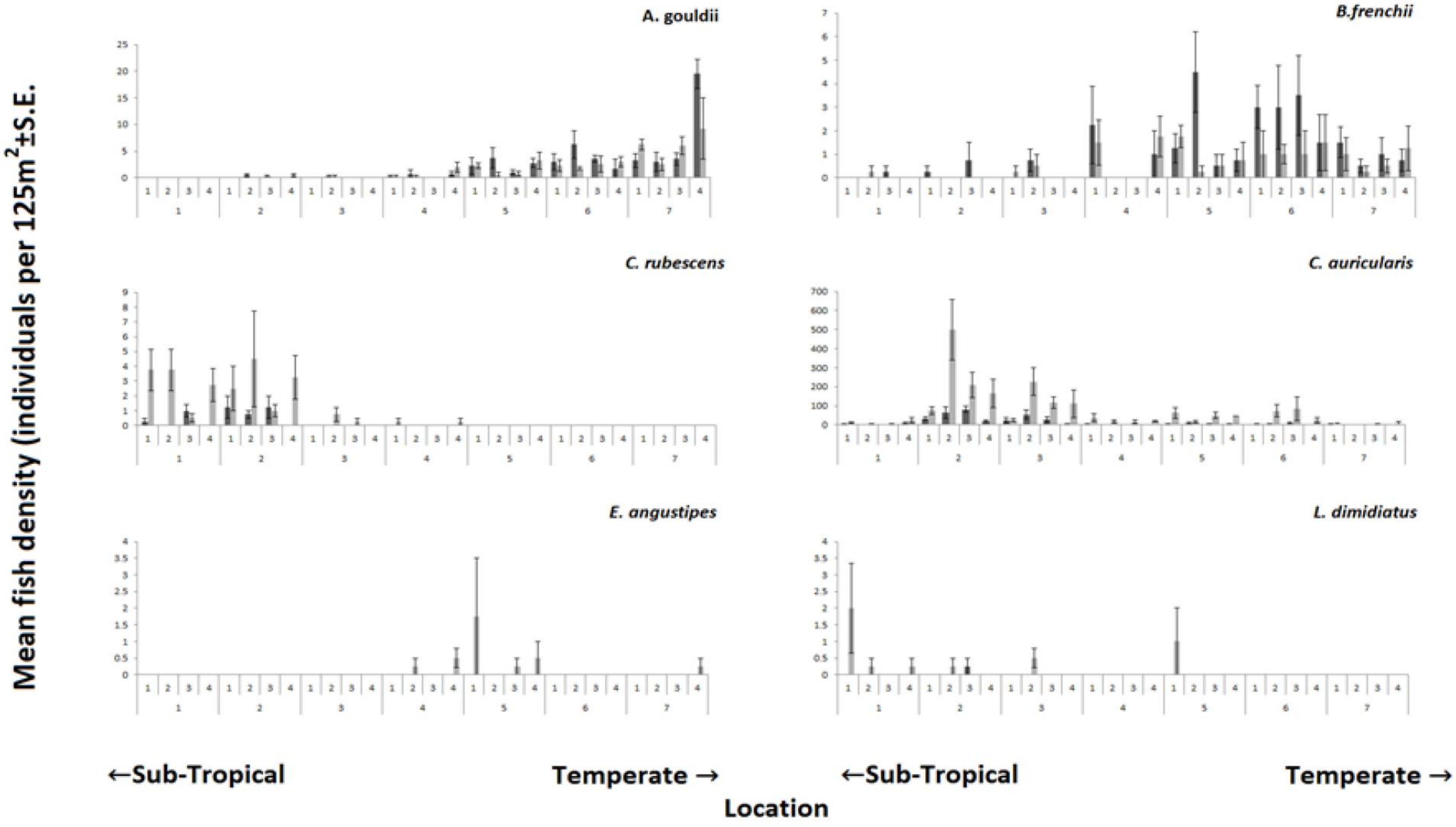
Geraldton		
t	P(perm)	Unique perms
Location 1		
5.7596	**0.0001**	9962
Location 2		
3.6834	**0.0001**	9955
Location 3		
3.4328	**0.0001**	9927
Location 4		
2.6701	**0.0006**	9957
Jurien Bay		
Location 1		
3.6087	**0.0001**	9968
Location 2		
5.2222	**0.0001**	9952
Location 3		
2.6473	**0.0001**	9952
Location 4		
7.1121	**0.0001**	9960
Perth		
Location 1		
2.3769	**0.0017**	9966
Location 2		
4.1056	**0.0001**	9953
Location 3		
4.241	**0.0001**	9967
Location 4		
4.7722	**0.0001**	9952
Capes		
Location 1		
2.9782	**0.0003**	9962
Location 2		
1.6965	0.0521	9956
Location 3		
2.7712	**0.0006**	9965
Location 4		
4.4008	**0.0001**	9951

Albany		
Location 1		
3.909	**0.0001**	9955
Location 2		
3.3468	**0.0001**	9954
Location 3		
3.5497	0.0001	9968
Location 4		
3.9595	0.0001	9950
Bremer Bay		
Location 1		
1.8087	**0.022**	9948
Location 2		
2.9088	**0.0002**	9956
Location 3		
2.4796	**0.0003**	9957
Location 4		
2.6893	**0.0005**	9951
Esperance		
Location 1		
1.9274	**0.0136**	9957
Location 2		
1.6059	0.0534	9959
Location 3		
3.0348	**0.0001**	9963
Location 4		
1.6093	0.0557	9962

Table App A: 2 Details of the splits in the MRT in Figure 2:3 and Figure 2:4. Assemblage column describes the splits and nodes in the tree, followed by the number of sites included at that level. The species that are most associated with that split or node based upon their Dufrêne and Legendre index (DLI) values. As a description of the assemblage at each terminal node the range of species richness (means ± s.e. site-1) and range of abundances (means ± s.e. site-1) within a species are also given.

