Department of Environment and Agriculture

Spatial ecology and ontogeny: incorporating fish size-classes into species distribution models

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Declaration

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

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 proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number # AEC_2014_21.

Signature: _______________________ Date: 2/08/2016

“Nothing works out according to plan, but it always works out”

-local motto in Chihuahua, Mexico, from the book
Born to Run by Christopher McDougall

“When eating an elephant take one bite at a time”

-Creighton Abrams

Abstract

The south-west coast of Australia is a well recognised global hotspot for terrestrial and marine biodiversity. The marine environment of this region is characterised by a high proportion of endemic species of demersal fish, invertebrates and algae. This region is also identified as a climate change hotspot with recently recorded unprecedented massive fish kills, southerly range extensions of tropical fish species and potentially permanent phase shifts of dominant temperate benthic ecosystems. With the frequency and intensity of environmental perturbations predicted to increase, identification of species-environment patterns across varying spatial scales can contribute to deeper understanding of spatial ecology of these threatened fish communities and improve local and regional management and climate change adaptation strategies.

The niche requirements and habitat resource partitioning by conspecific fishes of different sizes is a knowledge gap in spatial ecology and fisheries management. Many fish species undergo ontogenetic shifts in habitat use throughout their life-history. Ontogenetic movements between and among habitats are often driven by the need to find sufficient food of an appropriate size to support growth, to seek out new shelter to support a larger body size, to avoid predation and to encounter other sexually reproductive fish. Therefore, the ability to move between habitat patches may have consequences for the survivorship of a species, particularly at vulnerable life-history stages. As such, knowledge about ontogenetic habitat shifts and other growth-dependent processes is crucial to understand the processes that underpin abundance patterns and community composition.

The economic constraints often posed by limited resources for marine spatial management raise the question about what areas are most worthy of protection and what species could be used as ecological indicators of a phenomenon, or to monitor overall ecosystem health. Identifying key benthic areas that are crucial for multiple species of demersal fish, or for different life-history stages of same species (i.e. spawning grounds, fisheries refugia or nursery areas) may help to preserve vulnerable life-history stages of target species, optimise the limited resources for monitoring and management and to identify areas of high intrinsic value for spatial protection.

To address the questions above I begin this thesis by examining the bioregional patterns of demersal fish assemblage composition along the south-west coast of Australia (chapter 2). I use Multivariate Regression Trees (MRT) and Distance-based Linear Models (DistLM) to identify significant biological and/or environmental variables that are most correlated to the observed demersal fish assemblage patterns. Using multivariate statistical techniques on a set of 49 environmental variables I identify the six most influential variables (five benthic and one spatial variable) that combined explain 42 % of the variation in spatial patterns of fish community structure of demersal fish along 1600 km of this coast. In addition, using the MRT output, I identify key indicator species of each of the assemblages. These analyses reveal that the fish assemblages in the central part of the south-west are characterised by high proportion of endemic species that are closely associated with canopy forming seaweed habitats. These seaweeds have already been subject to large scale die-offs throughout the region.

Using a subset of the indicator species that I have identified in chapter 2 and Generalised Additive Models (GAMs), I examine the habitat resource partitioning and environmental niche requirements of conspecific individuals of different body length (i.e. ontogeny; chapter 3) and body mass (i.e. biomass; chapter 4). Continuous predictive rasters of individuals' size/biomass distributions across a broader unsampled geographical area highlight habitat partitioning and difference in the environmental niche for the ecological indicator species (chapter 3) and the fishery indicator species (chapter 4) throughout their life-histories. In addition, predictive hotspot maps that I have created have helped to identify potential areas that are important for numerous species and/or for different life stages of multiple species (e.g. fish nurseries or spawning stock hotspots). When compared to models based on abundance datasets for the same species, the biomass models had higher explanatory power (adjusted R^2). Using individual body length with ecological modelling can provide crucial information that link abundance patterns and community composition across benthic habitats.

The usefulness of some of the long-established methods in combination with the novel ecological modelling approaches should be revised due to the biases they may introduce with respect to habitat associations of fish. In chapter 5 I compare occurrence models developed from data collected from stereo-BRUVs (Baited Remote Underwater Stereo Video systems) and towed stereo-video. Models developed for the towed stereo-video data had consistently better predictive performance then stereo-BRUVs. I conclude that this method of data collection was deemed to more likely reflect more realistic species-habitat relationships than from data collected with baited underwater video. The lower cost associated with using towed video system for data collection in low-relief seascapes is an additional reason for considering this method for marine spatial management purposes.

In conclusion, I identified canopy forming seaweeds as being a crucial habitat which supports endemic fish assemblages in south-west Australia. This type of benthic habitat requires close monitoring throughout the region because it has already been documented that human induced climate change is reducing the extent of this habitat. Habitat loss may compromise the demersal fish biodiversity and the resilience of other endemic marine communities in the region. I demonstrate that where there are limited resources for monitoring and management, predictive modelling can be a valuable tool for spatial management of coastal fish and fisheries by identifying areas and habitats that are important for multiple species and identifying previously overlooked processes such as ontogenetic habitat shifts. This novel approach can help researchers and managers to focus on areas of high intrinsic value for multiple species, thus saving limited resources for monitoring and management programmes. In addition, conservation efforts can be further improved by applying robust, cost-effective methods for rapid data collection such as the towed stereo-video which can be useful for spatial ecological modelling.

Statement of Contributors

Chapters in review

Chapter 3: Galaiduk, R., Radford, B., Saunders, B., Newman, S., Harvey, E., (in review for Ecological Applications). Characterising ontogenetic habitat shifts in marine fishes: advancing nascent methods for applied marine spatial management.

Author contribution: EH and BR collected the data. RG designed the study based on the collected data with help from EH and BR. RG conceived and executed the data analyses, wrote and edited the manuscript. BR provided guidance with data analyses. BS edited the manuscript. SN helped to develop the structure of the manuscript. All co-authors reviewed and commented on the manuscript.

Chapter 5: Galaiduk, R., Radford, B., Wilson, S. N., Harvey, E., (in review for Marine Ecology Progress Series). Comparing two remote video survey methods for spatial predictions of the distribution and habitat suitability of demersal fishes.

Author contribution: RG and EH collected the data. RG designed the study with help from EH and BR. RG conceived and executed the data analyses, wrote and edited the manuscript. BR provided guidance with data analyses. SW helped to develop the structure of the manuscript. All co-authors reviewed and commented on the manuscript.

Chapters in preparation

Chapter 2: Galaiduk, R., Radford, B., Moore, C., Halford, A., Harvey, E. Regional-scale, environmental drivers of highly endemic, temperate fish communities located within a climate change hotspot.

Author contribution: EH and BR collected the data. RG designed the study based on the collected data with help from EH and BR. RG conceived and executed the data analyses, wrote and edited the manuscript. BR and AH provided guidance with data analyses. AH assisted with interpretation and structure of the manuscript. All co-authors reviewed and commented on the manuscript.

Chapter 4: Galaiduk, R., Radford, B., Harvey, E. The use of individual fish biomass models to map essential habitat for adult and juvenile targeted fishes.

Author contribution: RG and EH collected the data. RG designed the study with help from EH and BR. RG conceived and executed the data analyses, wrote and edited the manuscript. BR provided guidance with data analyses and helped to develop the structure of the manuscript. All co-authors reviewed and commented on the manuscript.

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Chapter 1 General Introduction

1.1 Background and rationale

1.1.1 Global biodiversity loss

A worldwide decline in biodiversity associated with anthropogenic activities such as global warming, biological introductions and pollution may cause major changes in ecosystem function and have a negative impact on the provision of ecosystem services (Sala & Knowlton, 2006). Recent studies demonstrate that the effects of climate change associated with global warming can range from the response of individual species through to changes in biomes (Bellard et al., 2012). Typical species specific responses could be physiological and phenotypical shifts to adapt to a new set of local environmental conditions (Parmesan, 2006) or range shifts in order to maintain the current ecological niche (Poloczanska et al., 2007; Booth et al., 2009). Biome scale responses may include major community phase shifts and loss of ecosystem functioning (Verges et al., 2014; Bennett et al., 2015; Graham et al., 2015; Wernberg et al., 2016). Atmospheric carbon dioxide concentration and sea surface temperatures in the 21st century are predicted to reach levels that have not been experienced for tens of thousands of years (Hoegh-Guldberg et al., 2007). In response to the rapidly changing climate, the rates of biodiversity loss and homogenisation of communities are predicted to increase (Butchart et al., 2010; García Molinos et al., 2015).

In the marine environment, the coastal fish communities are particularly vulnerable to anthropogenic influences such as overfishing and loss of habitat (Jackson et al., 2001). As a result, the decline in biodiversity can lead to poor water quality and fisheries collapse (Worm et al., 2006). At this stage, little is known about what effect local changes in biodiversity will have on the larger community processes at landscape levels. Current predictions about regional-scale concepts are still being drawn from the integration of smaller-scale observations (Buddemeier & Fautin, 2002). The threats to marine biodiverisity are often cumulative and poorly understood, generating multiscalar impacts on marine organisms and the habitats they occupy (Edgar et al., 2016). There is a need for new or improved tools to rapidly assess and predict the biogeographic patterns in marine ecosystems, and to generate knowledge that can be used in regional and national management strategies for mitigation of changes in demersal fish community structure and distribution as a result of climate change.

1.1.2 Knowledge gaps in the spatial ecology of fishes

Environmental gradients are fundamental drivers of animal movements and their distribution across a landscape (Nathan et al., 2008). At large spatial scales, biogeographic variation in fish assemblages distribution and composition may be dictated by physiological tolerances to variations in temperature (Cheung et al., 2012), oceanic currents (Figueira & Booth, 2010) or evolutionary processes like speciation (Wellenreuther et al., 2008). Regional and fine-scale heterogeneity in habitat type (Anderson & Millar, 2004), depth (Nemeth & Appeldoorn, 2009) and complexity (Hyndes et al., 2003) have been identified as important for influencing population dynamics and assemblage structure of demersal fish by moderating the effects of predation and competition (Jones, 1992).

Species will preferentially select environmental conditions (i.e. environmental niche) that optimise their survival, growth, and reproductive success (Martinez-Meyer et al., 2013). The bio-physical environment and physiological responses of species along the environmental gradients are not always linear or intuitive, which influences predictions about species responses to climate change (Helmuth et al., 2005; Feary et al., 2014). Therefore, knowledge about environmental processes that influence the spatio-temporal occurrence and abundance of species (i.e. spatial ecology; Legendre and Fortin 1989) is fundamental for understanding the structure and function of populations (Tilman & Kareiva, 1997), and for effective conservation and management efforts (Stamoulis & Delevaux, 2015). Studying the abundance and distribution of demersal fishes in space can facilitate the identification of critical habitats (Schmiing et al., 2013) and an understanding of inter-specific interactions (Galaiduk et al., 2013). By knowing how human-associated activities influence fish populations and their essential habitat (Nye et al., 2009) it is possible to develop effective management and conservation plans (Wise et al., 2009).

Until recently, data describing the distribution and abundance of marine organisms has been sparse, point-observations based, and expensive to collect (Edgar et al., 2016). Managers have been lacking the tools to adequately synthesise, visualise and extrapolate the limited data that is available to draw spatial conclusions about environmental health (Cooke et al., 2016). A lack of knowledge about how the environment influences the spatial ecology of demersal fishes can bias population assessments and potentially lead to ineffective, or counterproductive management actions (Edgar et al., 2016).

1.1.3 The evolution of species distribution models in marine research

Species distribution models (SDMs) have been used by spatial ecologists to quantify species-habitat associations at broad geographical scales in both the terrestrial and marine environments (Guisan & Zimmermann, 2000; Pittman et al., 2007; Young & Carr, 2015). They are particularly useful in cases when there are limited resources for large scale spatial sampling, and where the knowledge of focal species is reduced to a few sampled locations (Costa et al., 2014). By combining SDMs and Geographic Information Systems (GIS) it is possible to extrapolate models into non-surveyed areas to provide insights into species-habitat linkages. SDMs have been used to investigate patterns in fish occurrence, abundance and density (Moore et al., 2009; Monk et al., 2011; Harvey et al., 2013; Young & Carr, 2015). This facilitates the identification of priority areas for protection and the development of zoned marine management plans (Possingham et al., 2000; Pittman et al., 2007; Stamoulis & Delevaux, 2015).

Among the various techniques currently available for remote video sampling of fish occurrence and assemblage composition, baited remote underwater stereo-video systems (stereo-BRUVs) are probably the most established. Stereo-BRUVs have been used to monitor individual species targeted by fisheries (Malcolm et al., 2015), fish assemblage composition (Malcolm et al., 2007; Harvey et al., 2013) and assemblage changes over space and time (Cappo et al., 2006; Terres et al., 2015), the impact of closed area management (Watson et al., 2007), and the impact of seismic surveys and oil spills (www.aims.gov.au/docs/research/ monitoring/seabed/video-monitoring.html; accessed March 2016). The combination of stereo-BRUVs data with fine-scale benthic habitat data from the remote sensing systems in the SDM framework (see Moore et al. 2009; Chatfield et al. 2010; Fitzpatrick et al. 2012; Terres et al. 2015 for examples) have become a powerful tool for understanding the relationships between demersal fish species and their environments (e.g. Pittman et al. 2009; Moore et al. 2010; Monk et al. 2011). In addition, the fine-resolution predictive maps generated from the modelling can provide an important layer for integrated coastal and marine planning (Leaper et al., 2012; Stamoulis & Delevaux, 2015). However, there is a significant knowledge gap in species distribution modelling with respect to the size-specific habitat requirements and partitioning of habitat resources among conspecifics throughout life-history stages.

1.1.4 The importance of considering life-history stages of fish in SDMs

Many fish species occupy different habitats at different life-history stages (Jones, 1984a; Compton et al., 2012). As an individual fish grows, its morphology and behaviour changes, as does its prey size and type (Lukoschek & McCormick, 2001; Kimirei et al., 2013).This often requires the fish to change habitats to meet energy and resource needs (Huijbers et al., 2015). Important life-history traits such as growth, mortality and longevity could be dependent on the ability of an individual to move between suitable habitats, which requires a degree of functional connectivity between habitats (Evans et al., 2014; Nagelkerken et al., 2015). Inability to move between habitats is likely to impact survivorship of individuals or entire populations.

From a fishery management perspective, facilitating successful spawning of target species is critical to maintaining self-sustaining and productive fisheries (Cooke et al., 2016). Intuitively, management efforts will concentrate on adult stock where major reproductive capacity could be invested in relatively few, old, large-size individuals that could produce exponentially more eggs than smaller size conspecifics (Larkin, 1978; Bohnsack, 1990). However, it is essential to consider patterns of connectivity across a mosaic of habitats and between all life-history stages of an exploited stock. The geographic distribution and productivity of juvenile habitats are important drivers for the spatial distribution patterns of adult populations, where source sink relationships exist (Huijbers et al., 2013). Without such consideration, management plans may not encompass the essential habitat requirements of different life stages of a range of targeted species (Schmiing et al., 2013). Therefore, it is important to identify patterns of distribution of fishes at various life stages and maintain connectivity between nursery areas and adult populations (Olds et al., 2014; Nagelkerken et al., 2015).

SDMs that incorporate the identification of critical habitats for different life-history stages of targeted and non-targeted fish species will be more useful for effective management. Models based on individual body length can help our understanding of spatial ecology of the modelled species or to identify key areas of the seascape that are crucial for different life-history stages of a single species or for multiple species (e.g. nursery areas). Mapping, followed by management or protection of such areas may result in higher survival of vulnerable life stages, depending on threats and risks (Dugan & Davis, 1993). By preserving physical linkages between discontinuous habitats crucial for juvenile and adult populations and maintaining quality of nursery areas it is possible to enhance the abundance of target and other fish species which rely on healthy ecosystem functioning (Olds et al., 2014).

Failure to do so can potentially lead to incomplete or incorrect identification of critical habitats for different life-history stages of fish (Moore et al., 2010; Nagelkerken et al., 2015; Cooke et al., 2016), affect the ecological realism of predictive modelling (Guisan & Zimmermann, 2000; Robinson et al., 2011) and potentially lead to ineffective or counterproductive management actions (Edgar et al., 2016).

1.2 Research question

The overarching goal of this research project is to utilise the individual body length measurements of demersal fish species in order to improve our understanding of environmental processes that best determine ontogenetic environmental niche partitioning among conspecific individuals throughout their life-history. Capitalising on the capabilities of spatial modelling and GIS, I synthesize the complex predictive models and maps into a simple visual aid for effective marine spatial management that allows the identification of essential fish habitat for any single and multiple species throughout their life-history (Figure 1.1).

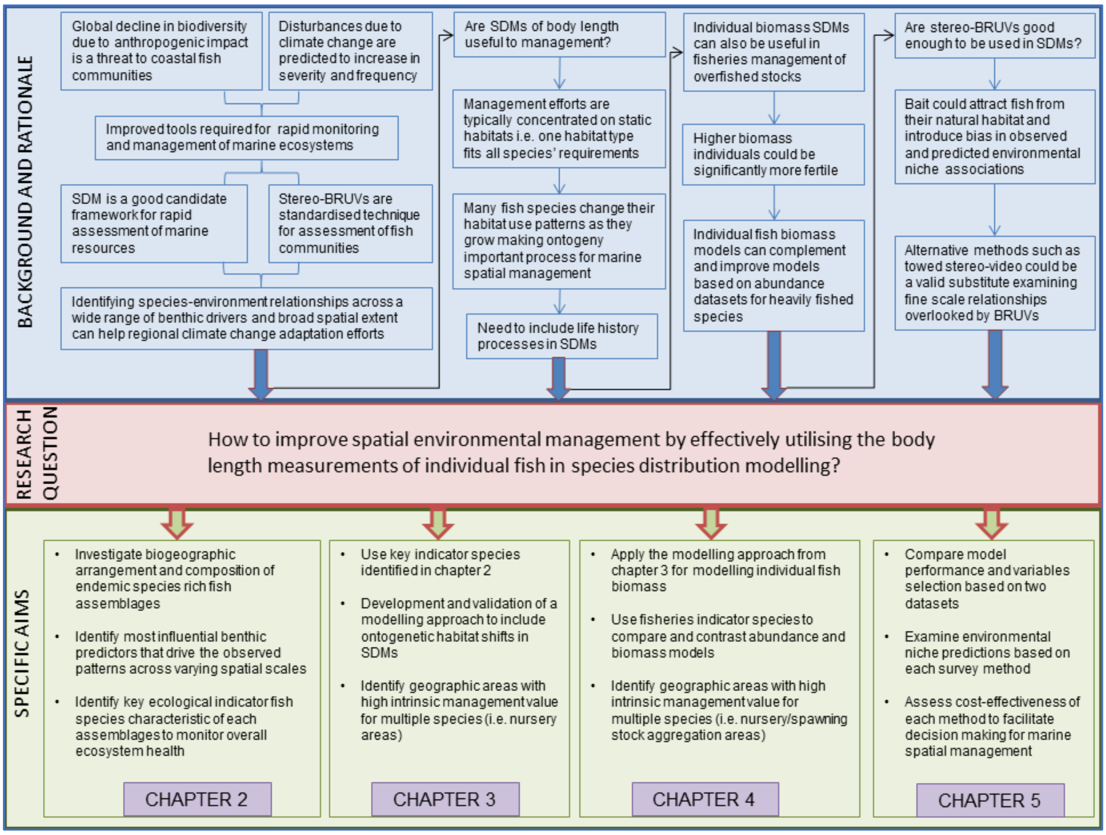


Figure 1.1 Flow diagram outlining the background, rationale and structure of the thesis.

I examine the biogeographic patterns in community structure and assemblage composition of demersal fish across a large number of explanatory environmental variables. This can help to identify the most important environmental variables that are driving patterns of distribution in marine communities as well as key indicator species that are characteristic of each assemblage. I then develop individual models for a number of indicator species that already are, or should become an object of spatial management for ecological or commercial reasons. In these models, I incorporate measurements of individual's body length to examine environmental niche requirements and habitat associations of the modelled species. Lastly, I examine some of the biases associated with using the baited underwater video method for collecting data for SDMs and compare the occurrence models developed from data collected using baited video and from an alternative towed stereo-video.

1.3 Study area

The work presented in this thesis was undertaken in south-western Australia Figure 1.2). This region is a well recognised terrestrial (Hopper & Gioia, 2004) and marine (Roberts et al., 2002) global biodiversity hotspot and has been suggested as a conservation priority area (Myers et al., 2000).

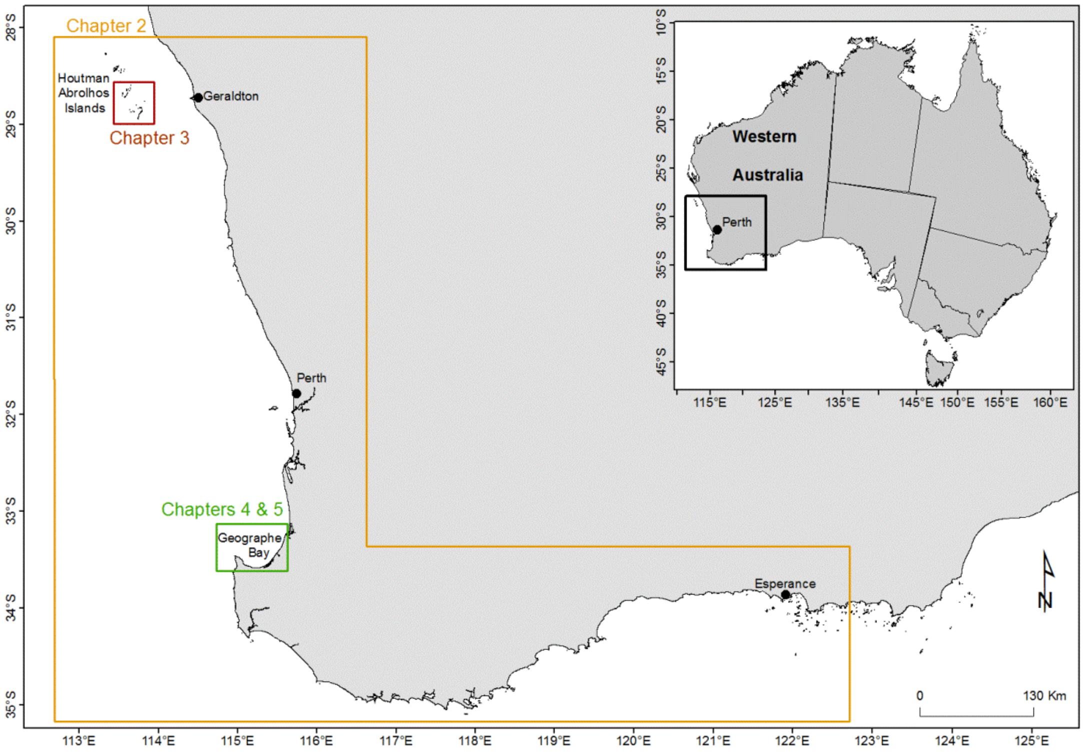


Figure 1.2 Map of south-west Australia with colour-coded panels showing the specific study areas for each chapter.

The stable geological and oceanographic history of the region has provided a relatively simple system in which speciation has been able to flourish along persistent environmental gradients (Hutchins & Pearce, 1994; Langlois et al., 2012b) resulting in the unique fish communities that have formed over millennia. Some of the families, such as the labrids and monacanthids are characterised by high diversity, narrow biogeographic ranges and high habitat specialisation (Hutchins & Pearce, 1994; Fairclough, 2005; Harvey et al., 2013).

However, the observed patterns and delicate balance of the entire region might be at risk due to synergetic effects of environmental and anthropogenic stressors. A steady increase in sea surface temperatures (SST) over the past 50 years has been observed for the West Australian continental shelf, indicating that this region is affected by SST change (Pearce & Feng, 2007). In addition, extreme climatic events, such as the 2011 marine heat wave, can significantly change the biodiversity patterns of temperate seaweeds, sessile invertebrates and demersal fish (Wernberg et al., 2013, 2016). These extreme environmental perturbations are predicted to increase in both frequency and intensity over time (Pearce & Feng, 2007; Poloczanska et al., 2007). The resilience of local fish communities may be compromised by abrupt community reorganisation (Wernberg et al., 2011; Bennett et al., 2015) due to predicted (Cheung et al., 2012) and documented (Wernberg et al., 2016) tropicalisation of fish communities in the region. Given that limited range endemics, fisheries targets or resource specialist species are often the most vulnerable to ocean warming (Last et al., 2011), knowledge about the environmental drivers and ecological niche requirements of such species is particularly crucial to develop adaptive fisheries management and conservation plans.