Assemblage	**Number of sites**	**Number of species**	**Species (DLI)**	**Species Richness Range**	**Species Abundance Range**
ALL	224	5	*N. parilus*(92), *C. auricularis*(79), *H. brownfieldi(*32), *A. maculatus*(30), *A. geographicus*(10)		
Sub-Tropical	100	0	N/A		
Temperate	124	5	*O. lineolatus*(83), *P. biserialis*(82), *A. gouldii*(69), *B. frenchii*(31), *P. laticlavius*(23)		
Geraldton-2006/2015	12	0	N/A	1-6 (2.5±1.5)	1-67 (11.1 ±18)
Geraldton- 2015	9	7	*S. ghobban/schlegeli*(48), *T. septemfasciatum*(37), *C. rubescens*(35), *L. dimidiatus*(32), *T. lunare*(18), *S. frenatus*(11), *C. sordidus*(9)	2-7 (5.7 ±1.6)	0-1028 (118.2±163.8)
Geraldton, Jurien Bay, Perth- 2006/ 2015	79	4	*T. lutescens*(14), *A. melanurus*(1) , *P. elongatus*(1), *S. bandanensis*(1)	0-13 (4.9±2.3)	19-148 (46.8±40.3)

Assemblage	**Number of sites**	**Number of species**	**Species (DLI)**	**Species Richness Range**	**Species Abundance Range**
Capes-2006/ Capes, Albany, Bremer Bay, Esperance-2015	23	1	*E. angustipes*(12)	1-10 (5.5±2.4)	7-241 (60.6 ±59.9)
Capes, Albany, Bremer Bay, Esperance- 2006/ Esperance-2015	*62*	0	N/A	1-10 (5.2±1.7)	3-149 (44.2 ±28.9)
Bremer Bay-2006/ Albany, Bremer Bay, Esperance-2015	39	3	*D. alleni*(9), *S. cyanolaemus*(3), *D. aurantiacus*(2)	2-11 (6.6±1.7)	26-372 (92 ±69.4)
Geraldton, Jurien Bay, Perth-2006/2015	88	0	N/A		
Capes, Albany, Bremer Bay, Esperance- 2006/ Capes, Esperance-2015	85	0	N/A		


Mean fish density (individuals per 125m²±S.E.
A. gouldii
0
5
10
15
20
25
B.frenchii
0
1
2
3
4
5
6
7
C. rubescens
0
1
2
3
4
5
6
7
8
9
C. auricularis
0
100
200
300
400
500
600
700
E. angustipes
0
0.5
1
1.5
2
2.5
3
3.5
4
L. dimidiatus
0
0.5
1
1.5
2
2.5
3
3.5
4
1 2 3 4
1
2
3
4
5
6
7
←Sub-Tropical
Temperate →
←Sub-Tropical
Temperate →
Location

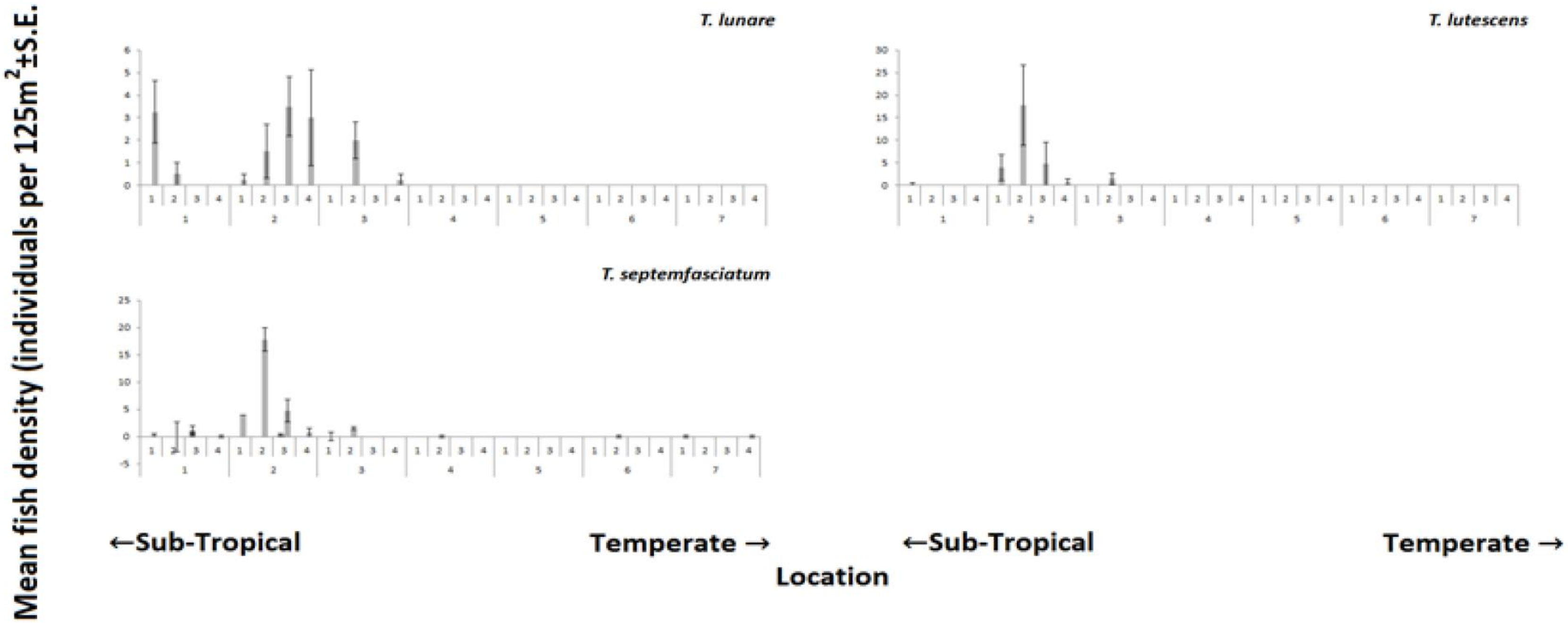


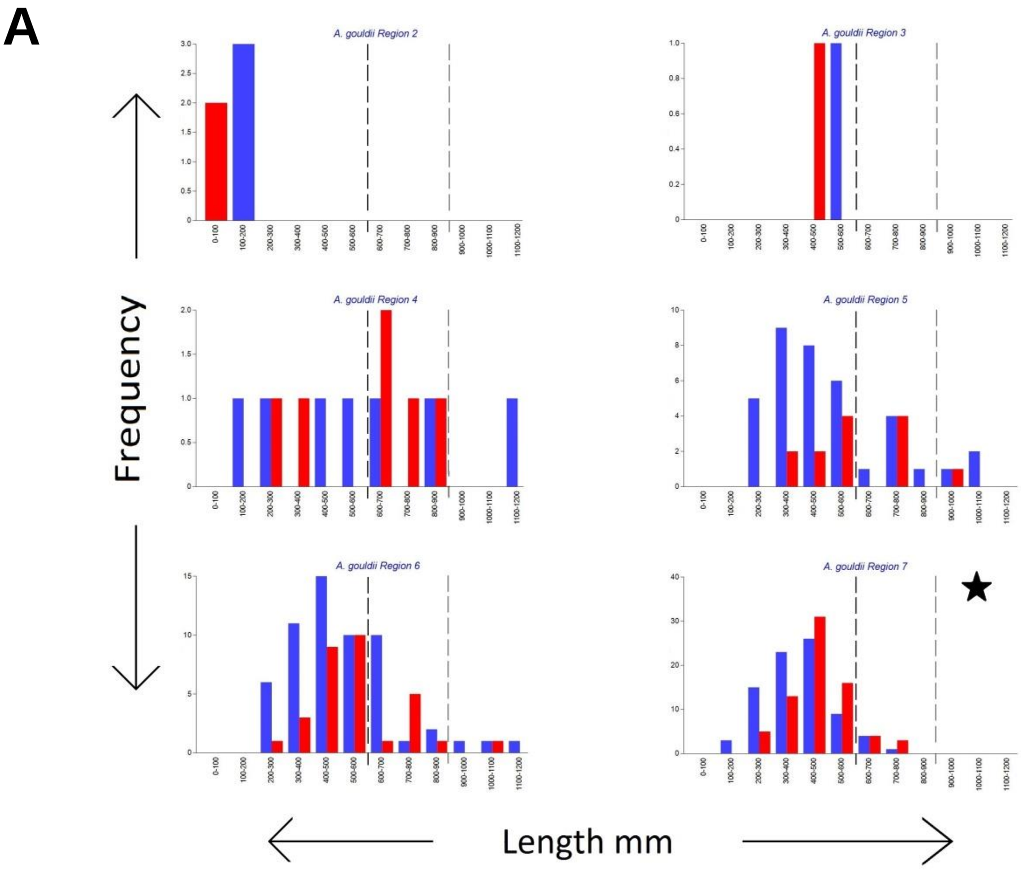
Figure App A: 2 Mean densities (per 125m2) in 2006 (dark bars) and 2015 (Light Bars) of the 15 most abundant indicator labrid species at each of the seven regions. The regions consist of four locations, which in turn have four sites nested within them (n-4).