Data for chapters 2 and 3 were collected along 1,600 km of coastline as a part of the Marine Futures project between March 2006 and February 2008 (see matrix-prod.its.uwa.edu.au/ marinefutures/research/project; accessed July 2016 for further project details). The project aimed to map the dominant marine habitats and conduct biodiversity surveys along the subtropical and temperate Western Australian coast to establish a baseline of key marine ecosystems. These surveys were performed within the shallow continental shelf waters (~100 m) between the Houtman Abrolhos Islands, 60 km offshore from the coast of Western Australia and Esperance on the south coast. The fieldwork for chapters 3 and 4 took place in December 2014 in Geographe Bay, located approximately 220 km south of Perth. Geographe Bay is the largest temperate water embayment in Western Australia with extensive cover of seagrass meadows. Part of the data used in these chapters was collected for the Marine Biodiversity Hub. Maps for each individual data chapter are presented in subsequent corresponding chapters, given that the survey aims and the experimental design differ between chapters.

1.4 Overview of data chapters

Below I present a short overview of each data chapter. The data chapters in this thesis have been written as four manuscripts and formatted according to specific formatting requirements of the targeted journals. Thus, chapters have their own specific formatting style, introduction and aim sections and consequently may include some elements of the background information presented here. References for all chapters are consolidated into one reference section at the end of the thesis.

1.4.1 Environmental factors driving bioregionalism

In chapter 2, I investigate the environmental and biological drivers of highly endemic temperate demersal fish community patterns located within a hotspot region for increasing sea surface temperature. I use Multivariate Regression Trees (MRT) to identify benthic variables most correlated to observed patterns of demersal fish assemblage structure along 1,600 km of coastline. Habitat associations and the proportion of the endemic species in all identified assemblages were examined and the Dufrêne-Legendre index (DLI) values on the MRT output calculated to identify those species most characteristic of each assemblage (Dufrene & Legendre, 1997). A subset of the identified indicator species were later used in the subsequent chapters of my thesis.

1.4.2 Modelling ontogeny of demersal fishes

In chapter 3, six of the key indicator species identified in the previous chapter are used to develop and validate a modelling approach to investigate the body-length driven environmental niche requirements and identify ontogenetic habitat shifts using SDMs. Generalised Additive Models (GAMs) are the most common and well developed method for investigating spatial ecology of fishes (Valavanis et al., 2008; Moore et al., 2009; Chatfield et al., 2010; Schmiing et al., 2013). GAMs were used to predict the validated models onto a spatial grid of the study area across approximately 200 km^2. Using these maps, the habitat resource partitioning between the conspecifics of different life-history stages can be visually assessed and provide a decision support tool for spatial management of areas with high intrinsic value. Finally, I combine six predicted layers for individual species to identify the location of key areas such as fish nursery or multiple species aggregations spots over the entire study area.

1.4.3 Using fisheries indicator species for biomass modelling

In chapter 4, the biomass estimates of individual fish obtained through body length measurements from the stereo-BRUVs are used with the modelling approach developed in the previous chapter to examine biomass-habitat associations of three iconic fishes which are highly prized by commercial and recreational fishers. I compare and contrast models developed for the individual fish biomass with models developed for abundance of the same species. In addition, I create continuous predictive distribution maps of the biomass of individual species as well as cumulative biomass maps to identify key areas for multiple species across the study area. Mapping size-specific ecological niche distributions of targeted fishes at regional spatial scale could be extremely relevant to informing marine spatial management and for designing successful fishery management strategies.

1.4.4 Comparing two remote video survey methods for use with SDMs

Chapter 5 is the final data chapter. Here, I examine how the commonly used stereo-BRUVs may impact SDMs. The accuracy and predictive power of models developed from the data collected with stereo-BRUVs could be affected because of the dispersal of the bait plume which is used to attract fish to a camera system. The distance that a fish travels to the cameras is unknown, resulting in the potential for the true fish-habitat relationships to be skewed. I examine the use of a towed stereo-video as an alternative method to collect data on fish-environment relationships. I compare variable selection, model performance and ecological niche predictions for models developed from each dataset. In addition, I assess the cost-effectiveness of each method for marine spatial management purposes.

Chapter 2 Regional-scale, environmental drivers of highly endemic, temperate fish communities located within a climate change hotspot

2.1 Abstract

Aim: To use detailed marine habitat maps and environmental data to identify important drivers of bioregional patterns of demersal fish assemblages, characterised by a high proportion of endemic species.

Location: Near–shore marine environment of south-western Australia. This region is a globally recognised biodiversity and climate change hotspot.

Methods: We used Multivariate Regression Trees (MRT) and Distance-based Linear Models (DistLM) to identify and model which biological and/or environmental variables, amongst an initial set of 49, were most correlated to observed patterns of demersal fish assemblage structure along 1,600 km of the southwest Australian coastline. Indicator species analysis was run on the MRT output to identify fish assemblage types associated with distinct combinations of environment and habitat. Results were correlated with expected levels of resilience to predicted changes in ocean temperature.

Results: The most parsimonious model defined eight fish assemblage types and was constrained by five benthic variables and one spatial variable which together explained 42% of the variation in spatial patterns of fish community structure. Canopy forming seaweeds were the major benthic drivers and when found on structurally complex hard habitat, supported the highest diversity of species after sites dominated by hard coral cover. Indicator species analysis revealed that 28 out of 35 (80%) significant species for this habitat type were endemics with the fish assemblages associated with these habitats often spatially limited to 10's or 100's of kilometres.

Main conclusions: Canopy forming seaweeds were identified as a key component of the habitat types favoured by high proportion of endemic fish species in the region. This benthic group has already been subject to catastrophic temperature related die-offs on reefs in the northern part of this study, indicating its vulnerability to temperature driven climate change.

The predicted changes can result in major regime shifts in temperate ecosystems as well as affect the associated commercial and recreational fisheries of iconic species in the region.

2.2 Introduction

Global declines in biodiversity driven by anthropogenic impacts such as burning of fossil fuels, deforestation and pollution are well documented (Butchart et al., 2010; Bellard et al., 2012; Hooper et al., 2012). Such declines can lead to major changes in ecosystem function, and a reduction in the resilience of ecosystems to environmental change (Chapin III et al., 2000; Sala & Knowlton, 2006). This loss of biodiversity and its flow-on effects extends to the marine environment where declining diversity has been closely linked to collapsing fisheries resources and poor water quality (Worm et al., 2006). Coastal fish communities have been particularly vulnerable, with serious declines in biodiversity through overfishing, eutrophication and loss of habitat (Jackson et al., 2001).

While many disturbances are locally-driven, climate change is imposing impacts on marine communities at scales not previously seen, with temperature-driven coral bleaching at regional, national and global scales a poignant example of this (e.g. Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007). However, most research remains targeted at local scales with landscape level understanding still being drawn from the integration of smaller-scale observations and concepts (Buddemeier & Fautin, 2002). A recent review of climate change impacts on marine life in Australia (where this study is based) has highlighted the lack of studies on species at regional or national scales (Poloczanska et al., 2007). Given the potential for climate change to affect sea temperature and chemistry, ocean currents, wind and precipitation patterns over large areas (Harley et al., 2006; Poloczanska et al., 2007) there is a renewed need for large-scale biogeographic studies that integrate multiscalar environmental variables and quantify their influence on community structure and distribution.

Australia’s temperate marine waters are unique for their disproportionately high levels of endemism, which persists across taxa. Long periods of climatic stability and geographic isolation have resulted in > 85% of fish, echinoderm and mollusc species, and 50% of algae species in southern waters being endemic (Poore, 2001; Roberts et al., 2002). The southwest region in particular is recognised as a global centre of endemism for fish, corals, snails and lobsters (Roberts et al., 2002). The fish communities along this coast are a unique combination of species of temperate origin, mixed with tropical and subtropical species that have migrated south under the moderating influence of the southward-flowing, Leeuwin current (Hutchins, 2001). While the species richness of some families such as the monacanthids and labrids is particularly high (Harvey et al., 2013) the majority of members of these families are characterised by very narrow biogeographic ranges and high habitat specialisation (Hutchins & Pearce, 1994; Hutchins, 2001; Fairclough, 2005; Lek et al., 2011).

Sea surface temperatures (SST's) have been increasing steadily along the south west coast of Western Australia for the past 50 years (Pearce & Feng, 2007), identifying this region as a climate change hotspot and hence pivotal location for observing the effects of rising temperatures on marine ecosystems. Extreme manifestations of this warming have already been seen, with a marine heatwave in 2011 pushing nearshore temperatures to ~5^0C above average resulting in devastating fish kills and transient southerly range extensions of tropical fish species and megafauna such as whale sharks and manta rays (Pearce & Feng, 2013; Wernberg et al. 2012). With the frequency and intensity of such environmental perturbations predicted to increase (Pearce & Feng, 2007; Poloczanska et al., 2007) the resilience of regional temperate water fish communities may be further compromised with endemic species mostly at risk.

Identification of significant species-environment patterns across varying spatial scales, and monitoring of shifts in these patterns relative to changing environmental conditions, can contribute significantly to local and regional climate change adaptation strategies. In this study, we set out to identify influential environmental and biological drivers of demersal fish assemblage patterns across 1,600 km of coastline covering four distinct bioregions in south-western Australia. A focus on landscape-scale patterns provides insights into climate change effects at a scale commensurate with the scale at which these effects are unfolding, addressing a clearly identified need. More specifically, we sought to identify whether the endemic component of the fish assemblages in this region were being influenced by a more constrained set of environmental and/or biological variables. A better understanding of the habitats and general environmental conditions specific to endemic fish assemblages in this uniquely diverse region will further our understanding of the processes of speciation and extinction (Lawton, 1993; Mora & Robertson, 2005), enabling more focused and effective management.

2.3 Methods

2.3.1 Study area and data collection

The coastline of Western Australia extends for almost 13,000 km, bordered by the Timor Sea in the north, Indian Ocean to the west and the Great Southern Ocean in the south (Cheung et al., 2012). The Leeuwin Current is the dominant poleward-flowing tropical-water ocean current in this region. It transports the larvae of algae, invertebrates and tropical fishes south along the west coast and eastwards into the Great Australian Bight (Maxwell & Cresswell, 1981). The stable geological and oceanographic history of the region has provided a simple system in which speciation has been able to flourish in both terrestrial and marine environments along persistent environmental gradients (Hutchins & Pearce, 1994; Hopper & Gioia, 2004; Langlois et al., 2012b). Benthic habitats in the region are dominated by rocky reefs interspersed with canopy forming kelp, fucalean and red algae communities (Wernberg et al., 2003).

All fish and habitat data used in our analyses were collected as a part of the Marine Futures project (matrix-prod.its.uwa.edu.au/marinefutures/research/project; accessed July 2016). The project aimed to map the dominant marine habitats and conduct biodiversity surveys along the subtropical and temperate West Australian coast to establish a baseline of key marine ecosystems. These surveys were performed within the shallow continental shelf waters (~100m) at seven regions of Western Australia, spanning four distinctive bioregions in this area (Figure 2.1). To maintain consistency in the interpretation of our findings we employ the same ecosystem-based classification of marine and coastal environments of the south-west region as was proposed in the Interim Marine and Coastal Regionalisation for Australia (IMCRA, 1998).

2.3.2 Available environmental variables

Hydroacoustic maps were developed after surveying approximately 1,400 km of the seafloor across the seven study regions between March 2006 and February 2008. Underwater towed video footage was also collected over > 210 linear km. The environmental database was constructed by combining the hydroacoustic maps, substrate and biological benthos observations from towed video imagery in a statistical modelling framework using Classification and Regression Trees (CARTS) to predict probabilities of occurrence of substrate and biota in areas with no observations (see Radford et al., 2008 for detailed methods on habitat modelling and uncertainty measures). For each area, all identified benthos classes with sufficient numbers of observations for modelling were mapped, including sediment texture and relief, reef structures, vegetation types, and different classes of sessile invertebrates, providing a total of forty five variables. These maps were used to develop sampling plans for baited remote underwater stereo-video systems (stereo-BRUVs) for fish surveys. The environmental variables for our analysis were extracted by querying an existing database and cross referencing it with the fish sampling data.

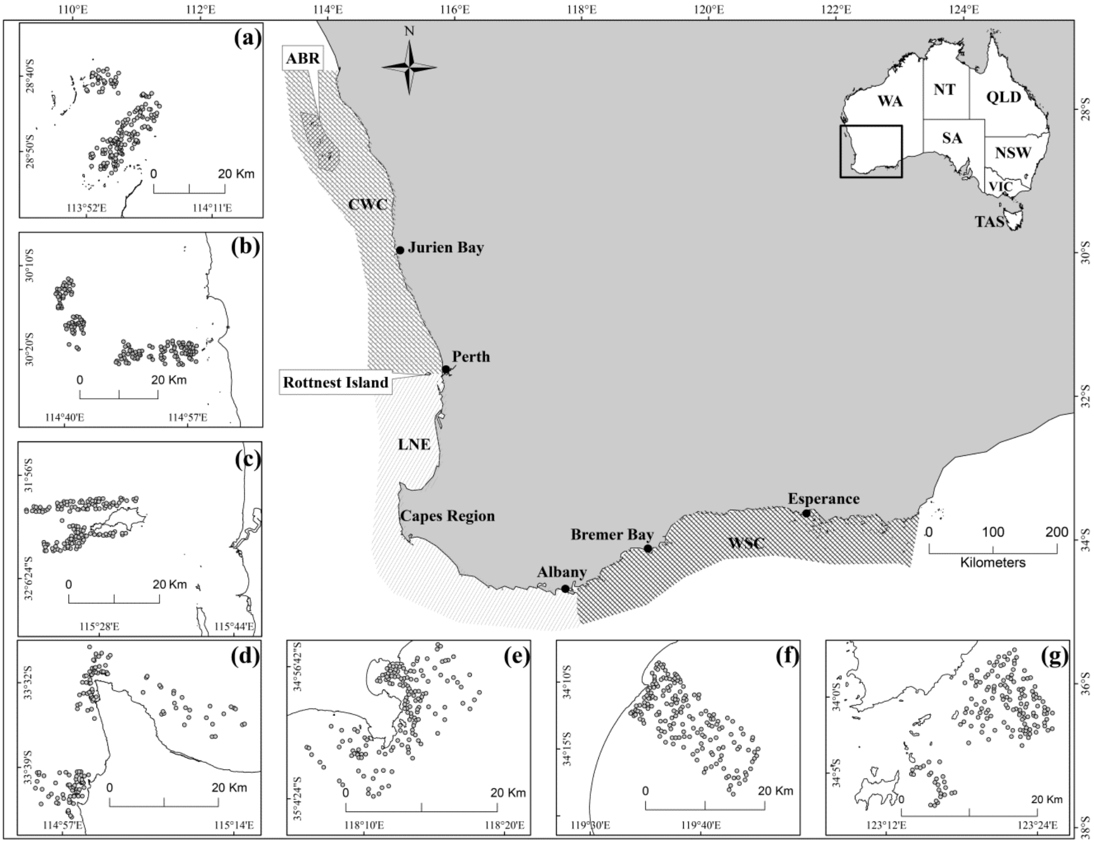


Figure 2.1 Map of the south-west coast of Western Australia (Geocentric Datum of Australia 1994 equal-area projection) showing four bioregions: ABR, Abrolhos Islands; CWC, Central West Coast; LNE, Leeuwin-Naturaliste; WSC, WA South Coast. The insets show position of seven sampling regions: (a) Abrolhos islands; (b) Jurien Bay; (c) Rottnest Island; (d) Capes region; (e) Albany; (f) Bremer Bay; (g) Esperance. Positions of individual stereo-BRUVs surveys in each region are marked by grey circles.

2.3.3 Sampling of fish assemblages

We analysed demersal fish assemblages recorded by stereo-BRUVs and assessed their relationships to biotic and abiotic environmental variables that had been modelled from multibeam and towed video surveys along 1,600 km of the south-west region of the continental shelf of Western Australia (Figure 2.1). Locations for sampling with stereo-BRUVs were chosen based on our overall goals of understanding fish biodiversity, benthic habitat relationships and frequency of occurrence. The modelled habitat maps, with probabilities of occurrence of various biota and substrate variables, were used to decide on locations for all sampling sites except those at the Abrolhos Islands, where timing meant stereo-BRUVs sampling was conducted before the habitat maps were completed. In this case, bathymetry alone was used for planning. To ensure sampling replication was appropriate, sampling was spatially stratified according to the size of the study area, benthic habitat (substrate and biotic benthos) and depth (see Radford et al., 2008 and matrix-prod.its.uwa.edu.au/marinefutures/research/project; accessed July 2016 for further details on site selection criteria). Within each combination of strata, sampling was randomly assigned and distance controls used to avoid spatial autocorrelation. The minimum separation distance of 500 m between the individual stereo-BRUVs is considered to be sufficient to minimise the possibility of attraction of individual fish between stations and keep the samples independent (Harvey et al., 2007).

Design, calibration (Harvey & Shortis, 1995; Shortis et al., 2009) and use of the stereo-BRUVs is presented in detail in the literature (Cappo et al., 2003). Each system was baited with approximately 800 g of crushed pilchards (*Sardinops sagax*), and lowered to the bottom for a 60 minute soak time. The video recordings from these deployments were analysed using the software EventMeasure (SeaGIS Pty Ltd). In order to avoid repetitive counts of individual fish in 1 hour long recordings, MaxN of individual species appearing at one time was used. This measure is considered to be conservative for estimating fish abundance (Cappo et al., 2003). All fish were identified to the lowest taxonomic level possible. The final dataset consisted of 1090 one-hour stereo-BRUVs deployments from which 54,908 individual fish from 219 fish species were identified. This represents approximately 64 % of the total diversity of neritic species recorded for the south-west of Western Australia (Fox & Beckley, 2005). Due to the unidirectional flow of the Leeuwin current, we also included a distance along shore (Das) variable in the analyses to account for this directionality. This distance was calculated as the Euclidean distance from a single point located north from the northern-most sampling area to any point where a stereo-BRUVs survey was performed, using ArcMap 10.1 (Borcard et al., 2011).

2.3.4 Data analyses

The responses of species along environmental gradients are not always linear. Consequently, linear and non-linear multivariate analysis techniques were used to investigate patterns in the spatial distribution of demersal fish assemblages. Environmental variables were extracted from the benthic habitat maps by intersecting with the stereo-BRUVs sampling locations in the shared database along with latitude, longitude, depth and the Das variable. This provided a total of 49 predictive variables for each assemblage sampling record (Supplement 2.7.1).

To avoid issues with correlation between explanatory variables in multiple linear regression analyses, Draftsman’s plots were created to examine continuous variable correlations. Where pairs of environmental variables had correlations greater than 0.7 one variable was excluded from the modelling (Moore et al., 2010). In addition, Variance Inflation Factor (VIF) analysis was performed with cut off variance values below 3 accepted (Zuur et al., 2010). We used a distance-based linear model (DistLM) and a CY dissimilarity matrix to perform a preliminary exploration of relationships between demersal fish assemblages and the normalised environmental variables (Cao et al., 1997; Anderson et al., 2008). The CY index is an appropriate dissimilarity measure for analysis of community composition data covering large spatial areas where beta diversity is high and there are many sites with few species in common (Anderson & Thompson, 2004). It is also a sensitive measure of dissimilarity that provides equal weighting for different types of multivariate variation in species abundance with minimal bias (Cao et al., 1997). Uncommon or rare species which were recorded only once or twice in the entire dataset (31 % of total species records) were excluded from the analyses. Rare species tend to amplify importance of rare habitat types. By removing rare species we avoided grouping sites with a shared common absence of rare species, instead concentrating specifically on common habitats found throughout the region (Gust et al., 2001). Backward model selection using AIC selection criterion was employed to obtain a preliminary model and to reduce a large number of predictors. The advantage of AIC when exploring variable contributions is that it tends to incorporate more variables within the model than other more strict selection criteria (Boyce et al., 2002). This enables all contributing variables to be considered based on the known ecology of species and, if needed, further tested by more parsimonious methods (Moore et al., 2010). A final list of 18 environmental explanatory variables produced by the exploratory DistLM model to be used in future analyses and a short description of each retained predictor variables is presented in Table 2.1.

To define hierarchies of groups of co-occurring species that form communities according to the influence of explanatory variables, we used multivariate regression trees (MRT) with the environmental variables chosen from the DistLM model (De’ath, 2002). MRT are a type of constrained clustering and a robust method for modelling complex linear and non-linear relationships (De’ath & Fabricius, 2000; De’ath, 2002). The CY dissimilarity matrix was calculated on the raw relative abundance data (excluding rare species) prior to running the MRT analysis. The most parsimonious tree was selected using cross-validation and the 1-SE rule (De’ath & Fabricius, 2000). Dufrêne-Legendre index (DLI) values were then calculated for all species across all leaves of the tree so that those species most typical of a node could be identified (Dufrene & Legendre, 1997). The DLI is defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups (specificity), multiplied by the proportion of sites within the group where the species occurs (fidelity), multiplied by 100 (DeVantier et al., 2006).

Table 2.1 Results of distance based linear model (DistLM; R^2 = 0.25, AIC = 684) based on CY dissimilarity measure identifying the preliminary environmental variables using backward model selection procedure. These environmental variables were further used in the multivariate regression tree analysis.

Predictor Code	Description & units
Das	Distance along shore. A relative distance in km along coastal gradient from an arbitrary point north of northern-most study site
depth	Water depth in metres relative to the Australian Height Datum
kelp	The kelp *Ecklonia radiata*. Probability of occurrence between 0-1
macalg	Mixed canopy foming macroalgae. Probability of occurrence between 0-1
othalg	Mixed unidentified algae. Probability of occurrence between 0-1
seagrass	Mixed seagrass. Probability of occurrence between 0-1
veget	Mixed vegetation (i.e. seagrass and algae). Probability of occurrence between 0-1
scytot	The seaweed *Scytothalia dorycarpa*. Probability of occurrence between 0-1
rhodo	Rhodolith beds (hard structures of coralline algae on sandy substrates). Probability of occurrence between 0-1
reef	Mixed undifferentiated reef. Probability of occurrence between 0-1
rfhigh	High profile reef (relief greater than 4 m). Probability of occurrence between 0-1
rflow	Low profile reef (relief less than 1 m). Probability of occurrence between 0-1
rfmed	Medium profile reef (relief between 2 and 4 m). Probability of occurrence between 0-1
obsrf	Obscured reef (hard substrate covered with sand veneer). Probability of occurrence between 0-1
sand	Undistinguished fine sandy substrate. Probability of occurrence between 0-1
sed	Unconsolidated sediment. Probability of occurrence between 0-1
grav	Substrate that have clearly grainy nature. Probability of occurrence between 0-1
figrav	Fine substrate of a clearly grainy nature. Probability of occurrence between 0-1

Each species is assigned to the leaf of the tree where its DLI value is highest. Species with the highest DLI values are considered representative of that assemblage, and the spatial extent of the assemblage indicated the region where the species was predominantly found (see DeVantier et al., 2006 for an example). This analysis was performed in R statistical software (R Core Team, 2014), using the packages mvpart, vegan and MVPARTwrap.

To examine the main trends in ordination of multivariate ecological communities in the form of continuous axes we submitted the data to an unconstrained ordination analysis using Principal Coordinates Analysis (PCO) and a CY dissimilarity matrix in PRIMER v.6 (Clarke & Gorley, 2006). The PCO is particularly well adapted to analyse data from ecological communities, which are naturally structured along gradients (Borcard et al., 2011). Environmental vectors and the species correlations (raw Pearson correlations > 0.3) were overlayed onto the PCO plot in order to identify the strength and direction of the relationships identified.

2.4 Results

2.4.1 Patterns in fish assemblages

DistLM analysis identified a model with 18 environmental variables, explaining 25 % of the variation in the data ($R^2 = 0.25$, AIC = 684, Table 2.1). These environmental variables were used as explanatory variables in the multivariate regression tree analysis (MRT). The MRT explained approximately 42 % of the variation in the species abundance data with a more parsimonious model than the DistLM, identifying six key environmental variables from the 18 submitted to the analysis. The final tree identified eight distinctive fish assemblages (Figure 2.2). The assemblage abbreviations, regional description and the list of Dufrêne & Legendre indicator (DLI) species are shown in Table 2.2.