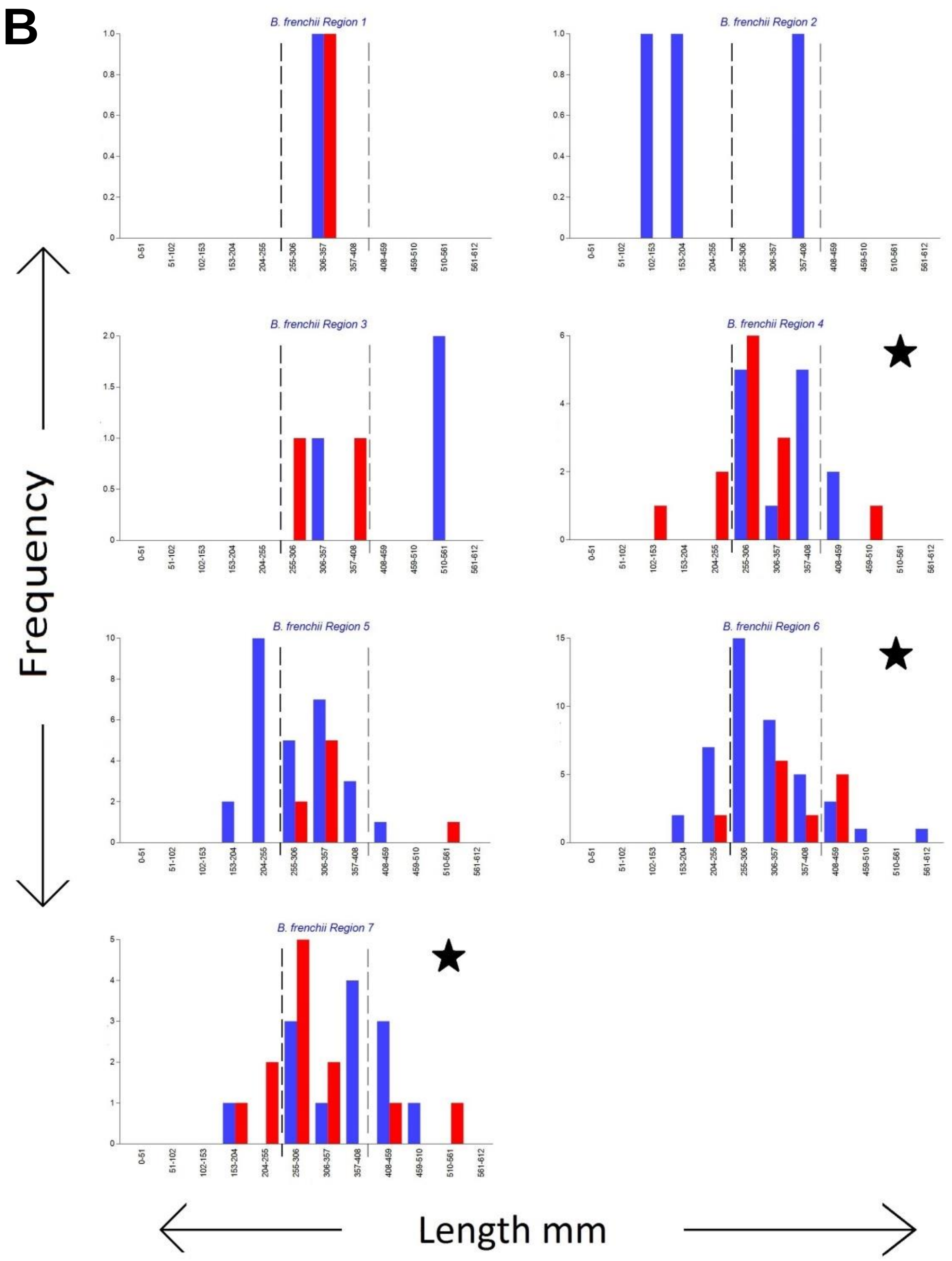
Appendix B Chapter 3

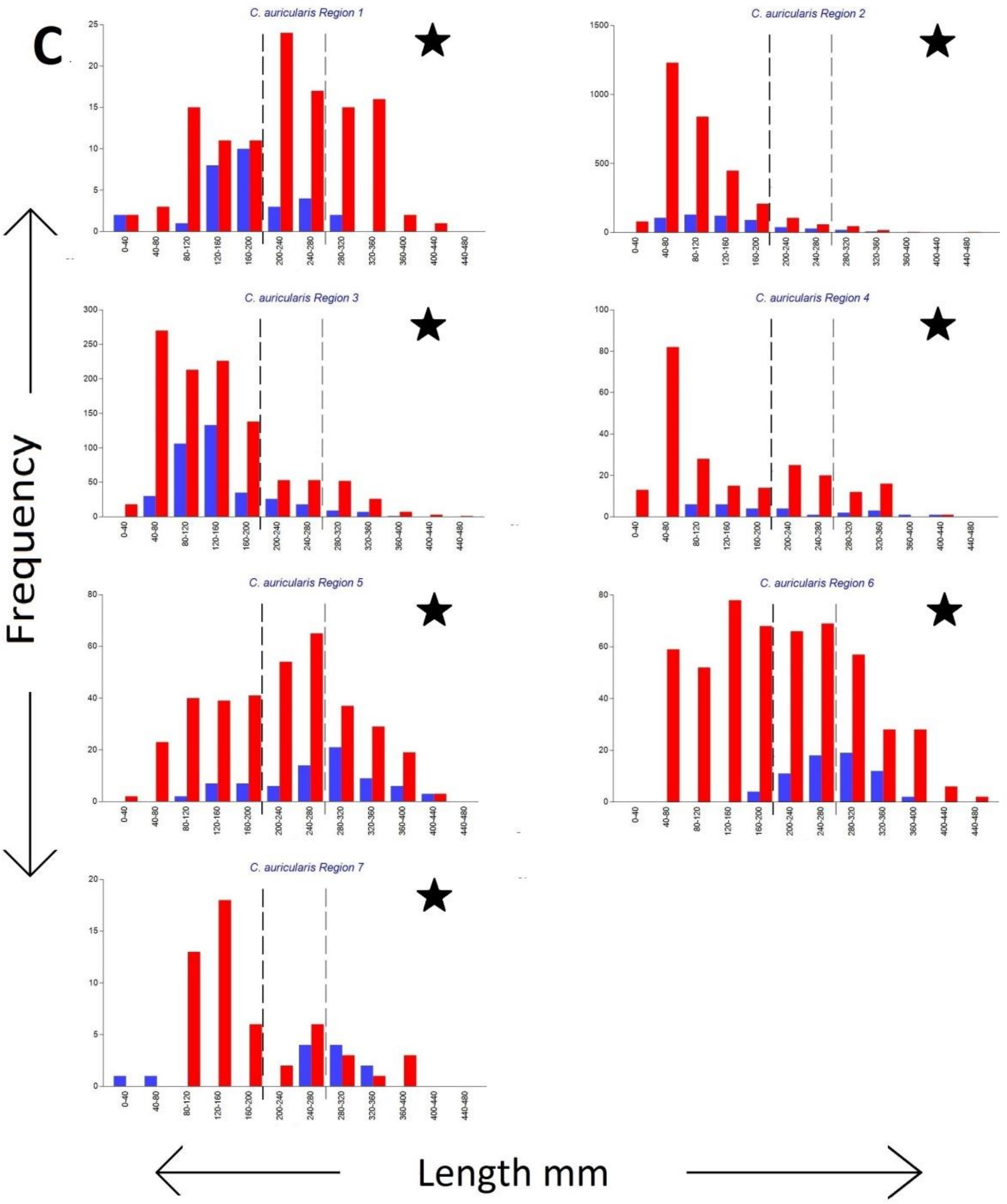
Appendix B contains tables and figures in support of Chapter 3.

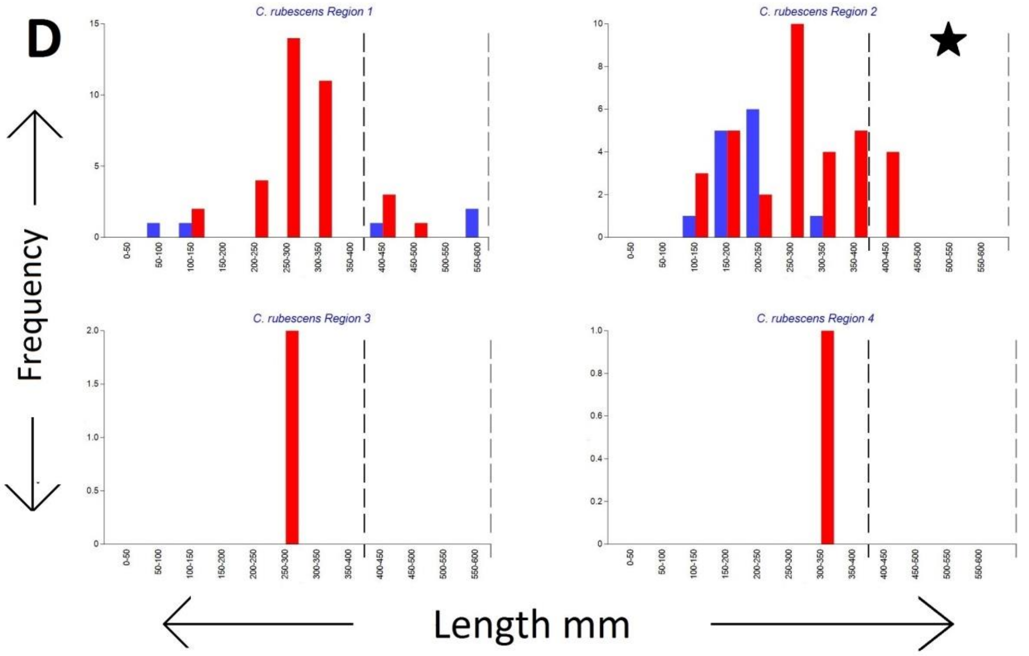
Table App B: 1 Supporting literature for labrid climatic affiliation and trophic groups

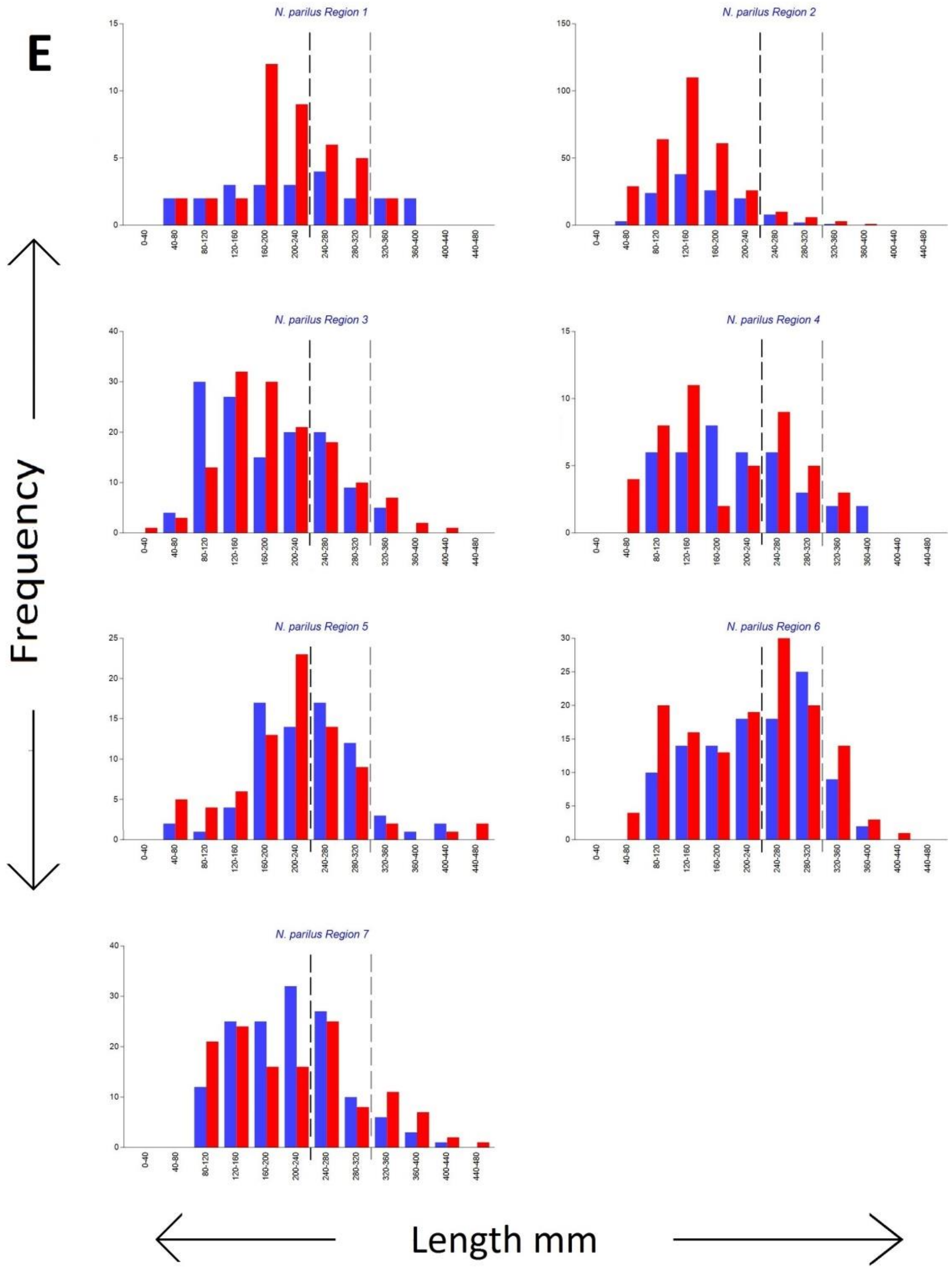
Species	**Climatic affiliation**	**Supporting reference**	**Trophic Group**	**Supporting reference**
Achoerodus gouldii	Temperate	Sheperd, 2007	Large Invertivores	Sheperd, 2007
Anampses geographicus	Tropical	Fish Base, 2018	Small Invertivores	Fish Base, 2018
Anampses melanurus	Tropical	Fish Base, 2018	Small Invertivores	Hodge *et al*. 2012
Austrolabrus maculatus	Temperate	Fish Base, 2018	Small Invertivores	Fairclough, *et al*., 2011
Bodianus frenchii	Temperate	Cossington, *et al*., 2010	Large Invertivores	Platell, *et al*., 2010
Chlorurus sordidus	Tropical	Fish Base, 2018	Herbivores	Fish Base, 2018
Choerodon rubescens	Sub-Tropical	Cure, *et al*., 2015; Cure, *et al*., 2018	Large Invertivores	Cure, 2016; Lek, 2004
Coris auricularis	Sub-Tropical	Lek, *et al*.,2011	Omnivores	Lek, *et al*., 2011
Dotalabrus alleni	Sub-Tropical	Fish Base, 2018	Generalist Carnivore	Bray, 2017
Dotalabrus aurantiacus	Temperate	Fish Base, 2018	Generalist Carnivore	Western Australian Museum, 2018