The primary split in the MRT occurred between assemblages where macroalgae cover was either high or low. Sites where macroalgae was sparse were further separated by distance along shore (Das ~ 93), which identified the sub-tropical Abrolhos Islands bioregion as a terminal node of the tree (ABR, Figure 2.2). The ABR, subtropical coral reef associated community is represented by a mix of reef, near-reef and sand dwelling species of Indo-Pacific origin and endemic species (WA and Australia) dominated by two highly abundant species of the Nemipteridae and a single species of Pinguipedidae (Table 2.2).

Sites with low algal cover south of the Abrolhos Islands bioregion were further split between reef and sand associated communities (sand ~ 0.89). The two leaves of the tree in the sand associated node separated western and eastern assemblages by distance along shore (Das ~ 1553).

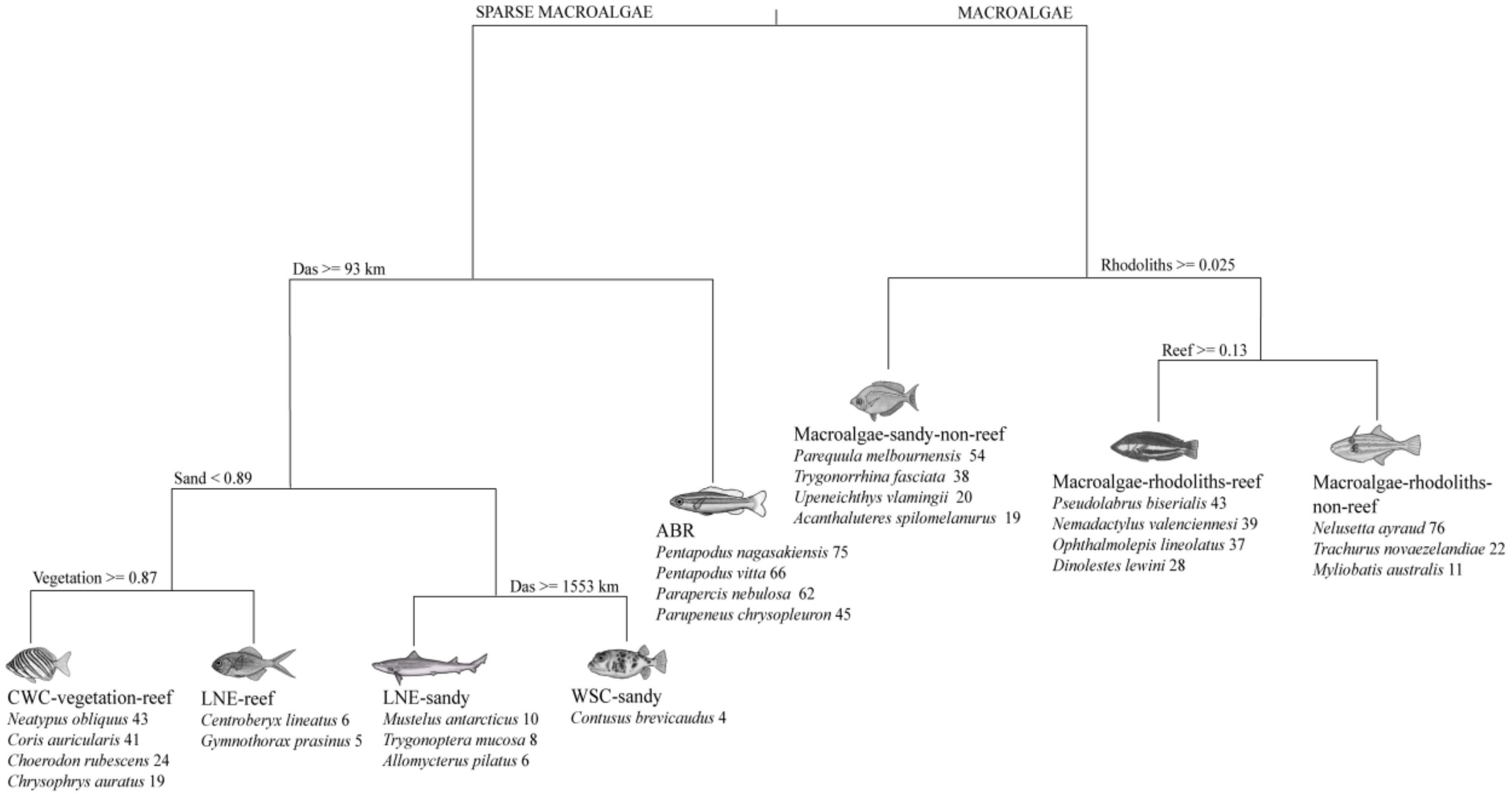


Figure 2.2 Pruned (1SE) Multivariate Regression Tree defining relative abundance of fish communities (CY dissimilarity index) constrained by six environmental variables indicated in the tree (Error: 0.566; CV Error:0.58; SE: 0.015). The terminal nodes represent eight communities scattered across four bioregions: ABR, Abrolhos Islands; CWC, Central West Coast; LNE, Leeuwin-Naturaliste WSC, WA South Coast. Four indicator species with highest values of the Dufrêne-Legendre index (DLI) are shown for each terminal leaf as well as a silhouette of the highest DLI species. The high DLI values represent 'indicative' species of a particular assemblage. Additional details of node names and full species DLI are given in Table 2.2.

The western sand associated assemblage of Leeuwin-Naturaliste bioregion (LNE-sandy) was mostly represented by low relief and soft substrate endemic demersal species, including the Australian endemic species of gummy shark *Mustelus antarcticus* and the shovelnose stingaree *Trygonoptera mucosa* (Figure 2.2 and Table 2.2). The eastern sandy assemblage of WA south coast bioregion (WCS-sandy) was characterised by the Australian endemic toadfish *Contusus brevicaudus* (Figure 2.2).

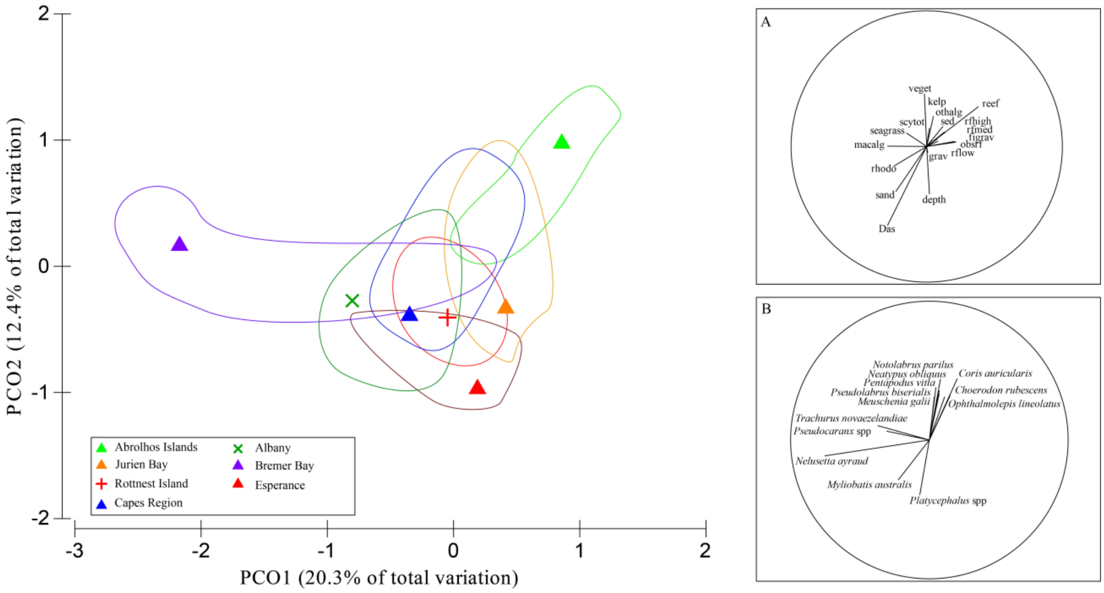


Figure 2.3 Principal coordinates analysis (PCO) on CY resemblance matrix of the relative abundances of fish communities in the 1090 survey sites and overlaid biplots of 18 normalised environmental variables (inset a) found significant in the DistLM and used in the MRT analyses, and the species affiliations vectors (raw Pearson correlations > 0.3; inset b). For convenience of interpretation, centroids of seven study regions are plotted and data range of individual regions is sketched. The length and direction of the vectors represent the strength and direction of the relationship. The separation along the PCO1 axis was based on occurrence of biotic features and topographic complexity and explained 20.3 % of total variation. The PCO2 axis explained 12.4 % of total variation and the separation of samples indicated a strong distance along shore and depth gradients with additional effect of various types of vegetative cover. The species vectors indicated higher affiliation to complex seascape environments. Additional details for environmental variables names and a short description are given in Table 2.1.

The reef node of the tree was further separated into offshore reefs along central west coast bioregion with patches of vegetative cover (CWC-vegetation- reef) represented by high abundance of endemic species from the Kyphosidae and Labridae families. In contrast, high wave impact rocky reefs with low or no vegetative cover (LNE-reef) were characterised by assemblages dominated by the ubiquitous members of the Berycidae and Muraenidae families (Figure 2.2, Table 2.2).

The high macroalgae cover node of the tree was further split into a node with intermediate to high cover of rhodoliths (Rhodoliths ~ 0.025) and a terminal leaf identifying low relief, soft substrate and macroalgae associated community (Macroalgae-sandy-non-reef) with high abundance of Australian endemic species (Figure 2.2, Table 2.2). An additional split in the tree separated reef sites (Reef ~ 0.13) from the low relief sites. Australian endemic ocean leatherjacket *Nelusetta ayraud* was highly abundant in the macroalgae covered non-reef sites with rhodolith beds (Macroalgae-rhodoliths-non-reef), whereas coastal reef sites covered by macroalgae (Macroalgae-rhodoliths-reef) were mostly dominated by Australian endemic species from the Labridae and Dinolestidae families (Figure 2.2, Table 2.2).

The two first axes of the unconstrained PCO explained almost 33 % of total variation in species relative abundance along the WA coast. The examination of overlayed eigenvectors of environmental variables portrayed sample separation along PCO1 axis based on positive association with an array of topographic complexity measures, such as various degrees of reef complexity. On the other hand, there were negative associations between the biotic features (seagrass, macroalgae and rhodoliths) and sample separation along the PCO1 axis. The separation along PCO2 axis was mainly negatively associated with depth and distance along shore and positively associated with various types of vegetative cover (Figure 2.3a, Table 2.1). The species vectors biplot have further demonstrated a high affiliation of species to reef and complex seascape environmental features, whereas none of the abundant species showed strong affiliation with low relief and deep water habitats (Figure 2.3b).

2.4.2 Key indicator species and MRT clusters richness

Across all terminal leaves of the MRT, only 6 % of species had a high DLI (≥50), while almost 23 % of species had moderately high DLI values (between 20 and 50). The CWC-vegetation-reef, ABR, Macroalgae-sandy-non-reef and Macroalgae-rhodoliths-reef assemblages had a small to intermediate number of sites (1-18 % of total number of sites), however they dominated the DLI analysis. The most noticeable groupings were ABR and Macroalgae-rhodoliths-reef assemblages, comprising only 15 % and > 1 % of all sites respectively, but including 35 % and 26 % of total species with moderate to high DLI (Table 2.2). These four assemblages and the LNE-reef assemblage, while spatially quite restricted, had relatively high species richness and were dominated by families associated with complex seabed structure such as subtropical and temperate reef habitats and/or macroalgae canopy cover (Figure 2.4). In addition, the complex relief and species rich assemblages of Central West Coast and Leeuwin-Naturaliste bioregions were characterised by high endemic species richness, while the Abrolhos Islands and Western Australian south coast bioregions had mostly low numbers of endemic species (Figure 2.4, Table 2.2).

Table 2.2 Summaries of all indicator species in the eight terminal fish communities of the multivariate regression tree (Figure 2.2). Values of the Dufrêne-Legendre index (0 < DLI ≤ 100) for each discriminant species are shown in brackets. The higher DLI value, the more 'indicative' the species is of a specific assemblage. The total number of sites and total number of the indicator species are shown for each terminal leaf. The asterisk symbols (*/**) next to DLI indicate WA/Australia endemic species respectively.

Assemblage abbreviation	**Regional and environmental description**	**No. of sites**	**No. of DLI species**	**Indicator species (DLI)**
CWC-vegetation-reef	Central coast, mixed seagrass and macroalgae, reef	202	11	*Neatypus obliquus (43**), Coris auricularis (41*), Choerodon rubescens (24*), Chrysophrys auratus (19), Trygonoptera ovalis (18**), Plectorhinchus flavomaculatus (13), Gymnothorax woodwardi (11*), Heterodontus portusjacksoni (9), Glaucosoma hebraicum (7*), Scorpis georgiana (5**), Pictilabrus laticlavius (5**)*
LNE-reef	Between Capes region and Esperance, reef	275	2	*Centroberyx lineatus (6), Gymnothorax prasinus (5)*
LNE-sandy	Between Capes region and Esperance, sandy bottom	128	3	*Mustelus antarcticus (10**), Trygonoptera mucosa (8**), Allomycterus pilatus (6)*
WSC-sandy	Esperance, sandy bottom	118	1	*Contusus brevicaudus (4**)*
ABR	Abrolhos Islands region	165	25	*Pentapodus nagasakiensis (75), Pentapodus vitta (66*), Parapercis nebulosa (62**), Parupeneus chrysopleuron (45), Torquigener vicinus (32), Lagocephalus sceleratus (32), Lethrinus genivittatus (21), Saurida spp (21), Caesioscorpis theagenes (19*), Choerodon jordani (13), Lethrinus miniatus (13), Diagramma labiosum (11), Chromis westaustralis (10), Carcharhinus obscurus (10), Scarus schlegeli (9), Plectropomus leopardus (8), Chaetodon assarius (7*), Parupeneus spilurus (7), Scombridae spp (7), Ammotretis elongatus (5), Lethrinus nebulosus (5), Echeneis naucrates (4), Pentapodus porosus (4), Decapterus russelli (4), Rhynchobatus djiddensis (4)*

Macroalgae-sandy- non-reef	Mixed macroalgae, sandy bottom, low complexity	49	11	*Parequula melbournensis (54**), Trygonorrhina fasciata (38**), Upeneichthys vlamingii (20), Acanthaluteres spilomelanurus (20**), Suezichthys bifurcatus (19**), Meuschenia scaber (12), Scobinichthys granulatus (10**), Sillaginodes punctata (8**), Sillago spp (7), Anoplocapros amygdaloides (6**), Aptychotrema vincentiana (6**)*
Macroalgae-rhodoliths-reef	Mixed macroalgae, rhodolith beds, reef	15	24	*Pseudolabrus biserialis (43*), Nemadactylus valenciennesi (39), Ophthalmolepis lineolatus (37**), Dinolestes lewini (28**), Notolabrus parilus (24**), Pseudocaranx spp (20), Meuschenia flavolineata (18**), Meuschenia galii (18**), Meuschenia hippocrepis (17**), Odax cyanomelas (16**), Caesioperca rasor (16**), Bodianus frenchii (16), Chromis klunzingeri (15*), Epinephelides armatus (14*), Scorpis aequipinnis (13**), Achoerodus gouldii (10**), Hypoplectrodes nigroruber (10**),Centroberyx gerrardi (8**), Aulopus purpurissatus (8**), Austrolabrus maculatus (8**), Parascyllium variolatum (7**), Cheilodactylus nigripes (7), Omegophora cyanopunctata (5**), Othos dentex (5**)*
Macroalgae-rhodoliths-non-reef	Mixed macroalgae, rhodolith beds, low complexity	138	3	*Nelusetta ayraud (76**), Trachurus novaezelandiae (22), Myliobatis australis (11)*

In contrast, LNE-sandy, Macroalgae-rhodoliths-non-reef, LNE-reef and WSC-sandy assemblages had moderate to high numbers of sites (11-25 % of total number of sites), but contained either single or no indicator species with moderate values (Table 2.2). With exception of the LNE-reef assemblage, such groups had mostly moderate to low species and endemic species richness.

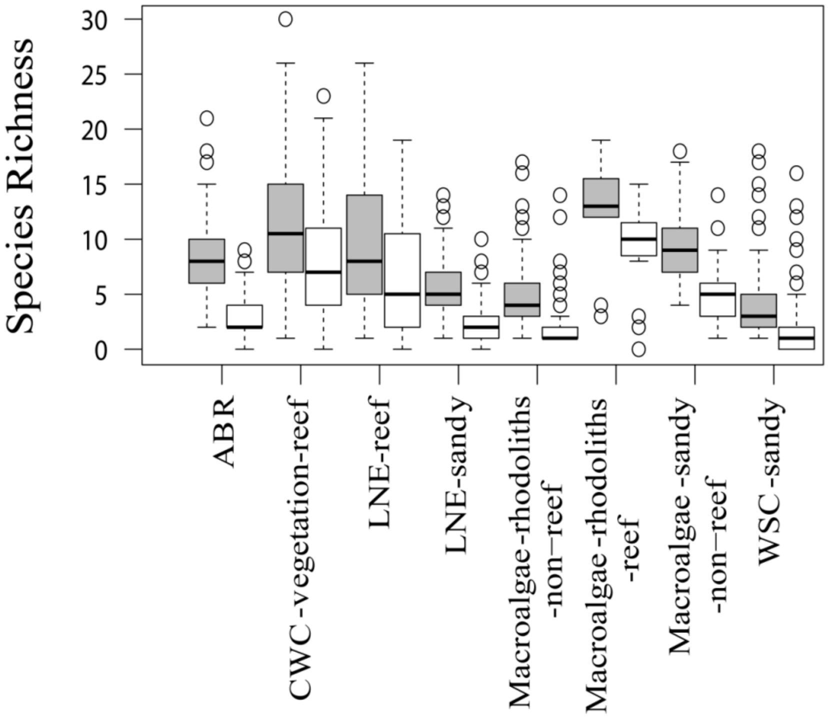


Figure 2.4 Mean species richness (■) and mean endemic species richness (□) +/- SE in eight fish assemblages resulted from the multivariate regression tree clusters and across four bioregions: ABR, Abrolhos Islands; CWC, Central West Coast; LNE, Leeuwin-Naturaliste; WSC, WA South Coast. The more structurally complex clusters are associated with higher endemic and overall species richness.

These groups were dominated by mobile individuals from families mainly associated with low relief seascapes, such as sandy habitats with some degree of cover of macroalgae (LNE-sandy, Macroalgae-rhodoliths-non-reef, WSC-sandy) or ubiquitous habitat generalist species that occur in high numbers elsewhere (LNE-reef). The south-east boundary of the study area had the lowest overall species richness and the lowest endemic species richness (Figure 2.4, Table 2.2).

2.4.3 Spatial arrangement of the assemblages

The spatial extent and arrangement of the demersal fish assemblages identified from the MRT along the south-western Australia coast are presented in Figure 2.5. The Abrolhos Islands bioregion was identified as a separate assemblage with only one site in the southern part of this region belonging to another assemblage (LNE-sandy, Figure 2.5a). The assemblages along the south-west coast were spread from north to south and gradually changed from those associated with the limestone reefs and vegetative cover characteristic of the Central West Coast to those associated with the granite reefs dominating the Leeuwin Naturaliste bioregion (Figure 2.5b-e). In addition, two fundamentally different assemblages were observed between western and eastern sites of the Capes region (Figure 2.5d). There was a clear change in dominance between assemblages on the south and south-west coasts that occurred between Albany and Bremer Bay (Figure 2.5e-f). This change closely aligns with the existing bioregions (Figure 2.1). Reef associated assemblages were replaced by macroalgae associated assemblages of the southwest and in turn by unique sand associated assemblages of the south coast bioregion (Figure 2.5e-g).

2.5 Discussion

Spatially extensive studies that parallel the landscape scales at which climate change is influencing the natural environment remain pivotal to understanding how regional communities will respond. Our study utilized data from 1,090 stereo-BRUVs samples that recorded ~ 55,000 individuals belonging to 219 demersal fish species spanning 1,600 km of the south-west Australian coast, inclusive of four bioregions (*sensu* IMCRA, 1998). MRT identified six key variables, one spatial (Distance along shore), three biological (macroalgae, rhodoliths, vegetation) and two geomorphological (sand, reef), which together explained 42 % of the observed variation in the demersal fish assemblage composition over the study area. The percentage of variation explained in this study was up to 18 % greater than three other similar large-scale studies undertaken within the same broader region (see Cappo et al., 2007; Langlois et al., 2012; Harvey et al., 2013) implying that our analytical approach had a great ability to discriminate the principal drivers of fish assemblage structure.

The most parsimonious MRT model defined eight fish assemblage types constrained by various combinations of the six significant explanatory variables. These assemblages were nested within our seven sampling regions with only the Abrolhos region containing a single assemblage type, defined by the most southerly extension of true coral reefs along this coastline (Smith, 1981). Presence of macroalgae was the primary driver of fish assemblage types explaining 13% of the total variation in the observed patterns, equating to 30 % of the variation explained by our model. This result concurs with earlier work in the region which found macroalgae to be a significant driver of spatial variation in local fish assemblages in the Recherche Archipelago which lies on the south-easterly fringe of our study area (Harvey et al., 2013).

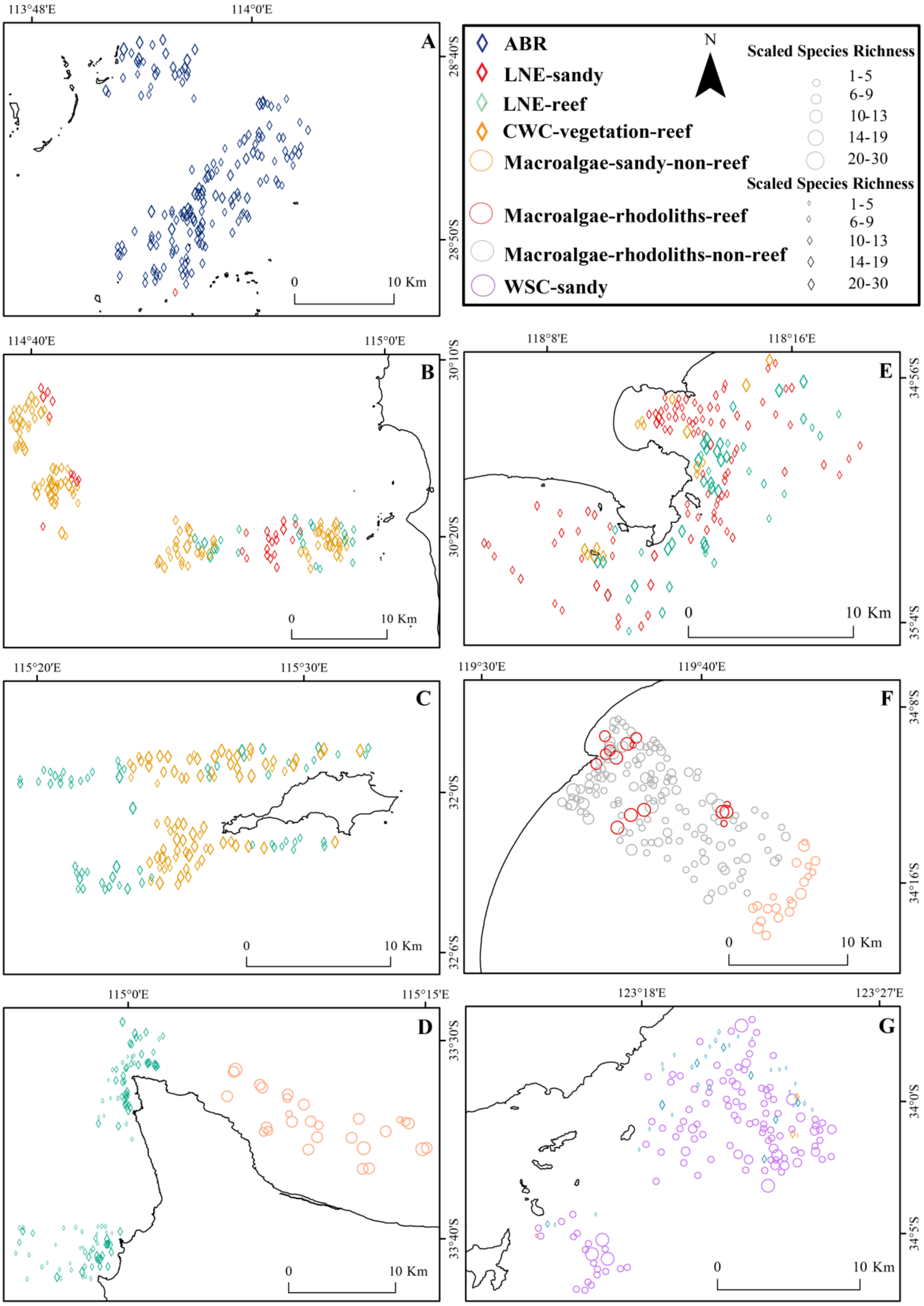


Figure 2.5 Spatial distribution of eight fish assemblages (Geocentric Datum of Australia 1994 equal-area projection) obtained from the multivariate regression tree analysis across seven sampling regions: (a) Abrolhos islands; (b) Jurien Bay; (c) Rottnest Island; (d) Capes region; (e) Albany; (f) Bremer Bay; (g) Esperance within four bioregions: ABR, Abrolhos Islands; CWC, Central West Coast; LNE, Leeuwin-Naturaliste; WSC, WA South Coast. The assemblage symbols are scaled by species richness.