Eupetrichthys angustipes	Temperate	Fish Base, 2018	N/A	N/A
Halichoeres brownfieldi	Sub-Tropical	Fish Base, 2018	N/A	N/A
Labroides dimidiatus	Tropical	Fish Base, 2018	Small Invertivores	Grutter, 1997
Notolabrus parilus	Sub-Tropical	Lek, *et al*.,2012	Omnivores	Lek, *et al*., 2011
Ophthalmolepis lineolatus	Temperate	Lek, *et al*.,2012	Omnivores	Lek, *et al*.,2011
Pictilabrus laticlavius	Temperate	Fish Base, 2018	Small Invertivores	Fairclough, *et al*., 2011
Pseudojuloides elongatus	Temperate	Fish Base, 2018	N/A	N/A
Pseudolabrus biserialis	Sub-Tropical	Fish Base, 2018	Small Invertivores	Fairclough, *et al*., 2011
Scarus frenatus	Tropical	Fish Base, 2018	Herbivores	Fish Base, 2018
Scarus ghobban / schlegeli	Tropical	Bennett, *et al*., 2015b	Herbivores	Bennett, *et al*., 2015b
Stethojulius bandanensis	Tropical	Fish Base, 2018	Small Invertivores	Dulvy, *et al*., 2002
Suezichthys cyanolaemus	Sub-Tropical	Fish Base, 2018	N/A	N/A
Thalassoma lunare	Tropical	Ackerman, 2004	Generalist Carnivore	Holmes, *et al*., 2012, Connell, 2000
Thalassoma lutescens	Sub-Tropical	Fish Base, 2018	Generalist Carnivore	Fish Base, 2018, Bray, 2017
Thalassoma septemfasciatum	Tropical	Fish Base, 2018	N/A	N/A