Of the 910 sites included in our final model 22 % (202) had fish assemblages significantly associated with the presence of macroalgae. These habitats were spatially constrained to only two regions; the Capes and Bremer Bay (Figure 2.5), where DLI indices indicated that their associated fish assemblages contained the greatest number of endemic species and the highest overall species richness (see Figure 2.4).

As sessile organisms with limited dispersal capabilities seaweeds have been identified as being particularly sensitive to climate change (Wahl et al., 2015; Wernberg et al., 2016). Light penetration and the requirements for seaweeds to photosynthesise eliminate the possibility of depth refugia for seaweeds and southerly range extensions are not possible because of the lack of habitat to the south of the Australian mainland. This provides limited opportunities for species to shift their geographical ranges poleward in response to sea surface temperature warming, resulting in a narrowing of geographical ranges (Wernberg et al., 2011). Mixed algal communities also become more monospecific with increasing temperature (Wernberg et al., 2011) with weedy species outcompeting the larger canopy-forming algae that are primary habitat providers for their associated fish assemblages (Gorman & Connell, 2009).

Endemism and habitat specialisation in this region has been attributed to the unique oceanography associated with Australia's boundary currents, and climatic stability over geological timescales (Adey & Steneck, 2001; Phillips, 2001; Kerswell, 2006). These same traits in demersal reef fish assemblages of southwest Australia are now recognised as indicators of vulnerability to extinction (Bender et al., 2013; Harvey et al., 2013). Nearly 41 % of the species recorded in this study were endemic either to Australia or Western Australia with life-histories, age and growth patterns of many of them still being unknown. However, some of the endemic species recorded clearly had traits that made them vulnerable to extinction, such as the long lived foxfish *Bodianus frenchii* (up to 78 years; Cossington et al., 2010) or long lived, slow growing endemics *Achoerodus gouldii* (up to 70 years; Coulson et al., 2009) and *Othos dentex* (up to 37 years; French et al., 2014).

Habitat loss, modification of habitat type or structural complexity become a common reason for changes in fish assemblage composition, rather than direct disturbance effect on the fish assemblage (Halford *et al*., 2004). Recent studies in the region demonstrate range contraction of 120 km in the northern range of kelp-dominated temperate reefs in the south-western Australia and climate mediated rapid regime shift to subtropical and tropical waters associated communities of seaweeds, invertebrates and fishes (Bennett et al., 2015; Wernberg et al., 2016). Whether the affected fish communities will shift their distribution further south and into the Great Australian Bight at this stage remains unclear.

In addition, the ecological changes may consequentially bear significant economic and social impacts to the commercial and recreational fisheries of species associated with the affected habitats. Some of the most iconic fishes targeted by commercial and recreational fisheries along the Central West Coast bioregion (e.g. *Glaucosoma hebraicum*, *Chrysophrys auratus* and *Choerodon rubescens*) were found in this study to be primarily associated with mixed vegetation covered reefs. A combined catch for these 3 species in the Central West Coast bioregion for the 2005/2006 season was well over 200 tonnes (Department of Fisheries, 2007). Limited biogeographic ranges in combination with the demographic attributes, where movement patterns of adults are typically limited by the extent and continuity of suitable habitat to which they first settle (Lenanton *et al*., 2009), could make these populations even more vulnerable to depletion.

The DLI identified a number of species which are characteristic of the key fish assemblages identified by the MRTs. These indicator species include both targeted by fisheries and non-targeted species, some of which may be vulnerable to climate associated changes (such as limited range endemic species). All the identified species could be used as surrogates (Harman et al., 2003) or ecological indicators (Garcia et al., 2000) for assessing health and stress responses of an entire fish assemblage and identifying significant changes in existing patterns of species richness and assemblage composition in the habitats they live in.

2.6 Conclusions

This study was able to demonstrate that species assemblage composition and biogeographical ranges in south-western Australia are influenced by a hierarchy of biotic and abiotic processes, including habitat availability, habitat complexity and indirect effects of temperature and/or oceanic currents, interacting at multiple spatial scales which often resulted in narrow environmental niche extents. Fish assemblages that were associated with structurally complex habitats, such as canopy forming seaweeds or reef, had more endemic species, high species richness and a higher proportion of key indicator species associated with these habitats. The composition and resilience of these assemblages may be prone to dramatic changes due to range contraction of habitat forming seaweeds and range expansion of tropical herbivores, causing further tropicalisation of this unique bioregion. The predicted changes can result in major regime shifts in temperate ecosystems as well as affect the associated commercial and recreational fisheries of iconic species in the region. Recent advances in macroecology, statistical analysis, and the compilation of global data will play a central role in improving conservation outcomes in an era of rapid global change (Edgar et al., 2016).

2.7 Supplementary material

Supplement 2.7.1 Description of the full set of environmental variables derived from bathymetry and used in data analysis

Predictor Code	Description & units
Das	Distance along shore. A relative distance in km along coastal gradient from an arbitrary point north of northern-most study site
depth	Water depth in metres relative to the Australian Height Datum
kelp	The kelp *Ecklonia radiata*. Probability of occurrence between 0-1
macalg	Mixed canopy foming macroalgae. Probability of occurrence between 0-1
othalg	Mixed unidentified algae. Probability of occurrence between 0-1
seagrass	Mixed seagrass. Probability of occurrence between 0-1
veget	Mixed vegetation (i.e. seagrass and algae). Probability of occurrence between 0-1
scytot	The seaweed *Scytothalia dorycarpa*. Probability of occurrence between 0-1
rhodo	Rhodolith beds (hard structures of coralline algae on sandy substrates). Probability of occurrence between 0-1
reef	Mixed undifferentiated reef. Probability of occurrence between 0-1
rfhigh	High profile reef (relief greater than 4 m). Probability of occurrence between 0-1
rflow	Low profile reef (relief less than 1 m). Probability of occurrence between 0-1
rfmed	Medium profile reef (relief between 2 and 4 m). Probability of occurrence between 0-1
obsrf	Obscured reef (hard substrate covered with sand veneer). Probability of occurrence between 0-1
sand	Undistinguished fine sandy substrate. Probability of occurrence between 0-1
sed	Unconsolidated sediment. Probability of occurrence between 0-1
grav	Substrate that have clearly grainy nature. Probability of occurrence between 0-1
figrav	Fine substrate of a clearly grainy nature. Probability of occurrence between 0-1
asp	Aspect, circular azimuthal direction of the steepest slope, calculated on 3*3 pixel area
curv	Curvature, Combined index of profile and plan curvature
hyp5^	Indicator whether a cell is a high or low point within the local neighbourhood (12.5 m radius)
hyp10^	Indicator whether a cell is a high or low point within the local neighbourhood (25 m radius)
hyp25^	Indicator whether a cell is a high or low point within the local neighbourhood (62.5 m radius)
hyp50^	Indicator whether a cell is a high or low point within the local neighbourhood (125 m radius)
morb5^	A weighted correlation coefficient used to detect spatial dependence. Calculated on the residuals from a linear trend surface (12.5 m radius)
morb10^	A weighted correlation coefficient used to detect spatial dependence. Calculated on the residuals from a linear trend surface (25 m radius)
morb25^	A weighted correlation coefficient used to detect spatial dependence. Calculated on the residuals from a linear trend surface (62.5 m radius)

morr5^	A weighted correlation coefficient used to detect spatial dependence. Calculated on the residuals from a linear trend surface (12.5 m radius)
morr10^	A weighted correlation coefficient used to detect spatial dependence. Calculated on the residuals from a linear trend surface (25 m radius)
morr25^	A weighted correlation coefficient used to detect spatial dependence. Calculated on the residuals from a linear trend surface (62.5 m radius)
plan	Plan curvature. Secondary derivative of elevation. Measure of concave/convexity perpendicular to the slope. Calculated on 3*3 pixel area
prof	Profile curvature. Secondary derivative of elevation. Measure of concave/convexity parallel to the slope. Calculated on 3*3 pixel area
resid	Depth residuals, depth minus trend
rng5^	Range (local relief). Maximum minus the minimum elevation in the local neighbourhood of 12.5 m radius
rng10^	Range (local relief). Maximum minus the minimum elevation in the local neighbourhood of 25 m radius
rng25^	Range (local relief). Maximum minus the minimum elevation in the local neighbourhood of 62.5 m radius
rng50^	Range (local relief). Maximum minus the minimum elevation in the local neighbourhood of 125 m radius
slp	Slope. First derivative of elevation. Average change in elevation, calculated on 3*3 pixel area
snip	Snippets. Second return from multibeam, indicator of sediment texture, density
std5^	Standard deviation of depth within a neighbourhood (12.5 m radius)
std10^	Standard deviation of depth within a neighbourhood (25 m radius)
std25^	Standard deviation of depth within a neighbourhood (62.5 m radius)
std50^	Standard deviation of depth within a neighbourhood (125 m radius)
trend	Trend. The linear trend calculated across the bathymetry dataset
rfflat	Flat reef. Probability of occurrence between 0-1
harcor	Undifferentiated hard coral. Probability of occurrence: 0-1
si	Undifferentiated sessile invertebrates. Probability of occurrence: 0-1
easting	Geographic coordinate
northing	Geographic coordinate

^ Local neighbourhood analysis: run on circles of kernel pixel radius 5, 10, 25, 100 original cell size is 2.5 m

Postscript: In the next chapter I use a subset of the key indicator species that I have identified in this chapter to develop a modelling approach for examining the ontogenetic environmental niche requirements of conspecific individuals.

Chapter 3 Characterizing ontogenetic habitat shifts in marine fishes: advancing nascent methods for marine spatial management

3.1 Abstract

The niche requirements and habitat resource partitioning by conspecific fishes of different sizes remain significant knowledge gaps in the species distribution modelling domain. Management efforts are typically concentrated on static habitats, or specific areas of interest, without considering movement patterns of species associated with ontogenetic shifts in habitat use. The body length-habitat relationships of six fish species were modelled using Generalized Additive Models. These models were used to identify subsets of environmental parameters that drive the continuous length-habitat relationships for study species with varying degrees of ecological and commercial importance. In addition, these models were used to create continuous predictive maps of the length distributions for the six study species across approx. 200 km^2 of the study area. The spatial patterns in habitat partitioning by individuals of different body lengths provide strong evidence for ontogenetic shifts for all six study species. This highlights the importance of considering ontogenetic processes for marine spatial management. Importantly, predictive hotspot maps were created that identify potential areas that accumulate individuals of similar life stages for multiple species (e.g. multispecies nursery areas). Where there are limited resources for monitoring and management, predictive modelling can be a valuable tool for studying previously overlooked processes such as ontogenetic habitat shifts. They provide crucial information that link abundance patterns and community composition across benthic habitats. This novel technique can contribute to the spatial management of coastal fish and fisheries by identifying areas that are important for multiple fish species and/or for different life history stages.

3.2 Introduction

The biogeographic distribution, assemblage composition and the abundance of marine organisms is known to be tightly associated with habitat type, its complexity and variability (Halpern et al., 2005; Kingsford & Carlson, 2010). The habitat is defined as an arrangement of environmental conditions that influences responses in the presence, abundance, growth and other important life-history traits of an organism (i.e. environmental niche, Hutchinson

1957; Martinez-Meyer et al. 2013). Habitat associations can vary among species and also within life history stages of the same species (Jones, 1984a; Compton et al., 2012). Species that are habitat specialists are inherently more susceptible to changes in habitat quality and cover as a result of climate change or other antropogenic stressors, such as sedimentation and eutrophication (Munday, 2004). This is particularly relevant for species that are dependent on a specific habitat for juvenile recruitment (Jones et al., 2004). For example, when canopy forming macroalgal fields and coral reefs co-occur, macroalgal fields can serve as recruitment and juvenile habitats for fish taxa that are typically associated with coral reefs as adults (Evans et al., 2014).

Many fish species undergo ontogenetic shifts in their habitat use and exhibit a degree of habitat specialization (Halpern et al., 2005; Fitzpatrick et al., 2012). Patterns in life history traits such as growth, mortality and longevity can vary within a single species of fish in association with subtle differences in habitat structure (Gust et al., 2001; Figueira et al., 2008). These variable size-species distribution patterns have particular implications for species that are the object of spatial management, whether for ecological or economic reasons. To address this ecologically important, but poorly studied topic in the spatial ecology realm, the novel approach introduced by Nagelkerken et al. (2015) was adopted. In this approach, a mosaic of functionally connected habitats creates a spatially explicit unit that allow animals to move from one patch to another as their requirements for food or shelter change (Nagelkerken et al., 2015). Ontogenetic habitat shifts are identified as one of the mechanisms that connect hotspots of animal abundance within a habitat mosaic.

Marine spatial management benefits from an understanding of species-habitat relationships such that the design and placement of spatial area closures can be optimized (e.g. Possingham et al. 2000). However, large scale spatial sampling is often limited by resources for monitoring and assessment, thus reducing knowledge of fish abundance to a few sampled locations (Costa et al., 2014). Being able to reliably predict this information across broader geographical areas is thus important, relevant and instructive (Schmiing et al., 2013). To this end, species distribution models are a powerful tool, as they combine observations of species occurrence or abundance with environmental and/or spatial variables. Species distribution models are widely used in terrestrial, freshwater and marine environments to support spatial planning arrangements (Elith & Leathwick, 2009; Moore et al., 2009). Furthermore, the results of predictive modelling can be readily illustrated in GIS and areas of specific interest for spatial management identified for individual or multiple species (Schmiing et al., 2013; Costa et al., 2014).

Generalized Additive Models (GAMs) are particularly suitable for predicting complex, often non-linear responses of marine species to environmental predictors (Leathwick et al., 2006). They have become the most common method for modelling fish-habitat relationships (Valavanis et al., 2008; Schmiing et al., 2013). Therefore, they are the natural choice to examine the size-specific shifts in habitat use or partitioning of habitat resources among conspecifics. This topic has received little attention in species distribution modelling (but see Lauria et al. 2011; Martin et al. 2012 for examples using GLMs). Models of size specific habitat associations can help to identify key areas of the seascape that are crucial for different life-history stages of a single species or for multiple species (e.g. nursery areas). Mapping, followed by management or protection of such areas may result in higher survival of vulnerable life stages (Dugan & Davis, 1993), and by preserving seascape connectivity patterns between nursery areas and adult populations it is possible to enhance the abundance of target and other fish species which rely on healthy ecosystem functioning (Olds et al., 2014).

This study set out to improve our understanding of the spatial ecology of the modelled species by identifying environmental parameters that best determine ontogenetic environmental niche partitioning among conspecific individuals. The body length measurements of individual fishes were modelled utilizing GAMs in order to produce predictive maps of the continuous spatial distributions of conspecifics across the study area. In addition, created predictive hotspot maps can help to identify critical areas for different life-history stages. Using these maps we aim to synthesize complex patterns into a simple single GIS layer resource for effective spatial management. This novel approach of modelling continuous body length of individual fishes in combination with the flexibility of GAMs is likely to improve the ecological realism of predictive modelling, the robustness and parameter performance of spatial models (Guisan & Zimmermann, 2000; Robinson et al., 2011), and the appeal of quantitative spatial ecology to marine resource managers.

3.3 Materials and methods

3.3.1 Study area

The Houtman Abrolhos Islands (hereafter HAI) are four clusters of islands (consisting of a total of 122 islands) approximately 60 kms offshore of the central-west coast of Western Australia. The islands run parallel to the mainland in a north–south orientation and span ~100 km. They exhibit a high species diversity of fishes with 184 species recorded, belonging to 42 genera derived from both tropical and temperate origins (IMCRA, 1998). The warm, southward flowing Leeuwin Current supports the southernmost coral reefs in the

Indian Ocean, giving this location a unique blend of temperate, tropical and Western Australian endemic fish species (Hutchins, 2001; Watson et al., 2009). This biodiversity rich area is influenced by environmental changes (Bornt et al., 2015) including a recent marine heat wave (Pearce & Feng, 2013). We surveyed the fish assemblage composition and developed detailed habitat maps in two areas that are open to fishing. Area 1 to the north of the Pelsaert Island group and Area 2 to the east of the Easter group (Figure 3.1).

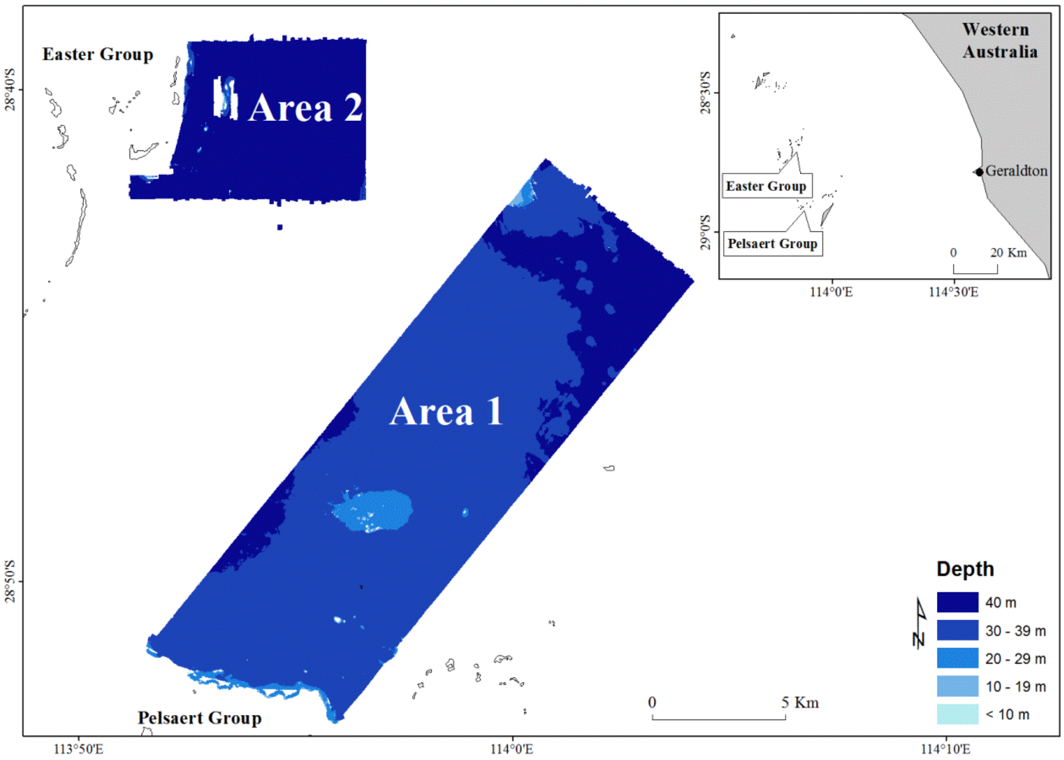


Figure 3.1 Map of the two study areas, north of the Pelsaert Group (Area 1) and east of the Easter Group (Area2). Inset: general location of the Houtman Abrolhos Archipelago off the coast of Western Australia.

3.3.2 Fish data collection and study species selection

Baited remote underwater stereo-video systems (stereo-BRUVs) were used to survey fish assemblages in the study area between the 15 and 19 May 2007. Design, calibration and use of the stereo-BRUVs are presented in detail in Harvey and Shortis (1995, 1998) and Harvey *et al.* (2013). To ensure that sampling replication was appropriate, sampling was spatially stratified according to the size of the study location and depth. In addition, sampling was randomly assigned and distance controls used to avoid spatial autocorrelation between samples (see Radford *et al.* 2008 for further details on site selection criteria). A total of 195 video recordings were analysed using the software EventMeasure Stereo (SeaGIS Pty Ltd).

The species chosen for modelling where amongst the most abundant species in the study area characterised by contrasting life histories, and/or were ecologically or commercially important (Table 3.1). The fork length was measured with precision constraints set to a 10 % cut off, which is achievable using stereo-BRUVs (Harvey & Shortis, 1995; Harvey et al., 2002).

3.3.3 Habitat mapping

Approximately 200 km^2 of the seafloor in the study area between depths of 10 and 40 m was hydroacoustically surveyed using a Reson 8101 Multibeam (Fugro Pty Ltd) between the 15 and 23 November 2006. In addition, underwater towed video footage was collected over more than 100 linear km between the 3 and 8 March 2007. The hydroacoustic surveys provided bathymetric information and a coarse distinction between various substrate textures, whereas the towed video imagery provided 'ground truthing' for the multibeam and allowed for fine scale habitat definition. The hydroacoustic maps and observations recorded from towed videos were combined in a statistical modelling framework using Classification and Regression Trees to predict the probabilities of occurrence of substrate and biota in areas with no observations (see Radford *et al.* 2008 for detailed methods). For both sites, all identified benthic classes were mapped, including sediment texture and relief, reef structures, different types of vegetation and sessile invertebrates, providing a total of 21 variables (Table 3.2). All probabilities of occurrence for benthic habitat and biota from the modelling were then predicted on a 2.5 m grid in ArcGIS using GDA94 datum MGA zone 50 equal area projections, allowing future querying and intersecting with the fish sampling data.

3.3.4 Preliminary data exploration

In order to achieve a continuous distribution of the response variable 'Fish Length' for each species, fork length measurements from both sites were analysed together. All exploratory and statistical analyses were performed using the packages lattice, mgcv, gamclass and raster in R software (version 3.2.0; R Core Team 2014). The initial data exploration followed procedures outlined in Zuur *et al.* (2007, 2010), examining potential outliers, homogeneity and co-linearity of covariates for individual fish species sequentially. For each species-specific data subset, the explanatory variables with Spearman's rank correlation > 0.7 to one-another and/or explanatory variables with a high percentage of zeroes (> 90 %), were excluded from further analyses of the specific subset (Moore et al., 2011).

3.3.5 Model fitting, cross-validation and final variable selection

The final subset of environmental variables was fit into a GAM for each species with a gamma error distribution with log link function (Hastie & Tibshirani, 1990; Wood, 2006). The predicted habitat data has probabilities of occurrence ranging from 0 to 1, as such, all explanatory variables were modelled with smoothers (knots) limited to $k = 3$. The number of knots determines the smoothness of the curve; the fewer knots used, the more smooth the curve (Wood, 2006; Sagarese et al., 2014). In addition, each model formula included a 'gamma = 1.4 loading to place a heavier penalty on each effective degree of freedom to counteract overfitting without compromising the model fit (Zuur et al., 2009; Drexler & Ainsworth, 2013).

The smoothing was performed automatically with cubic regression splines and a combination of shrinkage and double penalty approaches during the model fitting process (Marra & Wood, 2011). Shrinkage procedures are continuous processes, carrying out variable selection in one single step in such a way that smooth terms making no contribution to the model can be penalized away completely, and are considered to be a valid method for a variable selection in terms of both stability and prediction (Wood, 2006; Hesterberg et al., 2008). Hypothesis testing was used for final variable selection. Where the hypothesis testing indicated non influential variables (approximate $P > 0.05$) they were removed from the analysis and the model was re-fitted (Marra & Wood, 2011). When smoothers exhibit a linear behaviour, terms for these variables were fitted in a parametric manner. Response curves were visually inspected for ecological realism (Sagarese et al., 2014). Finally, we repeated 5-fold cross validation 50 times and then calculated normalized root mean square error (normalized RMSE) to examine the average magnitude of the predictive errors of all generated submodels (Potts & Elith, 2006; Costa et al., 2014).

To verify an absence of residual patterns, model residuals were plotted against each predictor variable included in the final model and excluded during variable selection procedures. Spatial independence was evaluated by plotting the model residuals against the spatial coordinates. Possible influential observations, outliers, homogeneity and normality of model residuals were investigated graphically following Zuur et al. (2010).

Table 3.1 The list of study species, with sample size and sample length range provided.