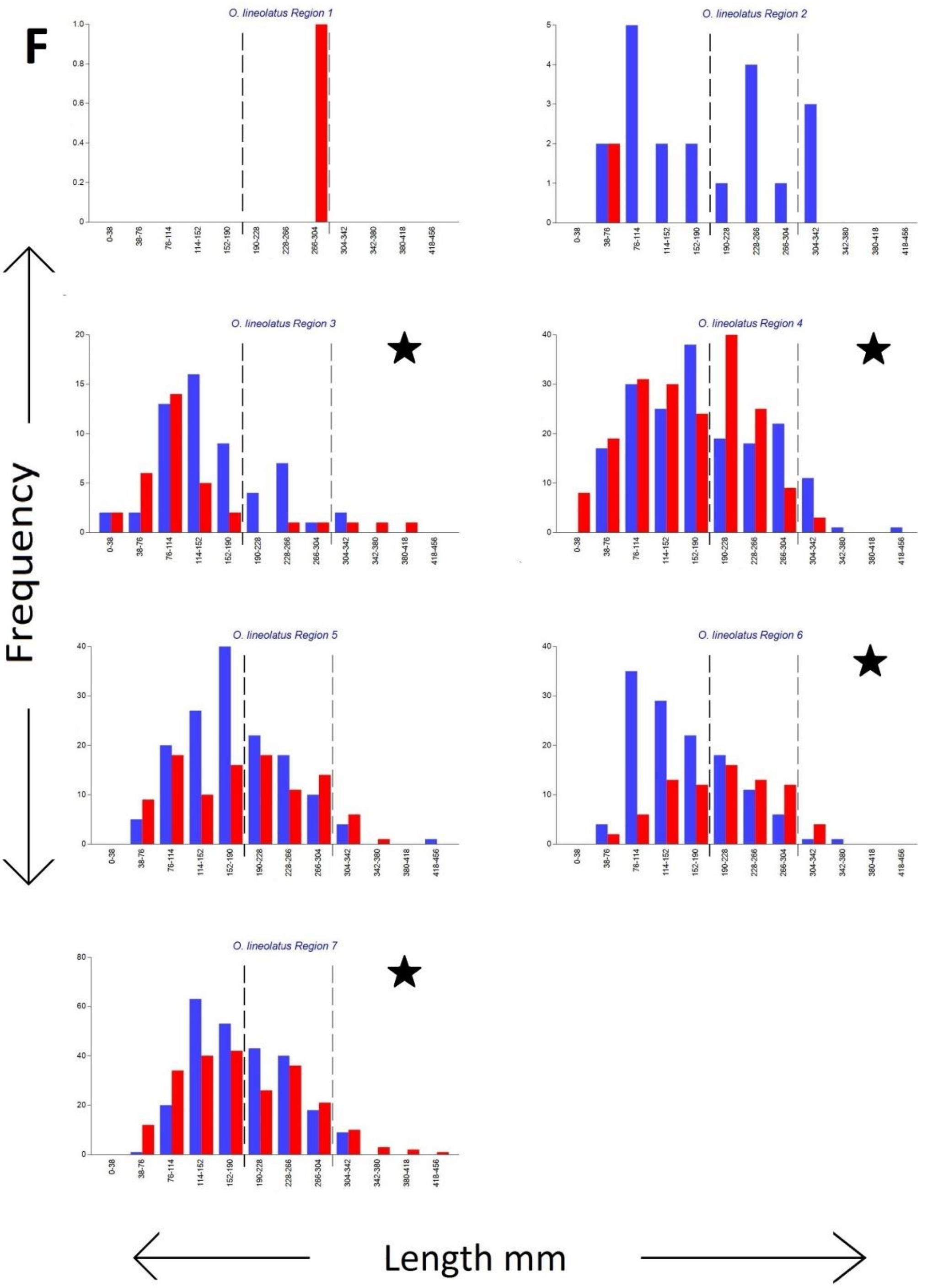

A
A. gouldii Region 2
A. gouldii Region 3
A. gouldii Region 4
A. gouldii Region 5
A. gouldii Region 6
A. gouldii Region 7
★
Frequency
Length mm
0-100
100-200
200-300
300-400
400-500
500-600
600-700
700-800
800-900
900-1000
1000-1100
1100-1200

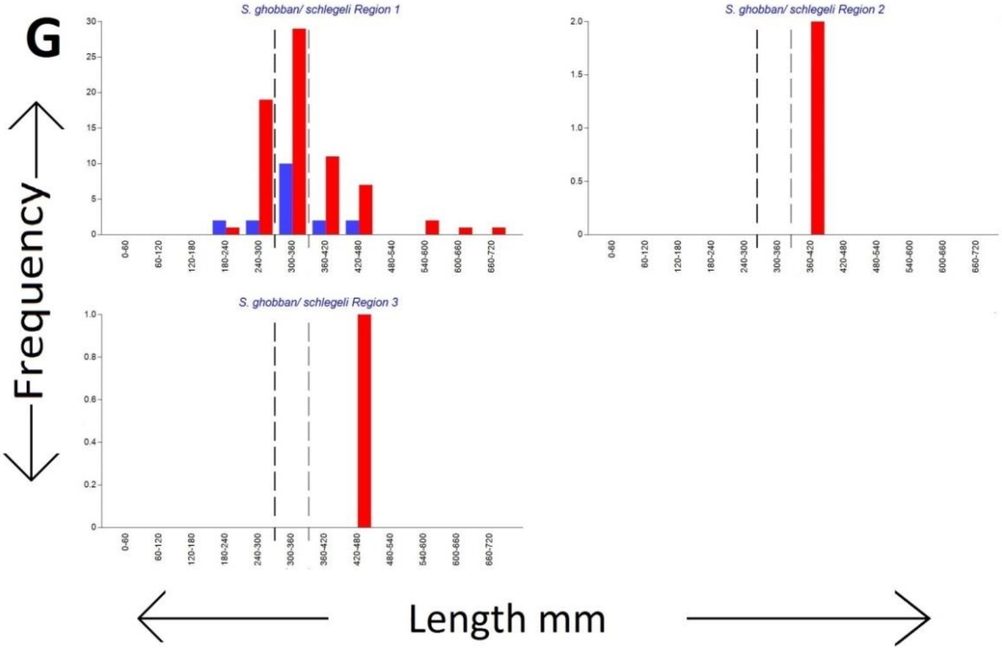

B
B. frenchii Region 1
B. frenchii Region 2
B. frenchii Region 3
B. frenchii Region 4
B. frenchii Region 5
B. frenchii Region 6
B. frenchii Region 7
Frequency
Length mm
0-51
51-102
102-153
153-204
204-255
255-306
306-357
357-408
408-459
459-510
510-561
561-612
★


C
C. auricularis Region 1
C. auricularis Region 2
C. auricularis Region 3
C. auricularis Region 4
C. auricularis Region 5
C. auricularis Region 6
C. auricularis Region 7
★
0-40
40-80
80-120
120-160
160-200
200-240
240-280
280-320
320-360
360-400
400-440
440-480
Frequency
Length mm


D
C. rubescens Region 1
C. rubescens Region 2
C. rubescens Region 3
C. rubescens Region 4
★
0
5
10
15
2
4
6
8
0.5
1.0
1.5
2.0
0.2
0.4
0.6
0.8
0-50
50-100
100-150
150-200
200-250
250-300
300-350
350-400
400-450
450-500
500-550
550-600
Frequency
Length mm


E
N. parilus Region 1
N. parilus Region 2
N. parilus Region 3
N. parilus Region 4
N. parilus Region 5
N. parilus Region 6
N. parilus Region 7
0-40
40-80
80-120
120-160
160-200
200-240
240-280
280-320
320-360
360-400
400-440
440-480
Frequency
Length mm


F
O. lineolatus Region 1
1.0
0.8
0.6
0.4
0.2
0
O. lineolatus Region 2
5
4
3
2
1
0
O. lineolatus Region 3
20
15
10
5
0
O. lineolatus Region 4
40
30
20
10
0
O. lineolatus Region 5
40
30
20
10
0
O. lineolatus Region 6
40
30
20
10
0
O. lineolatus Region 7
80
60
40
20
0
0-38
38-76
76-114
114-152
152-190
190-228
228-266
266-304
304-342
342-380
380-418
418-456
Frequency
Length mm


G
S. ghobban/ schlegeli Region 1
S. ghobban/ schlegeli Region 2
S. ghobban/ schlegeli Region 3
0
5
10
15
20
25
30
0.5
1.0
1.5
2.0
0.2
0.4
0.6
0.8
0-60
60-120
120-180
180-240
240-300
300-360
360-420
420-480
480-540
540-600
600-660
660-720
Frequency
Length mm