Scientific name	**Common name**	**Family**	**Number of individuals**	**Size range sampled (mm)**	**Max. size recorded (mm)**	**Size at maturity (mm)**	**Fisheries**	**Selection basis**
Lethrinus genivittatus	Longspine emperor	Lethrinidae	118	98-242	250	~ 105 (Mellin et al., 2007)	Recreational & Minor commercial	Key indicator species (Galaiduk, R., unpublished data), vulnerable to trawl gear (Kangas et al., 2007)
Coris auricularis	Western king wrasse	Labridae	327	45-298	400	~ 200 (Lek et al., 2012)	Casual recreational	Key indicator species (Galaiduk, R., unpublished data), limited range endemic (south-western Australia only)
Parupeneus chrysopleuron	Rosy goatfish	Mullidae	146	64-235	330	NA	Commercial & Recreational	Key indicator species (Galaiduk, R., unpublished data), commercially and recreationally fished , biology unknown
Torquigener vicinus	Orange spotted puffer	Tetraodontidae	86	43-193	220	NA	Not fished	Key indicator species (Galaiduk, R., unpublished data), non-commercial, biology unknown
Chrysophrys auratus	Pink snapper	Sparidae	65	145-809	940	~ 600 (Smallwood et al., 2013)	Major Commercial & Recreational	Key indicator species (Galaiduk, R., unpublished data), fisheries indicator (Kangas et al., 2007)
Pentapodus vitta	Western butterfish	Nemipteridae	667	57-294	310	~ 150 (Mant et al., 2006)	Recreational	Key indicator species (Galaiduk, R., unpublished data), vulnerable to trawl gear (Kangas et al., 2007)

3.3.6 Spatial prediction of species' size distributions

Once the final models were validated, the constrained size distributions of individual fish species were predicted on 2.5 m grids using R and these predictions were plotted in ArcMap 10.2. In addition, to identify 'hotspots' for multiple species, the continuous predictive rasters were reclassified into 2 size categories: juveniles/small size individuals and adults/large size individuals according to the known ontogeny of individual species. For *Lethrinus genivittatus*, *Chrysophrys auratus* and *Pentapodus vitta* the reclassification was based on an individual's length at maturity (Table 3.1). The ontogenetic shift for *Coris auricularis* is known to occur at approximately 200 mm total body length when juvenile females change sex (Lek et al., 2012), which provided the basis for raster reclassification in this study. When biological data on size distributions were not available from the literature (*Parupeneus chrysopleuron*, *Torquigener vicinus*), the size categories were assigned arbitrarily based on the observed size frequency distributions. For example, individuals with body length belonging to a first quartile were assigned into the juvenile/small size category, whereas individuals with body length belonging to a fourth quartile were assigned into adult/large category. The reclassified values were plotted again to illustrate potential multi-species 'hotspot' areas, where environmental niche conditions were suitable for juvenile/small or adult/large individuals of the modelled species. For example, a hotspot would have a maximum score of 6, corresponding to the six modelled fish species that could potentially associate with that particular area.

To guide the interpretation of the hotspot maps we also visually represented the relationship between the predicted hotspots and the recorded abundance of adult and juvenile fishes by overlaying them on the hotspot map. Based upon the same size categories as were used for reclassification of the predicted hotspot map, the observed abundance values for adults and juveniles of each species in each sample were standardized by expressing as a proportion of the total number of juveniles or adults recorded for that species. The values for each of the six species were then summed for each sample location and plotted on the hotspot map. We used Spearman's rank correlation (ρ) to assess the measure of association between the predicted hotspots and the recorded standardized abundances of adult and juvenile fishes.

3.4 Results

3.4.1 Species specific models and variable selection

Significant linear and nonlinear relationships for individual length distributions were observed for all six study species.

Table 3.2 Summary of the environmental predictors extracted from the hydroacoustic survey and the predictive modelling used for the generalized additive model fits.

Predictor	**Description & units**	**Predictor Code**
Bathymetry	Elevation relative to the Australian Height Datum (m)	bathy
Eastness	Trigonometric transformation of a circular azimuthal direction of the steepest slope (*sin*(aspect)), calculated on a 3 x 3 pixel area. Values close to 1 represent east-facing slope, close to -1 if the aspect is westward	eastness
Northness	Trigonometric transformation of a circular azimuthal direction of the steepest slope (*cos*(aspect)), calculated on a 3 x 3 pixel area. Values close to 1 represent north-facing slope, close to -1 if the aspect is southward	northness
Slope	First derivative of elevation. Average change in elevation, calculated on a 3 x 3 pixel area (steepness of the terrain, % rise)	slope
Range 5,10,25^	Maximum minus the minimum elevation in the local neighbourhood (local relief) of 5,10,25 m kernel radius	rng5, rng10, rng25
Plan curvature	Secondary derivative of elevation. Measure of concave/convexity perpendicular to the slope, calculated on a 3 x 3 pixel area	plan
Profile curvature	Secondary derivative of elevation. Measure of concave/convexity parallel to the slope, calculated on a 3 x 3 pixel area	prof
Curvature	Combined index of profile and plan curvature	curv
Trend	The linear trend calculated across the bathymetry dataset	trend
Low profile reef	Relief less than 1 m. Probability of occurrence: 0-1	LPR
Medium profile reef	Relief between 2 and 4 m. Probability of occurrence: 0-1	MPR
High profile reef	Relief greater than 4 m. Probability of occurrence: 0-1	HPR
Reef	Undifferentiated. Probability of occurrence: 0-1	reef
Sand	Undifferentiated. Probability of occurrence: 0-1	sand
Hard coral	Undifferentiated. Probability of occurrence: 0-1	hardcoral
Kelp	*Ecklonia radiata*. Probability of occurrence: 0-1	kelp
Seagrass	Undifferentiated. Probability of occurrence: 0-1	seagrass
Vegetation	Undifferentiated. Probability of occurrence: 0-1	veget
Sessile invertebrates	Undifferentiated. Probability of occurrence: 0-1	sessinvert

^ Local neighbourhood analysis: run on circles of kernel pixel radius 5, 10, 25 original cell size is 2.5 m.

The majority of the significant explanatory variables in the final models were associated with the physical descriptors of habitat complexity (i.e. local relief and/or slope) with some significant biotic variables (i.e. probability of occurrence of mixed undifferentiated vegetation, sessile invertebrates and reef; Table 3.3). The deviance explained by the final models ranged from 13.6 to 54.6 % (Table 3.3). The initial set of 21 explanatory variables was typically reduced to between two and five significant variables. The residual plots confirmed homogeneity, normality and independence for all six focal species. For only one species, *Chrysophrys auratus*, slight spatial clustering of positive residuals indicated that the GAM model over-predicted the length distributions for this species. This can be attributed to the relatively small sample size (65 observations) and the large range in the observed sizes (145 – 809 mm) for this species. The average difference between the predicted and observed size values (normalized RMSE) for all models varied between 13.5 – 23.1 % (Table 3.3). Higher error values were associated with lower explained deviance, suggesting poor model fits for *Torquigener vicinus* and *Coris auricularis*.

The presence of reef and vegetation and the habitat structural complexity ('reef', 'veget' and 'rng25' respectively) were the most common variables chosen by the fitted models across all modelled species (Table 3.3). The large individuals of *Lethrinus genivittatus* and *C. auratus* were predicted to be positively associated with the presence of reef and vegetation and high structural complexity (Figure 3.2). In addition, high structural complexity and presence of vegetation were positively associated with large individuals of *Pentapodus vitta* and presence of reef was positively associated with large individuals of *T. vicinus* (Figure 3.2). In contrast, small individuals of *C. auricularis* were predicted to be associated with presence of reef and vegetation and small individuals of *Parupeneus chrysopleuron* were predicted to be associated with high structural complexity of habitat. Large individuals of both species were associated with open areas of low structural complexity (Figure 3.2). Bathymetry was an additional environmental variable that appeared in models for three species. The smaller individuals of *P. vitta*, *C. auratus* and *P. chrysopleuron* were predicted to be associated primarily with shallow water (Table 3.3 and Figure 3.2).

3.4.2 Spatial predictions

While a degree of mixing between large and small size individuals was apparent for all six species, the spatial predictions of the habitat associations from the GAM models consistently showed spatial separation between large and small size individuals (Figure 3.3). The small size individuals of *L. genivittatus* were predicted to be found in the structurally complex near reef areas throughout most of study Area 1 and were particularly concentrated in the north-east and the south-east corners of Area 1 and in the western part of study Area 2 (Figure

3.3a, b). Large individuals of this species were mostly predicted to be associated with exposed near reef areas covered with vegetation in the central and south-west parts of Area 1 and throughout most of Area 2 (Figure 3.3a, b).

Small size *C. auricularis* were predicted at near reef areas with a low cover of sessile invertebrates and a high probability of vegetative cover in the north-western, southern and the central part of Area 1 and also in the central part of Area 2.

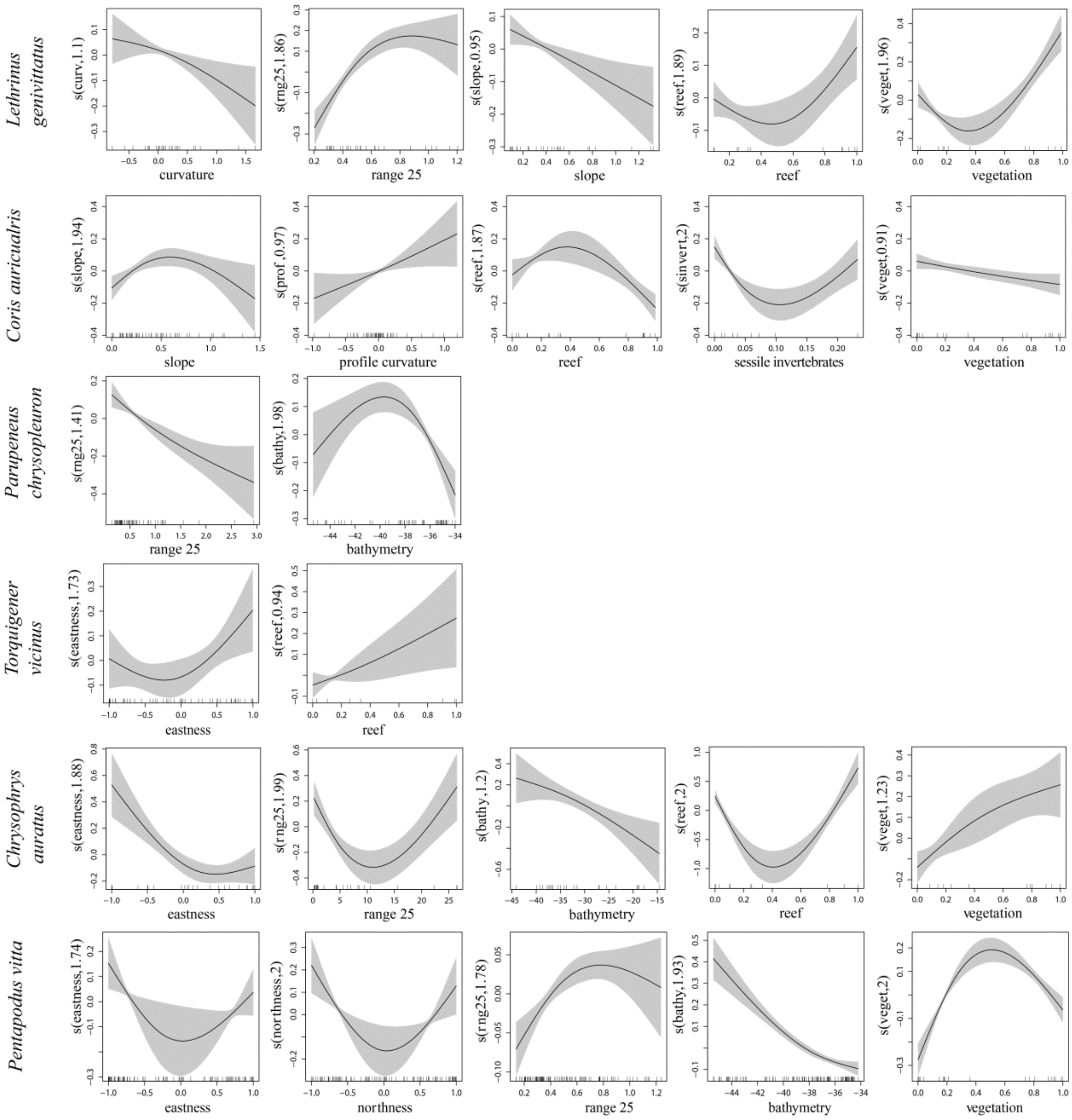


Figure 3.2 Smoother estimates (solid line) for the environmental predictors as obtained by generalized additive models for individuals of various body lengths of the six study fish species. The approximate 95% confidence envelopes are indicated (grey shading), marks along the x-axis are sampled data points. All explanatory variables were fitted with model smooths (knots) k = 3. Summary of the environmental predictors is provided in the Table 3.2.

Table 3.3 Variable selection for species-specific generalized additive model with percent deviance explained (Dev) and the normalized root mean square error (normalized RMSE) provided. Initial models are in *italics*. Final models are in **bold**. All explanatory variables were fitted with smooths (knots) k=3. When the smoothing symbol ('s') does not appear in the final model, that term was fit as parametric function. Summary of the environmental predictors is provided in the Table 3.2.

Species	**Variable selection procedure**	**Dev (%)**	**Normalized RMSE (%)**
Lethrinus genivittatus	*Length~ s(eastness)+s(northness)+s(curvature)+s(reef)+s(rng25)+s(slope) +s(vegetation)+s(sessinvert)+s(sand)+s(seagrass)* **Length~ curvature+slope+s(rng25)+s(reef)+s(vegetation)**	54.6	19.3
Coris auricularis	*Length~ s(eastness)+s(northness)+s(profile)+s(slope)+s(reef)+s(rng25) +s(sessinvert)+s(vegetation)+s(seagrass)* **Length~ vegetation+profile+s(reef)+s(sessinvert)+s(slope)**	15.8	20.4
Parupeneus chrysopleuron	*Length~ s(eastness)+s(northness)+s(curvature)+s(reef)+s(rng25)+s(slope) +s(bathymetry)+s(vegetation)+s(sessinvert)+s(seagrass)* **Length~ s(bathymetry)+s(rng25)**	21.1	18.2
Torquigener vicinus	*Length~ s(eastness)+s(northness)+s(curvature)+s(reef)+s(slope)+s(bathymetry)+s(vegetation)+ s(sessinvert)* **Length~ reef +s(eastness)**	13.6	23.1
Chrysophrys auratus	*Length~ s(eastness)+s(northness)+s(profile)+s(bathymetry)+s(reef)+s(rng25) +s(kelp)+s(vegetation)+s(sand)+s(seagrass)* **Length~ s(eastness)+s(rng25)+s(bathymetry)+s(reef)+s(vegetation)**	53.2	18.9
Pentapodus vitta	*Length~ s(eastness)+s(northness)+s(profile)+s(bathymetry)+s(reef)+s(rng25) +s(slope)+s(vegetation)+s(sessinvert)* **Length~ s(eastness)+s(northness)+s(rng25)+s(bathymetry)+s(vegetation)**	20.8	13.5

In contrast, the larger individuals of this species were predicted to be associated with areas of low vegetative cover and medium reef complexity throughout Area 2 and north-east and south-east parts of Area 1 (Figure 3.3c, d).

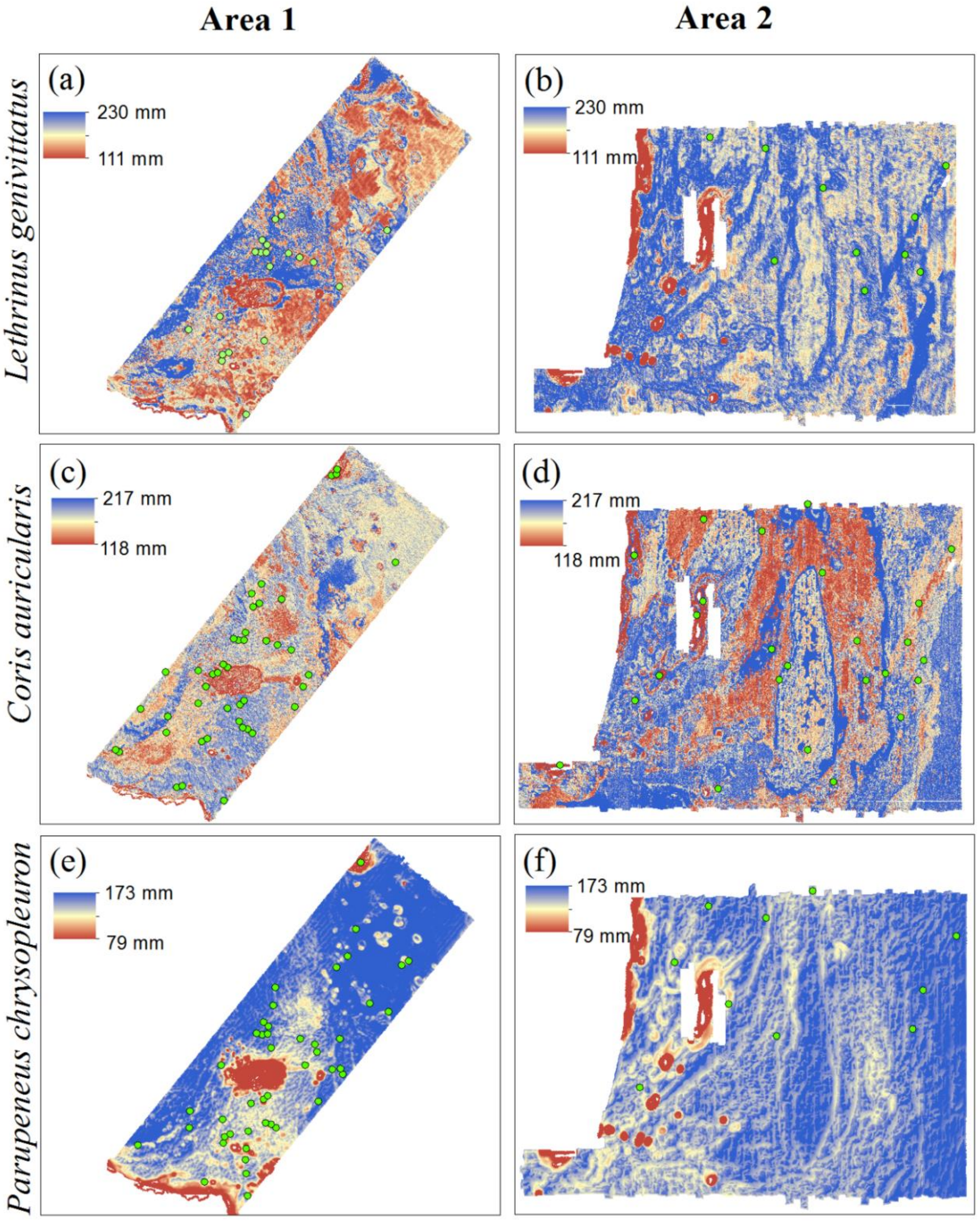


Figure 3.3 Predictive maps of habitat associations on a continuous size scale of individuals of the six study species as obtained by generalized additive models predicted on a 2.5 m grid. Positions of species specific observations from the individual stereo-BRUVs surveys are marked by green circles.

Water depth was important for *P. chrysopleuron* with medium to small size individuals of this species predicted to be scattered over reef slopes at intermediate water depth in the north-west, south-east and central parts of Area 1 and in the western part of Area 2. The larger size individuals of this species were predicted to be found throughout both study areas in deep water habitats characterised by low structural complexity (Figure 3.3e, f).

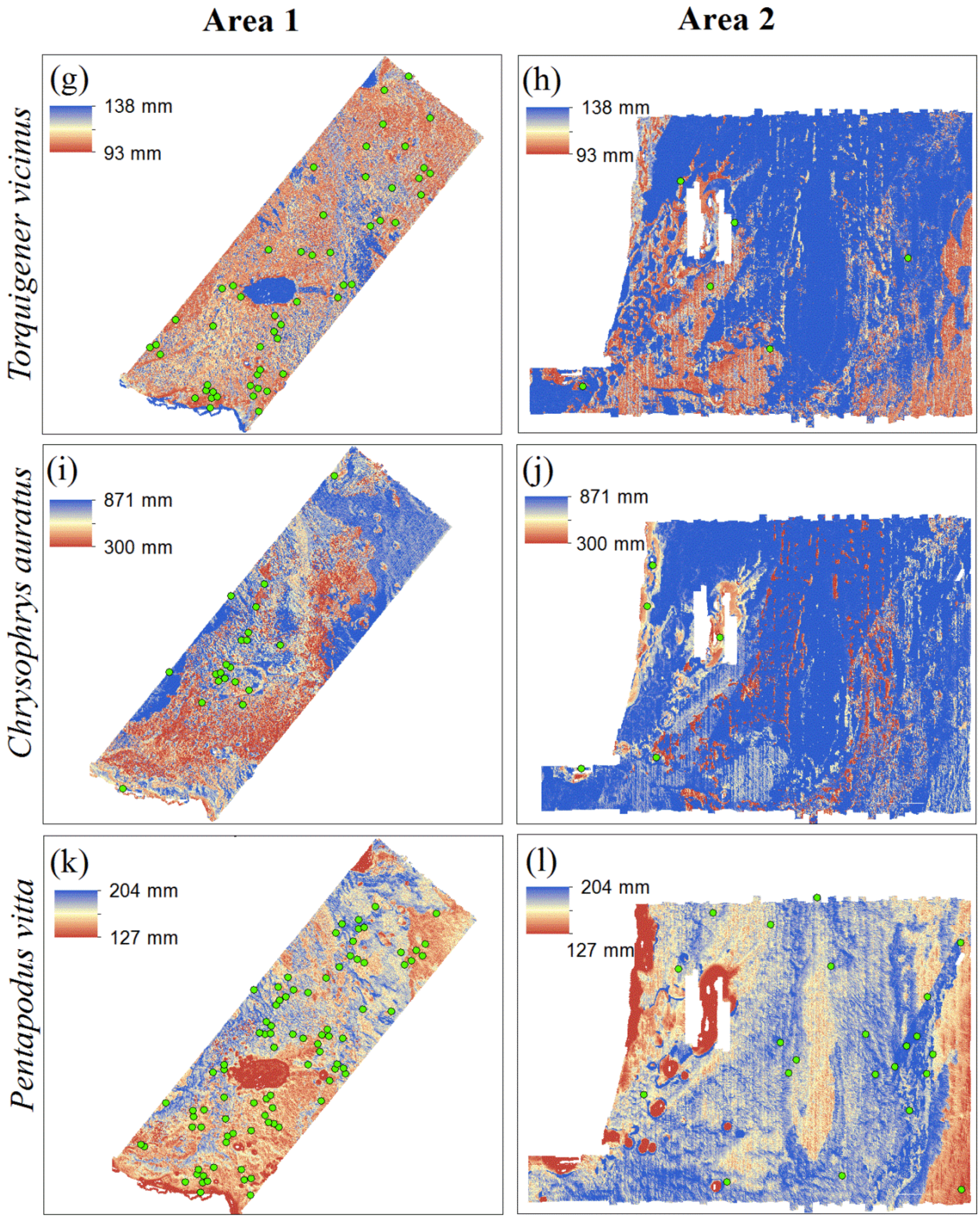


Figure 3.3 continued Predictive maps of habitat associations on a continuous size scale of individuals of the six study species as obtained by generalized additive models predicted on a 2.5 m grid. Positions of species specific observations from the individual stereo-BRUVs surveys are marked by green circles.

The exposed east facing reef areas throughout the central part of Area 2 and in a few distinctive patches in the central and north-western parts of Area 1 were predicted to be suitable for large size individuals of *T. vicinus*. In contrast, the small size individuals of this species were predicted to be found throughout most of Area 1 and on protected flat patches in the west and east parts of Area 2 (Figure 3.3g, h).

The larger sized individuals of *C. auratus* were predicted to be associated with west facing deep reef slopes covered by dense vegetation throughout most of Area 2 and the northern and western parts of Area 1. In contrast, smaller sized individuals of this species were predicted to be scattered throughout shallow, bare, east facing reef flats in the central part of Area 2 and in the central-south part of Area 1 (Figure 3.3i, j).

Both study areas were predicted to be highly suitable for small to medium size individuals of *P. vitta*. Protected reef flats at intermediate depths in the north-west, central and south of Area 1 and the western and eastern sides of Area 2 were predicted to be particularly suitable for small size individuals of this species. The large size individuals of this species were mostly predicted to be associated with deep high complexity reef slopes covered by vegetation throughout the central and eastern parts of Area 2 (Figure 3.3k, l).

Cumulative predicted fish distribution maps of the six study species combined identified hotspots of environmental niche conditions suitable for species aggregations of juvenile fish and adult fish in the study region. The spatial distribution of hotspots for adults and juveniles showed opposing patterns (Figure 3.4). Environmental niche conditions suitable for juvenile fish were predicted in the south-eastern part of Area 1 and in the many shallow pockets scattered throughout the area. In Area 2 conditions suitable for juveniles were predicted around the shallow reef edges in the western part of the study area (Figure 3.4a, b). In contrast, hotspots for species aggregations of adult fish were predicted in deeper, less structurally complex regions around the centre and north of study Area 1. In Area 2 environmental niche conditions suitable for adult fish were predicted in the eastern and the western regions of the area (Figure 3.4c, d). These patterns are supported by the observed standardized abundances of juveniles (Spearman's ρ = 0.23, P = 0.005) and adult fishes (Spearman's ρ = 0.17, P = 0.03), where areas of high recorded abundance are close to or within areas that were predicted as hotspots (Figure 3.4).

3.5 Discussion

3.5.1 Methodological approach

This case study successfully combined highly precise continuous fish length data obtained using stereo-BRUVs with modelled habitat maps derived from ground-truthed data to produce predictive maps of ontogenetic environmental niche associations of six abundant fish species with varying degrees of ecological and commercial importance. When examined next to each other these maps highlight habitat partitioning with body length for all study species. These maps graphically represent ontogenetic shifts in habitat use. Changes in habitat requirements with ontogeny, and patterns of population connectivity across a continuous mosaic of habitats is an often overlooked topic in spatial modelling of demersal fishes (Compton et al., 2012; Nagelkerken et al., 2015). However, it is a crucial link for understanding the processes that underpin abundance patterns and community composition across a mosaic of benthic habitats. For any given species, as an individual grows its morphology and behaviour change, as does its prey size and type (Lukoschek & McCormick, 2001; Kimirei et al., 2013). This often requires a change in habitat to meet energy and resource needs (Huijbers et al., 2015). As such, ontogenetic movement among habitat types is dependent on size of individuals and the relative complexity of structure for protection and/or availability of prey, which is also likely to be size structured. A failure to move between habitats is likely to adversely impact survivorship. Increasing the understanding of size-specific environmental niche partitioning among conspecifics and mapping the key areas of the seascape that are important for multiple species can inform management efforts directed towards specific or vulnerable life history stages of fish.

3.5.2 Habitat distribution of studied species

Fitting GAMs is a flexible modelling approach suitable for demersal fishes (Valavanis et al., 2008). The individual models fitted varied in their explanatory and predictive performance. The lowest deviance explained and the highest predictive errors were observed for models of size distributions fitted to *C. auricularis* and *T. vicinus*. The most plausible explanation for this poor model performance is related to the biological characteristics of these species, where mixed schools contain both juveniles and adults. This has been documented for *C. auricularis*, where various size females of this species come together under male-dominated harems or set up cleaning stations to remove skin parasites from other fish (Lek et al., 2012; Saunders et al., 2013).

High structural complexity provided by the reefs and canopy forming seaweeds were found to be among the most common environmental variables that drove the patterns in size distributions of the modelled species. These habitats are known to drive the distribution of fish species due to their influence on many demographic and community processes, for example by providing different sized shelters (Wilson et al., 2007; Nash et al., 2013), food sources (Lim et al., 2016), and nesting spaces (Azevedo et al., 1999) to individuals with varying degrees of habitat specialization (Munday, 2004).

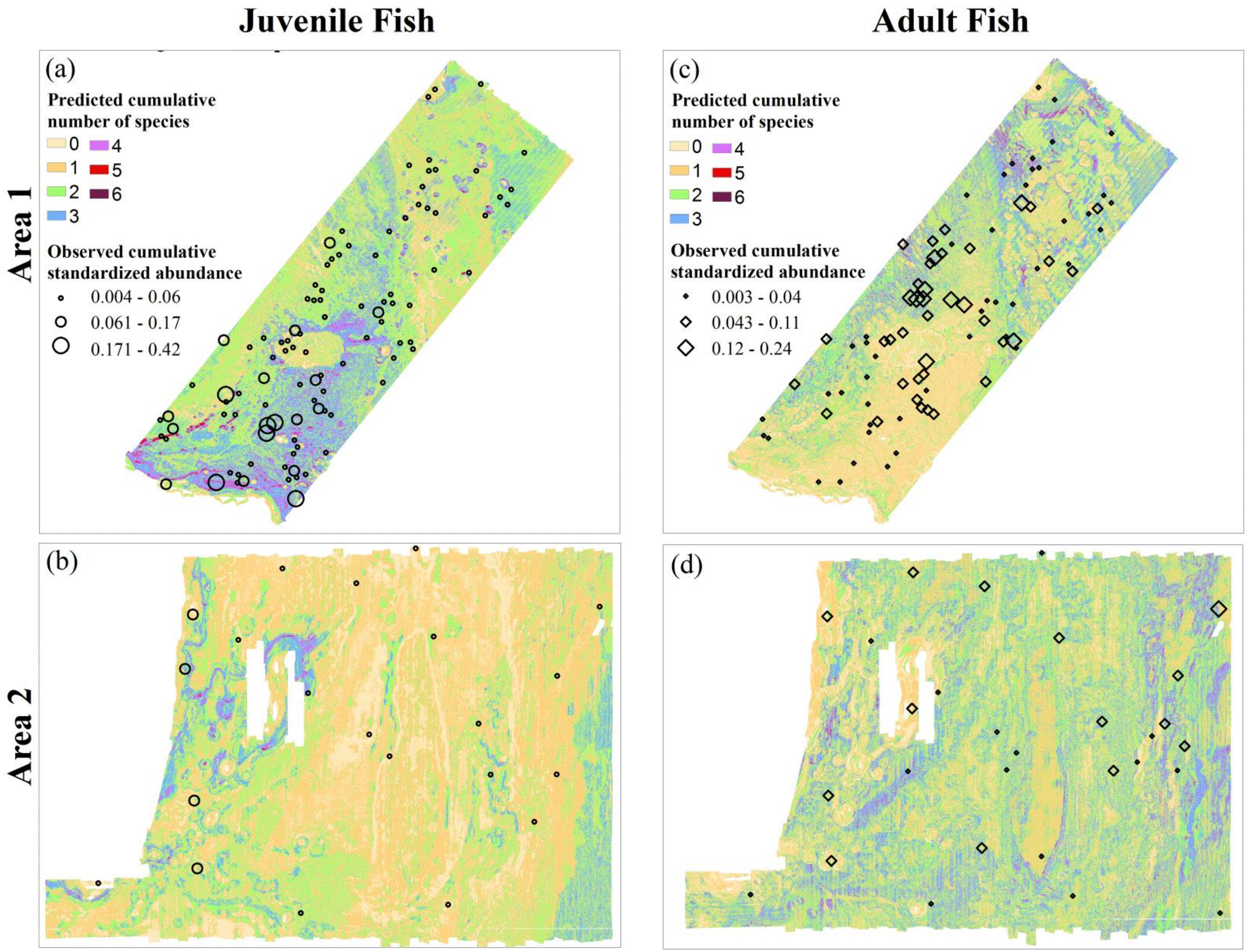


Figure 3.4 Hotspots map for cumulative environmental niche suitability for juvenile/small (a, b) and adult/large (c, d) size individuals of the six study species. Fish size classes for the rasters and the standardized abundance were assigned based on known ontogeny of the study species. There is apparent habitat partitioning between fishes of different life history stages/body lengths, suggesting ontogenetic shifts in habitat use for all six species.

These processes could explain the close associations of large individuals of four of the modelled species with deep reef habitats. Juvenile survivorship on deep reefs is typically lower than in shallow near shore areas due higher predation rates (Kimirei et al., 2013), a situation which is likely to favour higher abundance of larger individuals. In contrast, small individuals of *C. auricularis* and *P. chrysopleuron* were predicted to be associated with reefs and macroalgal habitats. Reef and macroalgal habitats support high density and diversity of fish assemblages (Bellwood et al., 2003; Mellin et al., 2007), are important recruitment areas (Jones, 1984b) or juvenile habitats (Evans et al., 2014; Grol et al., 2014) and contribute to adult population patterns (Huijbers et al., 2013).

3.5.3 Applicability of findings to spatial management

Understanding spatial population dynamics of marine animals is a vital step for successful marine spatial management. With fish populations being often patchily distributed in space and time (e.g. Newman & Williams 2001; Travers *et al.* 2012) and observation data being often limited by resources available for monitoring and/or to a few sampling locations, the use of predictive spatial modelling is a powerful tool for management. Mapping key areas such as fish nurseries or hotspots for multiple species aggregations can identify environmental niche requirements and resource partitioning between fish at different life stages. The geographic distribution and productivity of nursery areas are important drivers for the spatial distribution patterns of adult populations, with areas close to nurseries replenish more isolated areas (Huijbers et al., 2013). In addition, well-established global biodiversity patterns are changing rapidly in response to human activities such as ocean warming (Sala & Knowlton, 2006). To effectively address such issues, managers require advanced tools to identify geographic areas that have a high intrinsic management value. Our method for identifying hotspot areas demonstrates a useful decision support tool for spatially identifying benthic areas that are important for numerous species and/or for different life stages of multiple species (e.g. fish nurseries). Following *in situ* evaluation of the predicted hotspots, the hotspot maps can identify entire areas that may not require future in-depth surveys, thus optimizing limited management resources. Hotspot areas identified through quantitative analysis could be considered in zoning schemes and become priority areas for marine spatial monitoring and management (Schmiing et al., 2013). In addition, future re-zoning efforts should consider including hotspot areas. In conclusion, robust size-based predictive ecological modelling can further improve our knowledge of the spatial habitat use of demersal fishes at various life history stages. In turn this knowledge will contribute to marine spatial management efforts for rapid assessment and development of mitigation strategies for declining ecosystem condition.

Postscript: In the next two chapters I use a different spatial database which has no habitat maps constructed yet. Therefore, I use variables of habitat complexity as surrogates for various habitat types and for modelling the species-environment relationships. In the next chapter, I utilise the individual fish biomass to further extend the modelling approach developed in the previous chapter. I compare and contrast models developed for the individual fish biomass with models developed for relative abundance of the same species.

Chapter 4 The use of individual fish biomass models to map essential habitat for adult and juvenile targeted fishes

4.1 Abstract

Habitat resource partitioning and patterns of connectivity between different habitats by conspecific fishes of different life-history stages is a significant knowledge gap. We suggest that essential habitats of different life stages of fishes of the same species should be incorporated into spatial plans for fisheries and biodiversity conservation management. Species distribution models were used to examine patterns in the abundance and environmental niche requirements of different life stages of three iconic West Australian fishes. Generalised Additive Models on abundance and biomass data indicated that the bathymetry, the structural complexity of habitat and the direction of reef slope were the most common predictors for the observed patterns of distribution of *Glaucosoma hebraicum, Choerodon rubescens* and *Chrysophrys auratus*. The biomass models had higher explanatory power (adjusted R^2) than the abundance models for all three study species. The relative importance of all explanatory variables varied between species for abundance and biomass models suggesting that processes driving the abundance patterns could be different from the body length associated demographic processes throughout an individual's life cycle. Continuous predictive maps of biomass distributions identified shallow near shore areas as potential nursery habitat (lower biomass of individual fish) for two species and predicted large, sexually mature adults of the third species would be associated with these areas. Spatial distribution models developed from biomass data for individual fish are a useful decision support tool for identifying benthic areas that are important for different species and/or life stages of multiple species (e.g. fish nurseries or spawning stock hotspots).

4.2 Introduction

The goals of marine spatial management are usually the preservation of biodiversity and management of sustainable fisheries (Olds et al., 2014). These goals are often constrained by economic considerations, which raise the questions about where scarce conservation and fisheries management resources should be directed and what areas are most worthy of protection (Ferrier, 2002). Similarly, the decision about where to locate marine reserves and closed areas to maximise biodiversity conservation and sustainable fisheries management outcomes is challenging, as designated areas may not encompass the essential habitat requirements of different life stages of a range of targeted and ecologically important fishes (Schmiing et al., 2013). Identifying key areas of the seascape that are crucial for multiple species, or for different life-history stages of same species (i.e. spawning grounds, fisheries refugia or nursery areas) can help to optimise the design and placement of reserves (e.g. Possingham et al. 2000) and may help to preserve critical spawning stock biomass of exploited species and result in lower losses and higher survival of vulnerable life stages (Dugan & Davis, 1993). Furthermore, preserving functional seascape connectivity patterns between nursery areas and adult populations can enhance the abundance of target species as well as other fish species relying on healthy ecosystem functioning (Olds et al., 2014).

In the marine environment, describing patterns of species-habitat associations has been the focus of many ecological and fisheries associated studies (Curley et al., 2002; Lenanton et al., 2009; Lewis et al., 2012; Galaiduk et al., 2013). The amount, type and quality of habitat is known to influence the abundance, density and distribution patterns of many marine fishes (Gillanders & Kingsford, 1998). Consequently, the identification of essential fish habitat has become a key goal for marine spatial management (Compton et al., 2012). Species distribution models (SDMs) are a robust method for the rapid assessment of species-habitat associations at broad geographical scales (Guisan & Zimmermann, 2000; Pittman et al., 2007). In the recent years, SDMs have become a common tool for investigating patterns in fish occurrence, abundance and density in relation to benthic marine habitats (Moore et al., 2009; Monk et al., 2011; Harvey et al., 2013; Young & Carr, 2015). The results of predictive ecological modelling have helped to map and identify areas for spatial protection and to develop zoning and management plans for marine environments (Possingham et al., 2000; Pittman et al., 2007).

It is common for SDMs to use occurrence datasets to examine processes that produce the observed species and assemblage patterns (Brotons et al., 2004; Francis et al., 2005). However, as mechanisms that determine presence can be different to those that determine abundance (Ridout et al., 1998), examining other demographic processes such as species abundance, density or biomass estimates can enhance the potential benefits of using SDMs for spatial management applications. More specifically, since many demersal fish species undergo ontogenetic habitat associations as they grow (Jones, 1984a; Compton et al., 2012), incorporating the continuous body-length or biomass measurements of individual fish could help to characterise the relationships between different life-history stages of individual conspecific fishes and the environment. The biomass of fish is often used in fisheries management, where major reproductive capacity could be invested in relatively few, old, large-size individuals that could produce exponentially more eggs than smaller size conspecifics (Larkin, 1978; Bohnsack, 1990). The use of individual fish biomass in the SDMs could improve their relevance to applied ecological studies, our understanding of the habitat associations of the modelled species, and conservation efforts associated with management of the vulnerable life-history stages (e.g. juvenile fish, spawning stock) of fish.

In this study, we use a species distribution modelling approach to investigate the relationships of individual fish biomass estimates and benthic habitat structure at spatial scales relevant to informing marine spatial management. The specific aims of this study were:

1) To develop models of fish biomass-benthic habitat relationships for three iconic fish species (*Glaucosoma hebraicum, Choerodon rubescens* and *Chrysophrys auratus*) in Geographe Bay, Western Australia;

2) To compare and contrast the performance of fish biomass models with models of fish abundance;

3) To generate reliable spatial extrapolations of species biomass across the seascape;

4) To create a single GIS layer to identify key areas for multiple species (i.e. nursery areas or spawning stock biomass hotspot), which can be informative for marine spatial management and planning.

4.3 Methods

4.3.1 Study area

Geographe Bay is a ~100 km wide, relatively shallow, north-facing embayment with seagrass cover that can at times exceed 60% (McMahon et al., 1997). The bay is located in south-western Australia, approximately 220 km south of Perth (Figure 4.1). It is part of Ngari Capes Marine Park with approx. 3500 ha (< 4 % total bay area) zoned as no take marine sanctuary (Department of Environment and Conservation, 2013). The majority of the seafloor is covered by unconsolidated sediments that have been deposited over older clay layers. There is also a series of discontinuous limestone ridges, dominated by canopy-forming brown macroalgae, that run parallel to the coast (Wernberg et al., 2003; Van Niel et al., 2009).

4.3.2 Fish abundance and biomass data

We collected data on the patterns of abundance and biomass of three iconic West Australian fishes: West Australian dhufish (*Glaucosoma hebraicum*), Baldchin groper (*Choerodon rubescens*) and Australasian snapper (*Chrysophrys auratus*). These are indicator species for fisheries management in Western Australia and account for the majority of the total nearshore and estuarine catch by commercial and recreational fishers (Smallwood et al., 2013; Johnston et al., 2014). Stock assessments classify these species as being overfished along the central west coast region of Western Australia (Wise et al., 2009; WA Department of Fisheries, 2013) despite the implementation of common fisheries management strategies, such as bag and size limits licensing and quotas.

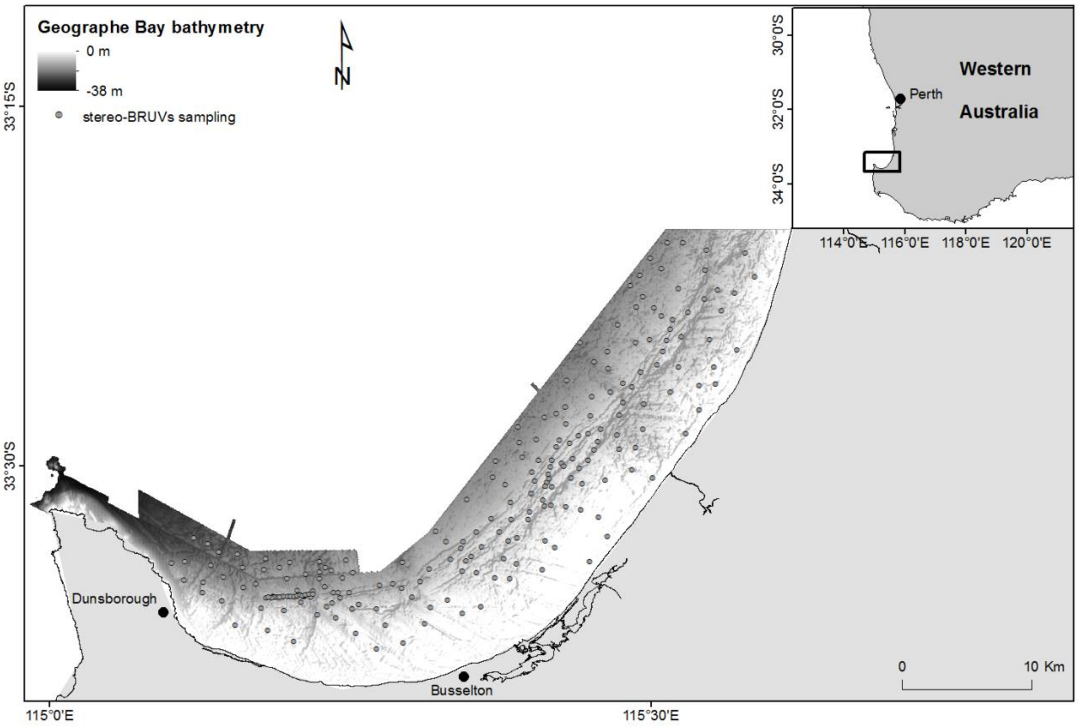


Figure 4.1 Bathymetry of Geographe Bay with grey dots indicating the stereo-video deployment sites. Inset: The location of the Geographe Bay study area on the south-west coast of Western Australia.

The abundance and biomass of these three target fish species was surveyed between the 9 and 17 December 2014 using baited remote underwater stereo-video systems (hereafter stereo-BRUVs). This method of data collection is thought be optimal for sampling large, mobile, carnivorous fish that are low in abundance (Cappo et al., 2004; Lewis et al., 2012). Each stereo-BRUV system comprised two wide-angle Sony CX12 high-definition video cameras that had been baited with approximately 1000 g of crushed pilchards (*Sardinops sagax*), and lowered to the bottom for a 60 minute soak time. The 217 video recordings from these deployments were analysed using the software EventMeasure (SeaGIS Pty Ltd). For sample unit standardisation purposes and to ensure high measurement accuracy and precision we only included fish within 7 m in front and 3 m into the water column above the system. Additional information on design, calibration (Harvey & Shortis, 1995; Shortis et al., 2009) and use of the stereo-BRUVs is presented in detail in the literature (e.g. Cappo et al. 2003; Langlois et al. 2012 and references therein). To ensure that sampling replication was appropriate, random stereo-BRUVs deployments were spatially stratified according to the size of the study area, habitat availability and depth. In addition, distance controls were used in the planning stage to avoid bait plume overlap and reduce the likelihood of fish moving between stereo-BRUVs, with each pair of stereo systems at least 400 m apart from each other on the day of deployment. The relative abundance of study species was estimated using MaxN (Cappo et al., 2007; Harvey et al., 2007, 2012). This measure is considered to be conservative for estimating fish abundance and avoiding repetitive counts of individual fish in 1 hour long recordings (Cappo et al., 2003). The fork length of individuals at the MaxN of each species was measured for each stereo-BRUVs deployment with the EventMeasure software (www.seagis.com.au) with precision constraints set to a 10 % cut off, which is achievable using stereo-BRUVs (Harvey & Shortis, 1995; Harvey et al., 2002). The biomass estimates for individual fish observed in the video recordings were obtained with known length-weight relationships (Smallwood et al. 2013 and references therein). For *Glaucosoma hebraicum*, the length-weight relationships are different for males and females. We were unable to sex the individual fish in the video recordings, therefore the biomass estimates were averaged for male and female individuals of this species.

4.3.3 Environmental variables

The bathymetric data was extracted from a mosaic of LiDAR and multibeam surveys collected by Fugro Corporation Pty Ltd gridded to a cell size of 4*4 m. The LiDAR hydrographic survey was performed between April and May 2009 on behalf of the Department of Planning as a part of a national coastal vulnerability assessment. The LiDAR area extended seaward from the coastal waterline to the 20 m marine nautical navigation chart contour and constituted the majority of bathymetric data (for details on LiDAR collection and processing see www.planning.wa.gov.au, accessed May 2016). In addition to the LiDAR, a small area of deeper water was surveyed during March-April 2006 using Reson 8101 multibeam in the north-west part of the study area as part of the Marine Futures biodiversity surveys (see Radford et al. 2008 and matrix-prod.its.uwa.edu.au/marinefutures; accessed May 2016 for further details). In addition to the bathymetric data, we derived five additional environmental variables that describe the structure and complexity of the seafloor and were previously shown to influence the distribution of fish using the Spatial Analyst toolkit in ArcGIS 10.2.2 (Moore *et al.* 2009; Monk *et al.* 2011; Table 4.1).

Table 4.1 Description of the seafloor variables used in model building.

Environmental Predictor	**Description**
Bathymetry	Elevation in metres relative to the Australian Height Datum.
Eastness	Trigonometric transformation of a circular azimuthal direction of the slope (sin(aspect)). Values close to 1 represent east-facing slope, close to -1 if the aspect is westward.
Northness	Trigonometric transformation of a circular azimuthal direction of the slope (*cos*(aspect)). Values close to 1 represent north-facing slope, close to -1 if the aspect is southward.
Slope	First derivative of elevation. Average change in elevation, steepness of the terrain, % rise.
Range 10	Maximum minus the minimum elevation in the local neighbourhood (coarse scale local relief). Calculated at window size of 10*10 cells, which equates to ground area of 1600 m^2.
Curvature	Combined index of profile (parallel to the slope) and plan (perpendicular to the slope) curvature relative to the analysis window.

4.3.4 Species distribution modelling

To infer the effect of habitat complexity on the abundance or biomass of three fish taxa we applied generalised additive models (GAMs) developed for individual study species and the full subsets approach (Zuur et al., 2009). GAMs are the most common and well developed method for modelling fish-habitat relationships (Pittman et al., 2007; Valavanis et al., 2008; Schmiing et al., 2013) and the full subsets method provides an unconstrained approach for fitting ecological responses to the predictor variable (Zuur et al., 2009; Fulton et al., 2014). The initial data exploration followed procedures outlined in Zuur et al. (2007, 2010), examining potential outliers, homogeneity and co-linearity of covariates for subsets of data for individual fish species. There were large slope values observed in the exploratory stage. However, we decide to keep these potential outliers, as they represent true nature of the benthos of the bay which is mainly characterised by low relief seascape with occasional reef ridges.

The GAMs for abundance estimates, which were characterised by large proportion of zeroes, were fitted with negative binomial error distribution and logarithmic link function. The decision to use the negative binomial error distribution was made after comparing the observed frequency distribution of abundance values to theoretical density curves from a negative binomial and a Poisson distributions (which are most common types of statistical distributions for analysing count data; Zeileis et al. 2007) for similar mean and dispersion parameters (Tu, 2006; Zuur et al., 2009). The frequency distribution for the observed abundance values for all focal species best resembled the distribution of theoretical values from the negative binomial density curves. The biomass GAMs were fitted with gamma error distribution and logarithmic link function, which is a suitable statistical distribution for analysis of a continuous positive response variable (Murase et al., 2009; Zuur et al., 2009).