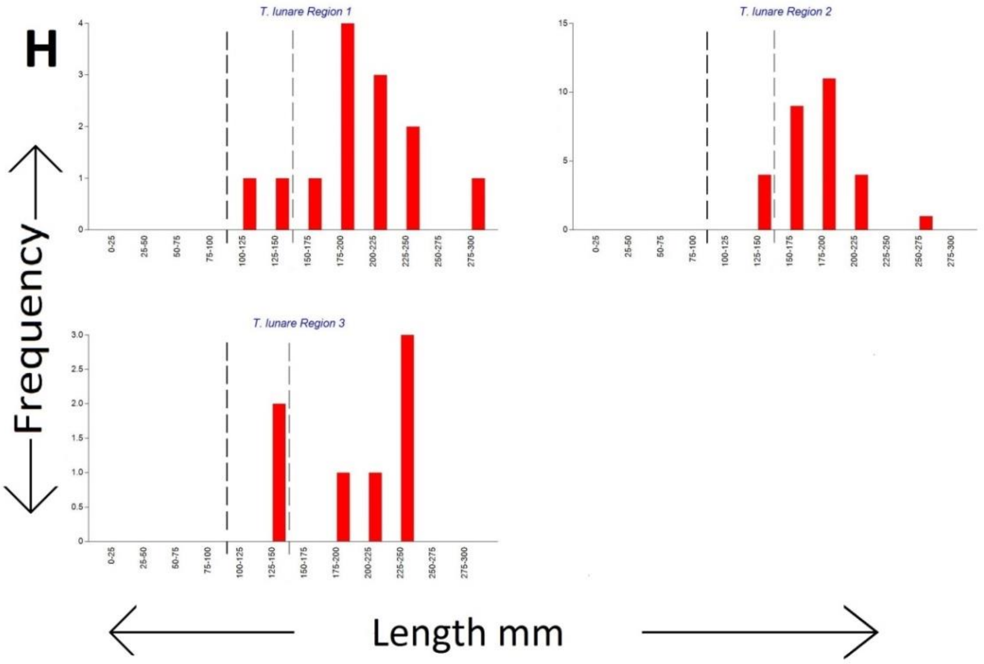


Figure App B: 1 Length frequency analysis for select labrid species A (A. *gouldii*), B (*B. frenchii*), C (*C. auricularis*), D (*C. rubescens*), E (*N. parilus*), F (*O. lineolatus*), G (*S. ghobban / schlegeli*) and H (*T. lunare*). The figure depicts 2006 lengths (blue) and 2015 lengths (red). Graphs were overlaid with age of estimated maturity from literature however they are highly variable; darker indicates length when juveniles first become mature females and lighter were females change to males A Pairwise test between year × region was run and a black star was placed over that region to indicate a significant result at that region however this could not be done for region when a species was not present for either 2006 or 2015.

Table App B: 2 PERMANOVA tests differences in the length frequency distributions of species across different regions and years of the labrid climate association that were analysed above in Figure 3:2 and the individual species length frequency's Figure App B:1. Bold P-Values indicate significant result (P-value < 0.05).

Tropical affiliated species

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	2776	5.4866	**0.0042**	9969	
Region	6	5261	1.7329	0.0663	9920	
YearxRegion	6	3994	1.3155	0.2075	9942	
Residual	42	21251				

Sub-Tropical affiliated species

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	3.153E+05	5.7021	**0.0075**	9960	
Region	6	1.3675+E6	4.1218	**0.0006**	9939	
YearxRegion	6	6.9417E5	2.0923	**0.0264**	9943	
Residual	42	2.3224E6				

Temperate affiliated species

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	2833.4	3.0047	**0.0469**	9959	
Region	6	48603	8.5905	**0.0001**	9933	
YearxRegion	6	3015.4	0.53296	0.9009	9929	
Residual	42	39605				

Achoerodus gouldii

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	109.29	1.9245	0.118	9939	
Region	6	2102.7	6.1715	**0.0001**	9913	
YearxRegion	6	251.21	0.73732	0.7946	9922	
Residual	42	2385				

Bodianus frenchii

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	6343.6	0.66898	0.6254	9956	
Region	6	97583	1.7152	**0.0367**	9901	
YearxRegion	5	75102	1.584	0.0654	9908	
Residual	22	2.0861E5				

Coris auricularis

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	25476	5.0907	**0.0001**	9944	
Region	6	1.13E+05	3.7611	**0.0001**	9898	
YearxRegion	6	80015	2.6649	**0.0001**	9906	
Residual	39	1.9517E5				

Choerdon rubescens

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	35618	4.7463	**0.0022**	9948	
Region	3	65179	2.8952	**0.0014**	9912	
YearxRegion	1	21299	2.8382	**0.0102**	9938	
Residual	10	75044				

Notolabrus parilus

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	2871.4	0.66886	0.6791	9953	
Region	6	63541	2.4669	**0.0003**	9903	
YearxRegion	6	15659	0.60793	0.9551	9889	
Residual	42	1.803E5				

Ophthalmolepis lineolatus

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	15792	2.9076	**0.0152**	9951	
Region	6	93287	2.8627	**0.0001**	9903	
YearxRegion	5	37724	1.3891	0.1164	9924	
Residual	32	1.738E5				

Scarus ghobban

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	1	8565.5	1.18	0.3604	440	
Region	2	58185	4.008	**0.0201**	947	
YearxRegion	0	0	No test			
Residual	4	29035				

Thalassoma lunare

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Unique perms**	**P(MC)**
Year	0	0	No test			
Region	2	14036	0.77824	0.6536	104	0.582
YearxRegion	0	0	No test			
Residual	4	36070				

Appendix C Contributions to Chapter 2

To Whom It May Concern,
I, Jack Ryan Cripps Parker, developed concepts and interpretation, wrote and edited the manuscript, analysed and executed the data analysis and developed the figures and tables. I also contributed to the design of the study and collection of raw data for the paper/publication entitled “Shifts in Labridae geographical distribution along a unique and dynamic coastline. Submitted to the Journal of Diversity and Distributions”.

I, as a Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate.

Benjamin John Saunders	
Scott Bennett	
Joseph DiBattista	Joey DiBattista
Tanika Cian Shalders	
Euan Sinclair Harvey	E-S Harvey