Due to the number of degrees of freedom available for model fitting, the maximum number of explanatory variables across all fitted models was limited to four, which increases the ability to make ecological interpretation of the observed patterns in the numeric data. In addition, in order to produce conservative models (Wood, 2006), the maximum number of knots was also restricted to k = 4. To minimise the probability of model overfitting, model fits for all possible combinations of variables were compared using the Akaike Information Criterion corrected (AICc), which is a recommended criterion for finite sample size (Burnham & Anderson, 2003). In addition, to rank the fitted models we computed the Akaike weights (Buckland et al., 1997) to examine the weight of likelihood in favour of a model being the best in the given set of models. To explore the relative importance of each variable, we summed the weighted AICc values across all possible models. When number of candidate models tied for best for data analysis (arithmetic difference between a model AICc and the minimum AICc for all models, denoted ΔAICc < 2), the model of best fit was selected based on having the highest Akaike weight ranking for likelihood of evidence across all possible models (*sensu* Burnham & Anderson 2003). Response curves were visually inspected for ecological realism (Sagarese et al., 2014). All models were fitted in R version 3.2.0 (R Core Team, 2014).

4.3.5 Model validation

Models of best fit for biomass and abundance estimates were cross-validated using 5-Fold cross validation 50 times (Lehmann et al., 2002). We then calculated normalized root mean square error (normalized RMSE) to examine the average magnitude of the predictive errors of all generated submodels (Potts & Elith, 2006; Costa et al., 2014). Plots of model residuals were visually investigated for patterns following the procedures outlined in Zuur et al. (2009; 2010).

To investigate any residual spatial patterns not accounted for with the relationships between the observed biomass/abundance and values predicted by the models of best fit, we fitted geographically weighted regression (GWR) and examine the spatial patterns in the distribution of the local standardized residuals (Brunsdon et al., 1996). The GWR allows for nonstationarity in the relationships between the dependent (observed biomass/abundance) and the explanatory (predicted biomass/abundance) variables and is a useful explanatory technique for interpretation based on spatial context and known characteristics of the study area (Goodchild & Janelle, 2004).

4.3.6 Spatial prediction of species' biomass and abundance

Once the best fit models were validated, the constrained biomass and abundance estimates of individual fish species were predicted on 4 m grids using R and these predictions were plotted in ArcMap 10.2.2. To identify hotspot areas where large fertile adults, or small juvenile fish of the three species tended to aggregate, the continuous predictive biomass rasters were reclassified into these two categories according to the known biology and the life history of individual study species. The cut-off points for the reclassification process were based on the fecundity (number of eggs), length and biomass values summarized for the three species in Smallwood et al. (2013). The reclassified values were plotted again to map the hotspot areas where juvenile or mature adult fish of the modelled species aggregate. For example, a hotspot for juvenile/mature fish will have a maximum score of 3, corresponding to juvenile/mature individuals of the three modelled fish species that can potentially associate with that particular area. In addition, the predictive fish abundance rasters were summed for all study species to identify areas of Geographe Bay associated with high cumulative abundance of individuals of the modelled species.

4.4 Results

4.4.1 Model selection and variable contributions

Non-linear responses were frequently observed between the biomass or abundance of the study species and the explanatory environmental variables (Figure 4.2). These non-linear responses provided strong support for using GAMs in studies of the relationships between demersal fish and their environment. The relative importance of the explanatory variables across all model fits was similar between the biomass and abundance models for *Glaucosoma hebraicum* and *Chrysophrys auratus* but differed for *Choerodon rubescens* (Figure 4.3).

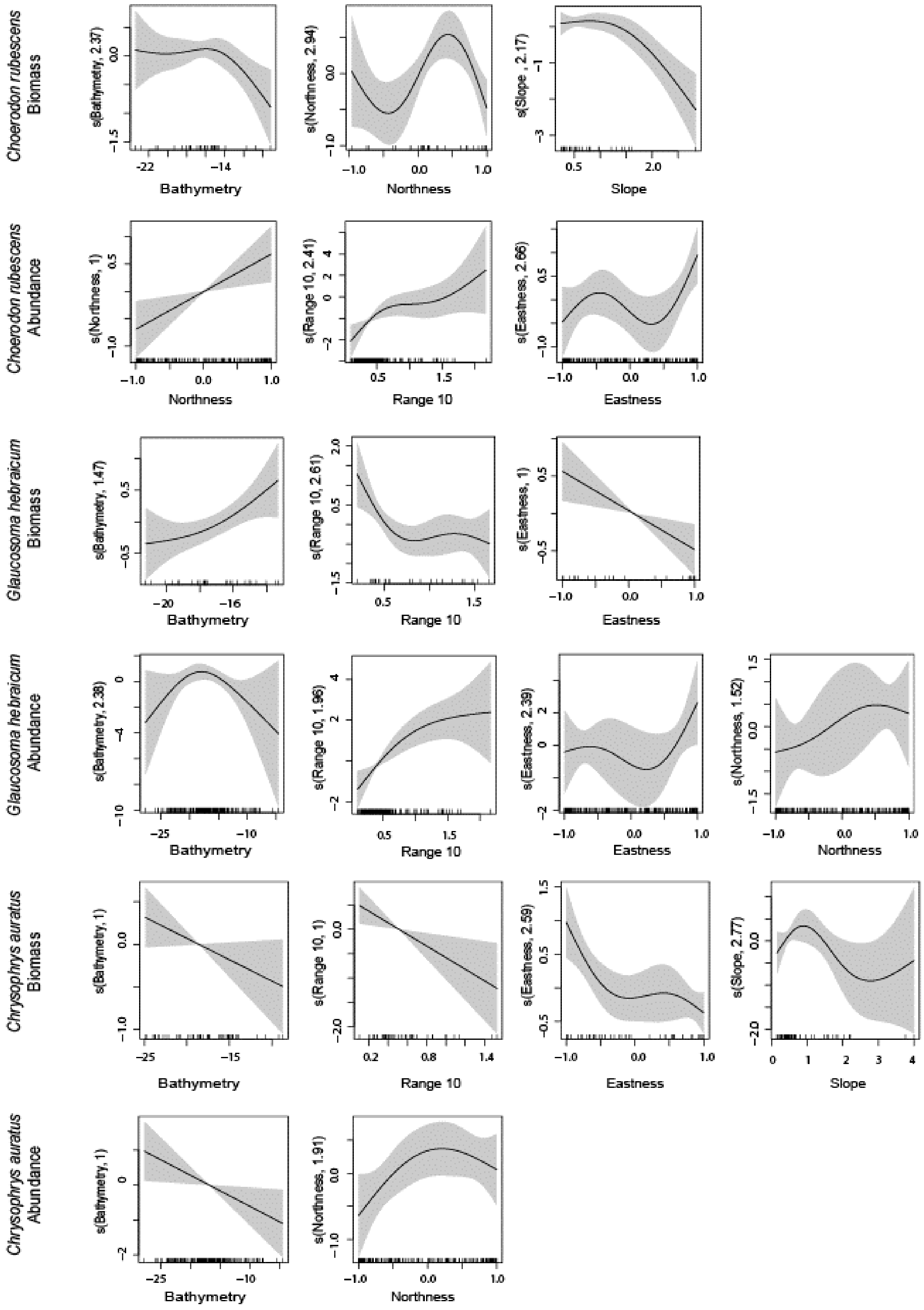


Figure 4.2 Smoother estimates (solid line) for the environmental predictors as obtained by generalised additive models for biomass and abundance of the three study fish species. The approximate 95% confidence envelopes are indicated (grey shading), marks along the x-axis are sampled data points. All explanatory variables were fitted with model smooths (knots) k = 4. Summary of the environmental predictors is provided in Table 4.1.

The most commonly chosen variables across all models fits for all study species were bathymetry, range (indication of structural complexity of the relief) and eastness (azimuthal direction of the reef slope) followed by northness and slope (Table 4.2 and Figure 4.3).

Bathymetry was an important environmental variable for abundance and biomass of all modelled species except abundance of *C. rubescens* where it was assigned low importance (Figure 4.3). Best fit models predicted lower biomass and lower abundance in shallow areas for *C. rubescens*, *G. hebraicum* and *C. auratus*, with exception of biomass of *G. hebraicum* where higher biomass was predicted in shallow water (Figure 4.2).

Range was an important variable for the abundance of *C. rubescens* and *G. hebraicum*, where higher abundance of these species was predicted near reef edges (Figure 4.2). Range was also important for biomass of *G. hebraicum* and *C. auratus*, where higher biomass of these species was predicted for the areas of low complexity (Figure 4.2). These results are particularly interesting for of *G. hebraicum*, which exhibited reversed patterns in the abundance and biomass distributions. Similar patterns were observed for eastness variable. A higher abundance of *C. rubescens* and *G. hebraicum* and a lower biomass of *G. hebraicum* and *C. auratus* was predicted on the east-facing slopes (Figure 4.2).

The explanatory power of the best models was notably higher for the biomass models (Table 4.2). However, the biomass models had slightly higher cross-validation errors (normalized RMSE). The best fit model developed for biomass of *C. rubescens* had the highest explanatory power across both the biomass and abundance datasets (adjusted R^2 = 61 %) and intermediate predictive error for the biomass model (normalized RMSE = 23.5 %; adjusted R^2 = 28 %). While the predictive error for model of abundance of this species was highest with intermediate explanatory power (normalized RMSE = 20 %; Table 4.2). Despite the fact that the best fit models developed for the biomass and abundance of *C. auratus* had the lowest associated predictive errors (normalized RMSE = 19.9 and 11.5 % respectively), the explanatory power of these models was lowest across both the biomass and abundance datasets (adjusted R^2 = 33 % and adjusted R^2 = 6 % respectively; Table 4.2). The amount of cross-validation error could be associated with the sample size and the range of sampled biomass and abundance values. For example, the observed abundance values of *C. rubescens* and *C. auratus* ranged between 1-3 and 1-13, resulting in the highest and lowest error terms respectively. Similarly, the sample sizes for biomass of *C. rubescens* and *G. hebraicum* were 34 and 35 individuals respectively in the study area, with the range of observed biomass values almost twice larger for *G. hebraicum*, which evidentially resulted in the highest cross-validation error for the biomass models of this species. Sample size is known to have a major impact on model performance (Pearce & Ferrier, 2000).

Table 4.2 Summary of candidate models (within 2 ΔAICc from the minimum AICc value) for predicting biomass and abundance distribution of the three study species. GAMs of best fit identified by ΔAICc = 0 and highest Akaike weights for evidence support.

	Species	Intercept	Bathymetry	Northness	Curvature	Range10	Eastness	Slope	Adjusted R^2	df	AICc	ΔAICc	Akaike weights	Normalized RMSE (%)
BIOMASS	*Choerodon rubescens*	6.45	+	+				+	0.61	9.48	501.0	0	0.40	23.5
	Choerodon rubescens	6.48		+				+	0.48	6.98	501.3	0.29	0.34	
	Choerodon rubescens	6.47		+	+			+	0.52	7.95	501.8	0.82	0.26	
	Glaucosoma hebraicum	6.84	+			+	+		0.45	7.08	552.9	0	0.38	27.9
	Glaucosoma hebraicum	6.82			+	+	+	+	0.5	8.34	553.6	0.65	0.27	
	Glaucosoma hebraicum	6.83	+			+	+	+	0.48	7.99	554.2	1.28	0.20	
	Glaucosoma hebraicum	6.84	+		+	+	+		0.47	7.95	554.8	1.83	0.15	
	Chrysophrys auratus	7.14	+			+	+	+	0.33	9.36	1788.2	0	0.38	19.9
	Chrysophrys auratus	7.15	+			+	+		0.3	8.28	1789.0	0.79	0.26	
	Chrysophrys auratus	7.16				+	+		0.29	7.29	1789.6	1.35	0.19	
	Chrysophrys auratus	7.16				+	+	+	0.28	6.78	1789.9	1.69	0.16	

ABUNDANCE	*Choerodon rubescens*	-1.71		+		+	+		0.18	8.68	256.0	0	0.51	20
	Choerodon rubescens	-1.74	+	+		+	+		0.2	11.06	257.2	1.18	0.28	
	Choerodon rubescens	-1.70		+		+	+	+	0.18	9.30	257.8	1.82	0.21	
	Glaucosoma hebraicum	-2.38	+	+		+	+		0.28	11.58	220.8	0	0.34	14
	Glaucosoma hebraicum	-2.28	+			+	+		0.26	9.88	221.2	0.42	0.27	
	Glaucosoma hebraicum	-2.35	+			+	+	+	0.27	11.05	221.2	0.45	0.27	
	Glaucosoma hebraicum	-2.29	+	+		+		+	0.26	10.94	222.8	1.96	0.13	
	Chrysophrys auratus	-0.66	+	+					0.06	5.29	426.7	0	0.27	11.5
	Chrysophrys auratus	-0.69	+	+			+		0.08	6.64	427.1	0.39	0.22	
	Chrysophrys auratus	-0.66	+				+		0.07	5.68	427.1	0.39	0.22	
	Chrysophrys auratus	-0.60	+						0.04	3.00	427.5	0.76	0.18	
	Chrysophrys auratus	-0.69	+	+		+			0.08	7.54	428.6	1.83	0.11	

4.4.2 Model validation

The visual examination of residuals of models of best fit for abundance of all modelled species, identified high frequency of negative residuals, which could be attributed to a large amount of zeroes observed in these datasets. In the exploratory stages of our analysis we examined the possibility of applying the zero inflated Poisson GAMs to the abundance dataset. However, the zero inflated models with Poisson error distribution did not resolve the negative skewness in the residuals and produced higher cross-validation errors. At this stage, only one package compatible with R statistical software is still under development that will allow fitting zero inflated GAMs with negative binomial error distribution that could provide a potential solution to the negatively skewed residuals (VGAM; Yee 2015).

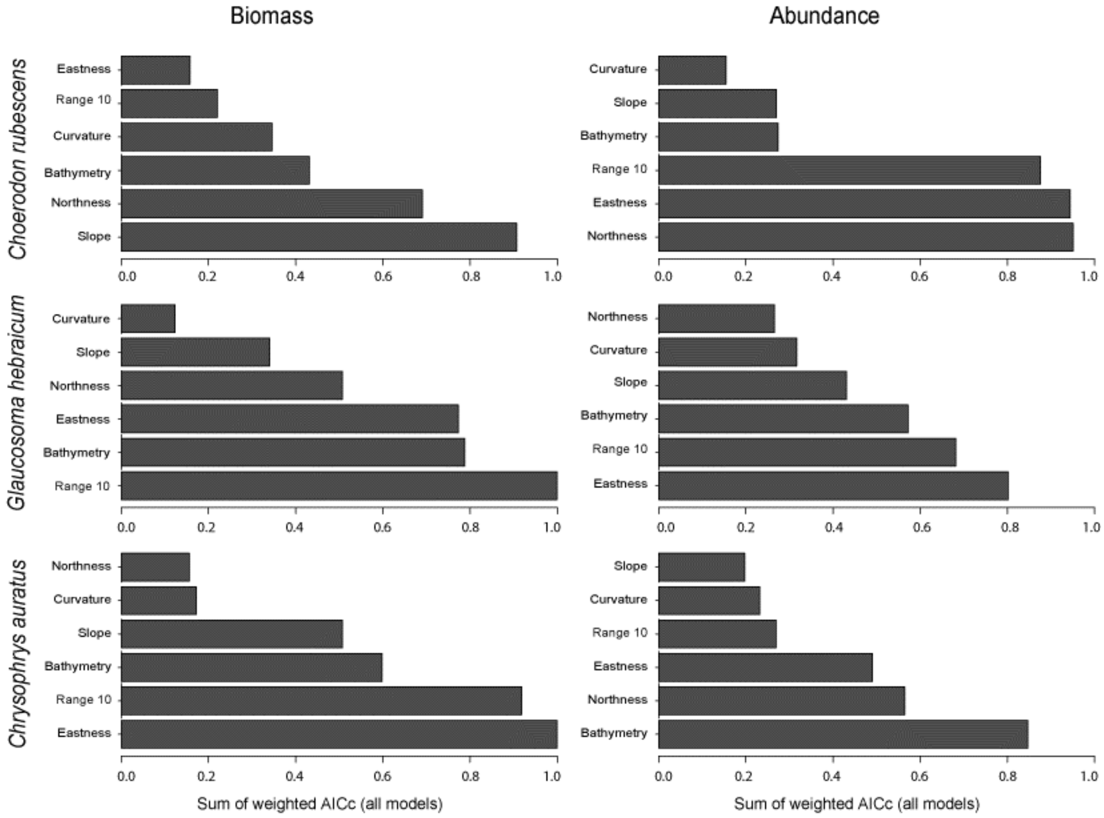


Figure 4.3 Relative importance of all environmental variables as indicated by the sum of weighted AICc for each variable across all fitted models.

The spatial patterns in distribution of the local standardized residuals from the GWR analysis can be found in plots in Figure 4.4. There was small amount of spatial clustering of high residuals in the north-eastern part of the bay in GWR model fit for biomass of *Chrysophrys auratus*. In addition, there was some degree of spatial clustering of the high and low residuals in GWR models fitted for abundance of all study species. However, the Moran's I analysis on the standardised residuals of all GWR models did not indicate spatial correlation in model residuals (all Z scores represented the expected outcome and all *P* > 0.05). Thus we conclude that the observed high/low residual patterns are due to local habitat characteristics and/or missing covariates, that are known to produce patterns in model residuals (Fotheringham et al., 2003; Zuur et al., 2009).

4.4.3 Spatial predictions

The predictions from the models of best fit provided a continuous representation of biomass and abundance distributions of the study species across entire Geographe Bay (Figure 4.5). The small biomass individuals of *Choerodon rubescens* were predicted to be associated with shallow, protected south or east facing reef edges, whereas the large biomass individuals were predicted to be found in deeper, flat areas of the bay (Figure 4.5a). The high abundance of this species was predicted for exposed reef edges particularly in the western part of the bay (Figure 4.5d).

The large biomass individuals of *Glaucosoma hebraicum* were predicted to be found in shallow, low relief westward sloping areas of the bay. In contrast, small biomass individuals of this species were predicted to be associated with deeper protected near reef areas of the bay (Figure 4.5b). The high abundance of *G. hebraicum* was predicted for the north or east facing near reef areas at intermediate depths (Figure 4.5e).

The small biomass individuals of *Chrysophrys auratus* were predicted to be associated with shallow, east facing high relief reef areas of the bay, whereas the large biomass individuals of this species were predicted to be found in deep flat areas in the west part of the bay (Figure 4.5c). The high abundance of this species was predicted in the deep and exposed western part of the bay (Figure 4.5f).

Cumulative predicted maps of abundance and biomass of small/juvenile and large/mature adults of all three study species identified shallow coastal areas of the bay as being a hotspot for aggregation of small fish biomass (Figure 4.6b). In addition, small local pockets of aggregations of juvenile and adult fish biomass were identified from the cumulative maps across the bay. However, no additional distinctive hotspots for the study species could be assumed from the cumulative maps of biomass (Figure 4.6a, b). The reef ridge areas that spans across most of the bay was predicted to be characterised by high abundance of individuals of the study species with higher cumulative predicted abundance in the western part of the bay (Figure 4.6c).

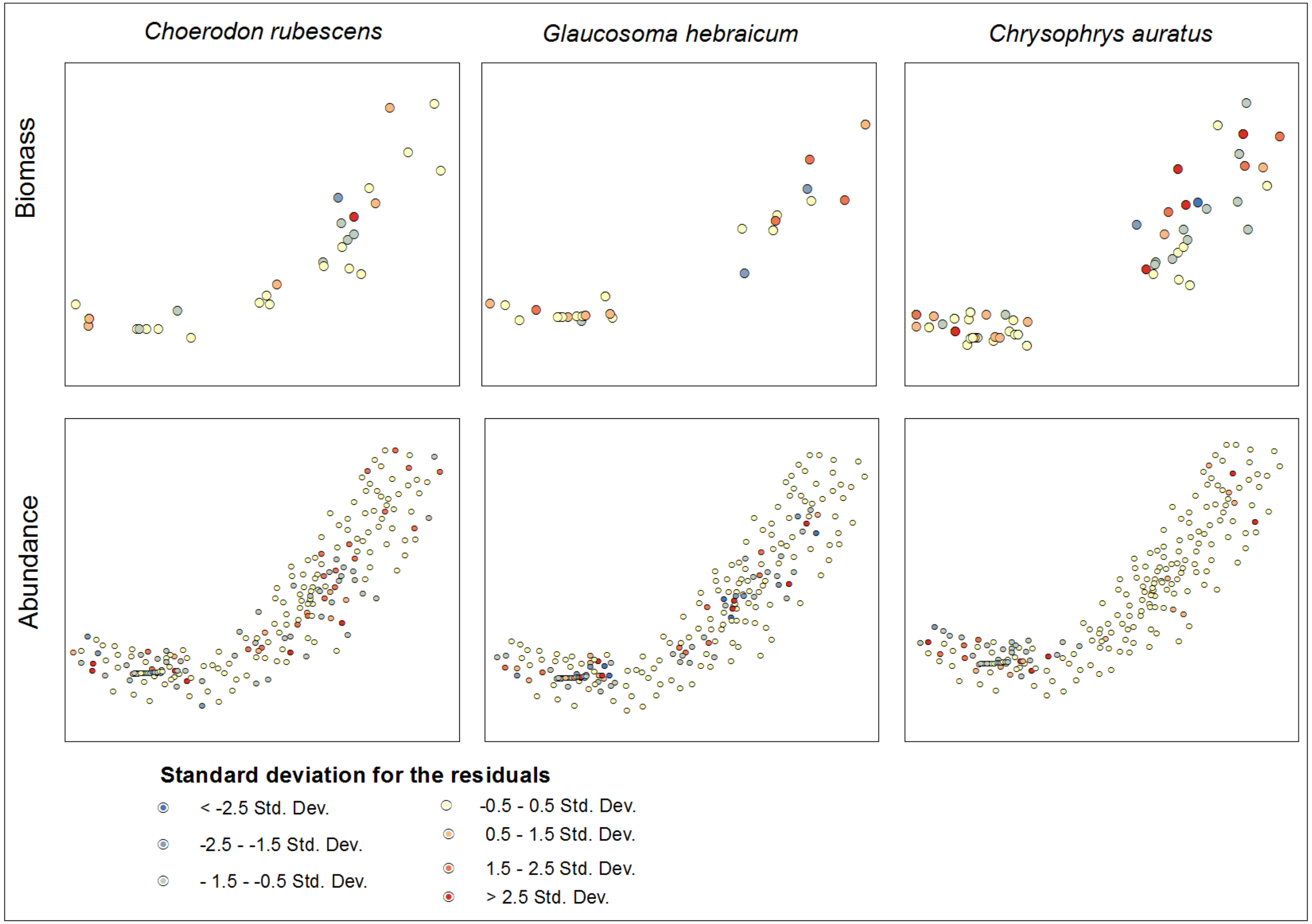


Figure 4.4 Distribution of the local standardised residuals from the Geographically Weighted Regression analysis.

4.5 Discussion

4.5.1 Most important environmental variables

Estuaries and shallow, sheltered coastal embayments play a central role in the population dynamics of many inshore fish species acting as juvenile nurseries or adult spawning grounds (Francis et al., 2005). We found that bathymetry, structural complexity of habitat and direction of reef slope were the most common predictors for the observed patterns in abundance and biomass distribution of the three study species. Bathymetry and structural complexity are also indicative of key processes that relate to resilience in other systems, such as regime shifts on coral reefs (Graham et al., 2015) and they should be considered as part of selection criteria for spatial planning of marine reserves. However, the relative importance of all explanatory variables varied between species for either abundance or biomass models suggesting that a different hierarchy of environmental processes dictates patterns in species-specific abundance and biomass distributions. Small scale habitat characteristics have previously been documented to influence the abundance and diversity of reef fishes (Syms & Jones, 2004; MacNeil et al., 2009) and to drive species-specific response to the environment (Almany, 2004).

4.5.2 Patterns in abundance of the modelled species

The abundance of the three study species was predicted to be higher in the western part of the bay, identifying these areas as a hotpot for cumulative abundance. In addition, higher abundances of West Australian dhufish (*Glaucosoma hebraicum*) were predicted along the limestone reef ridges across the bay. The observed high abundance gradient of the three species in the ocean-ward part of the bay could be driven by the large-scale population dynamics of these species. The pre-settlers of the three species were recorded to utilise major regional oceanic currents such as south-ward flowing Leeuwin Current or north-ward flowing Capes Current for enhanced larval transport from the source of populations further along the coast (Lenanton et al., 2009; Cure et al., 2015). Therefore, higher abundances of the three species could be expected in the areas close to the source of transport, gradually declining in the inner part of the bay. Similar patterns were documented in case of the Mediterranean wrasse, with a greater abundance of this species observed in the areas that were closer to the source of population (Guidetti et al., 2002). High structural complexity and higher prey availability on reef habitats could be additional factors that explain high abundance of *G. hebraicum* near the reef ridges. This carnivorous fish is known to favour reef habitats at various life-stages (Fairclough, 2005).

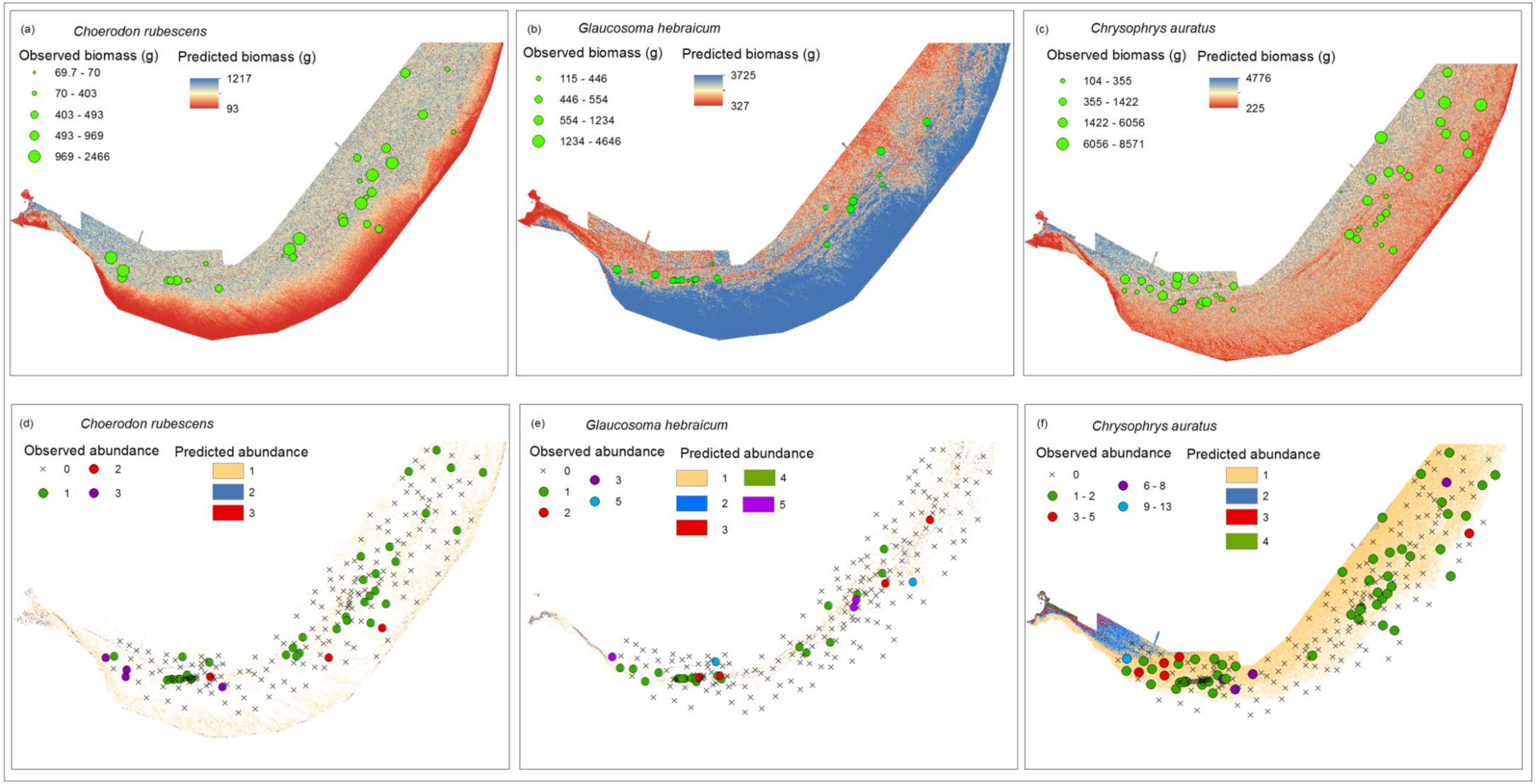


Figure 4.5 Predicted maps of continuous distributions of the three species across Geographe Bay for the biomass and abundance as defined by the GAMs of best fit for individual study species. Observed biomass and abundance estimates plotted as well.

4.5.3 Patterns in biomass distribution of the modelled species

The predicted distribution and the extent of ecological niches across the bay were similar for biomass of the Baldchin groper (*Choerodon rubescens*) and Australasian snapper (*Chrysophrys auratus*) identifying shallow coastal areas with high structural complexity as the most suitable hotspot area for juveniles of these species. Deeper areas of the bay with high complexity relief were also found to be good predictors of biomass distribution of juvenile *G. hebraicum*. In contrast, mature adults of this species were predicted to be associated with shallow coastal waters. However, the hotspot maps of cumulative biomass of large, sexually mature fish did not indicate any parts of the bay as being crucial for this stage of the species' life history. This outcome is somewhat expected, as a variety of juvenile fish are known to use structurally complex habitats such as canopy forming macroalgae or coral reefs as their nursery areas (Evans et al., 2014). In addition, small-size fish typically have smaller home ranges and are less likely to move as far as larger bodied conspecifics (Nash et al., 2015), which may have helped to identify the environmental niche requirements of juvenile fish more accurately. Many juveniles use near shore habitats as predation refugia and as a trade-off between high prey availability and low juvenile survivor rates on reefs (Kimirei et al., 2013). Our findings highlight the potential vulnerability of both the juvenile and the sexually mature adults of the three species which rely on the near shore areas. This important outcome would have been missed if only the abundance patterns of these species had been considered.

4.5.4 The benefits of using individual fish biomass in spatial modelling

The biomass model fits had notably higher explanatory power in comparison to the abundance models. The higher explanatory power of biomass is particularly beneficial for models developed for overfished and/or rare species where a high proportion of zeroes in datasets could result in poor model fits, and consequentially low explanatory power. While new methods for modelling non-linear relationships between rarely recorded marine species and their environment are being developed (e.g. VGAM package), we suggest using biomass and abundance models to complement each other. Such an approach could be extremely useful for spatial management when mapping distribution patterns in fish diversity and for understanding population dynamics of endangered species. In many cases, abundance and biomass patterns could produce very different curves for the same species (Thibault et al., 2004).

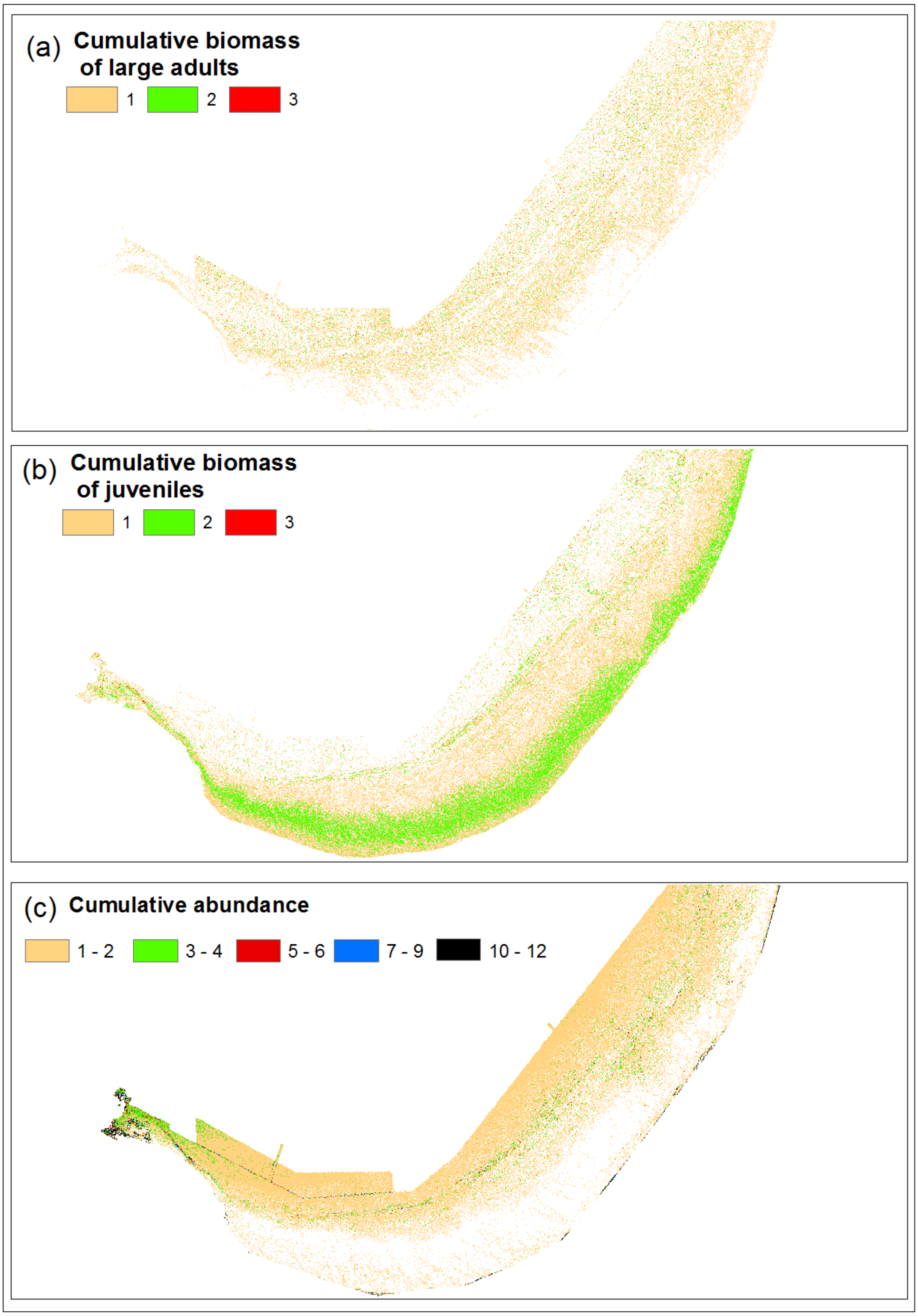


Figure 4.6 Hotspots map for cumulative biomass of large sexually mature adults (a), juveniles (b) and cumulative predicted abundance (c) of the three study species. Rasters reclassified based on known biomass estimates of the study species.

There is often a shift associated with establishment of marine reserves, where fished sites are characterised by higher abundance than biomass and protected sites by higher biomass of large-bodied species than the relative abundance of species (Edgar & Stuart-Smith, 2009; Anticamara et al., 2010). While species' abundance is clearly an important measure, biomass estimates could be more relevant for explaining patterns of resource use or niche partitioning among conspecifics than abundance models (McGill et al., 2007).

4.5.5 Benefits to management

As a fisheries management tool, mapping key areas of seascape that are crucial for different life-history stages of the same species or multiple species followed by relevant management actions, may result in lower losses and higher survival of vulnerable life stages, which in turn can preserve critical spawning stock biomass of exploited species, and enhance fishery yields (Dugan & Davis, 1993). Nursery areas contribute to adult population patterns (Huijbers et al., 2013). Enhancing the ability to monitor juvenile recruitment variability in areas of critical juvenile habitat would, for some species, allow predictions of future strength of cohorts to be made before they enter the fishery (Lewis et al., 2012). By creating temporary closures of adult breeding grounds during spawning season, it is possible to enhance the reproductive dynamics of the entire population of the target species. For example, longer spawning season and larger amount of eggs per batch is documented for large mature females of *G. hebraicum* in comparison to the smaller mature females, making them extremely vulnerable to fishing during the spawning period (WA Department of Fisheries, 2013). Protecting the crucial areas of seascape for large sexually mature females could enhance the abundance and biomass of depleted stocks (Polacheck, 1990; Denny et al., 2003), which in turn can benefit other fish species relying on healthy ecosystem functioning (e.g. Olds et al., 2014). Our study provides a novel approach that can be incorporated into efforts to address this knowledge gap for a wide variety of species. The hotspot maps can optimise limited management resources by identifying entire areas that may not require future in-depth surveys. Following *in situ* evaluation of the predicted hotspots, these areas should be considered in zoning schemes and become priority areas for marine spatial monitoring and management (Schmiing et al., 2013). They should also be included in any future re-zoning plans.

4.6 Conclusions

In this study we used spatial modelling to examine patterns in the abundance and biomass distributions of three iconic fish species across a continuous mosaic of habitats in order to identify niche requirements and resource partitioning between fish at different life stages.

The biomass models in this study were characterised by higher explanatory power for all modelled species, supporting future use of this novel approach for examining spatial ecology of other demersal fish species. Pairing video observations and measurements with remotely sensed (hydroacoustic or LIDAR) benthic habitat data with species distribution models has tremendous potential for understanding fine-scale species-environment relationships of demersal fish. In addition, mapping key areas of seascape that are crucial for different life-history stages of the same species, or multiple species may benefit actively fished species, particularly those species that exhibit high site fidelity and relatively localised movement patterns. By implementing management actions in the hotspot areas that provide protection from disturbance, such as bycatch or undersize fishing, it is possible to preserve the critical spawning stock biomass of exploited species. This in turn can result in higher survival of vulnerable life stages of targeted and non-targeted species, enhance fishery yields outside the protected hotspot areas and promote healthy ecosystem functioning. Furthermore, the hotspot areas may preserve critical spawning stock biomass of exploited stocks more effectively than size limits and catch quotas for some species by preserving natural size distributions and densities (Dugan & Davis, 1993).

Postscript: In the next chapter I examine the performance of stereo-BRUVs as data collection method on fish occurrence in combination with the ecological spatial modelling. I compare between models based on data collected using this method with models based on towed stereo-video datasets.

Chapter 5 Comparing two remote video survey methods for spatial predictions of the distribution and habitat suitability of demersal fishes

5.1 Abstract

Marine spatial management often utilises an array of survey and data analyses methods in order to answer specific research questions and to improve conservation efforts. With recent developments of ecological spatial modelling as a decision making tool, the usefulness of some of the long-established survey methods for species distribution modelling should be revised due to the biases they may introduce with respect to habitat associations of fish. Generalised additive models were used to model the probability of occurrence of six focal species after surveys that utilised two remote underwater stereo-video sampling methods (i.e. baited and towed video). Models developed for the towed stereo-video method had consistently better predictive performance for all study species, except for one. The relative importance of habitat variables for explaining variation in distribution patterns of fish differed between survey methods, the most important variables across the two survey methods being bathymetry followed by structural complexity. Models based on baited video dataset regularly included large-scale measures of structural complexity, suggesting fish attraction to a single focus point by bait. Conversely, models based on the towed video data often incorporated small-scale measures of habitat complexity and were more likely to reflect true species-habitat relationships. The lower cost associated with the use of the towed video systems for surveying low-relief seascapes provides additional support for considering this method for marine spatial management purposes. Our study provides evidence that towed stereo video is a robust, non-intrusive, low cost method for fine-scale data collection that can be useful for spatial ecological modelling.

5.2 Introduction

Finfish are widely recognised as an important component of marine systems with crucial roles in terms of ecological processes, tourism, and fisheries (Andrew & Mapstone, 1987; Morrison & Carbines, 2006). Anthropogenic influences such as climate change, habitat loss and increased fishing pressure alter the biodiversity, abundance and distribution of finfish, potentially compromising their ecological roles and services (Sala & Knowlton, 2006;

Butchart et al., 2010). Good fisheries management is crucial for building the adaptive capacity and resilience to climate-driven changes (Ogier et al., 2016). However, the extent of these changes is not always apparent over spatial scales relevant to management. Hence identification of significant species-environment patterns across varying spatial scales and monitoring shifts in these patterns relative to changing environmental conditions can contribute to local and regional climate change adaptation strategies and overall goal of preserving biodiversity.

Remote video systems provide a way to non-destructively survey fish assemblages at depths beyond the limits of SCUBA diving and is a common method for surveying patterns of assemblage composition and population dynamics of fish (Cappo et al., 2006; Terres et al., 2015). Models that pair video observations data with benthic habitat data that has been remotely sensed using hydroacoustic or LiDAR technologies have become a powerful tool for understanding the relationships between demersal fish species and their environments (e.g. Pittman et al. 2009; Moore et al. 2010; Monk et al. 2011). Furthermore, pairing these species-distribution models (SDMs) with GIS and extrapolating models into non-surveyed areas has tremendous potential for the assessment of ecosystem dynamics and marine spatial management (Stamoulis & Delevaux, 2015). Among the various techniques currently available for remote video sampling of fish, baited remote stereo video (stereo-BRUVs) are probably the most established. Stereo-BRUVs have been used to monitor individual species targeted by fisheries, fish assemblage composition (Malcolm et al., 2007; Harvey et al., 2013), the effectiveness of marine protected areas (Watson et al., 2007) and the impact of seismic surveys and oil spills (www.aims.gov.au/docs/research/monitoring/seabed/video-monitoring.html; accessed March 2016). In recent years, data obtained from stereo-BRUVs has also been widely used in SDMs (see Moore et al. 2009; Chatfield et al. 2010; Fitzpatrick et al. 2012; Terres et al. 2015 for examples). However, there are problems associated with this method that limit the precision and predictive power of the models.

Baited video systems attract fishes to a bait plume or camera station, making it impossible to estimate true abundance or density of sampled species and it is common practice to deploy the individual stereo-BRUVs systems at least 250-500 m apart to keep observations independent (Cappo et al., 2003; Harvey et al., 2007; Terres et al., 2015). Hence the premise for spatial analysis for data collected with stereo-BRUVs is that this method samples fish assemblage composition in 200 m radius increments or greater (Moore et al. 2011). This could create a discrepancy when modelling species-habitat relationships and reduce the accuracy of the ecological niche predicted by the model for each species. For example, in the study by Moore et al. (2009), sand-affiliated species were predicted to be present over reef probably due to an aggregation effect introduced by the stereo-BRUV system.

Small-scale landscape heterogeneity has ecological value, supporting different and diverse communities (Healey & Hovel, 2004) or key community processes such as distribution and abundance of prey or risk of predation (Laurel et al., 2003). At larger scales, landscape heterogeneity that considers combinations of both patchy and contiguous habitats is required to maximise fish diversity and abundance (Pittman et al., 2009). Thus, while models based on broad-scale habitat classification provide a good fit and predictive accuracy, fine-scale models explain a greater proportion of observed patterns in distribution and provide greater insight into spatial ecology of demersal fish species (Chatfield et al. 2010). Furthermore, environmental variables that are significant at coarse spatial scales may not be at finer spatial resolution (Chatfield et al., 2010). These studies highlight the importance of fine-scale habitat information when modelling species distributions and the potential biases that stereo-BRUVs can introduce.

Towed stereo-video has advantages similar to baited video systems, as it can be deployed at great depths, is non-destructive and provides a permanent record of fish lengths. In addition, towed stereo-video produces comparable results to diver-operated video transects (Stobart et al., 2007; Warnock et al., 2016) and is thought to be the least biased method for sampling abundance and biomass of sparids across multiple size ranges (Morrison & Carbines, 2006). Additional benefits of the towed stereo video are that they bear low rick for whale entanglement, continuously capture data over seascape transition zones (Spencer et al., 2005) allowing sample boundaries to be accurately estimated. The transition zones between different benthic substrates have previously been identified as important determinants of the structure and diversity of fish assemblages (Moore et al., 2011) because they provide a broader array of refuges and increased foraging and spawning opportunities (Friedlander & Parrish, 1998). Furthermore, towed video is a useful technique for rapid surveys of low-relief seascapes, vastly reducing manpower and vessel time (Watson et al., 2005; Monk et al., 2010) and providing comparable results to alternative survey methods such as bottom trawl and diver operated video (McIntyre et al., 2015; Warnock et al., 2016). Known limitations of towed video are typically associated with movement of the system through the water column. Fish that exhibit avoidance behaviour to moving objects could be frightened by the camera system which could result in low estimates of abundance and species richness (McIlwain et al., 2011), while other species may be attracted to moving objects. Towed video may also get tangled and underestimate cryptic fish especially when the system is towed over highly rugose reef or dense macroalgal canopy and consequentially bias model predictions by including false absences (Hirzel et al., 2001; Monk et al., 2010).

In this study we compare fish species-environment relationships derived from either stereo-BRUVs or towed stereo video systems (hereafter BV and TV, respectively) and use these to develop species distribution models. The specific aims of this study were: 1) To identify fish-habitat relationships and compare environmental variables from best-fit models for each survey method. 2) To develop predictive maps of fish distributions based on habitat presence (i.e. predicted ecological niche) in the study area and compare these predictions across two survey methods. 3) To assess cost-effectiveness of each method to facilitate decisions about which method is most suitable for marine spatial management.

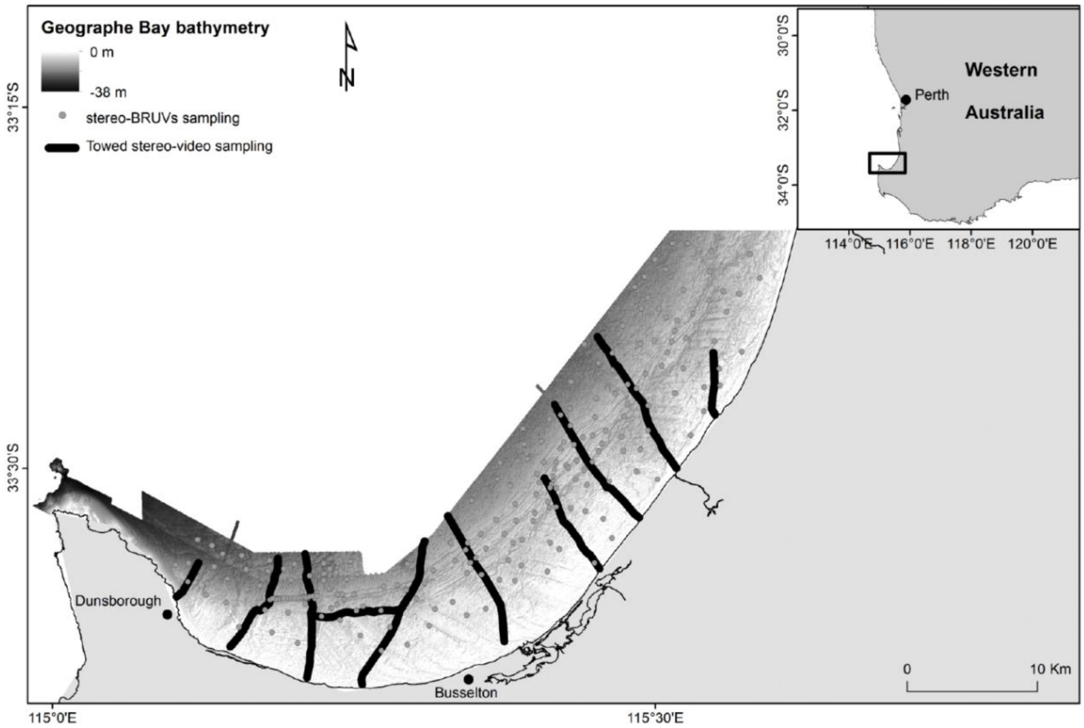


Figure 5.1 Inset: The location of the Geographe bay study area on the south-west coast of Western Australia. Main map: Shading indicates bay's bathymetry. Black lines indicate towed stereo-video transects. Grey dots indicate baited remote stereo-video deployments.

5.3 Methods

5.3.1 Study area

Geographe Bay is a ~100 km wide, relatively shallow, north-facing embayment with seagrass cover that can at times exceed 60% (McMahon et al., 1997). The bay is located in southwestern Australia, approximately 220 km south of Perth (Figure 5.1). The majority of the seafloor is covered by unconsolidated sediments that have been deposited over older clay layers. There is also a series of discontinuous limestone ridges, dominated by canopy-forming brown macroalgae, that run parallel to the coast (Wernberg et al., 2003; Van Niel et al., 2009).

5.3.2 Fish occurrence data

Fish occurrence data was collected between the 9 and 17 December 2014. Two methods were used for sampling fish assemblages in Geographe Bay: a point observation method using BV and a transect method using TV. The BV sampling was spatially stratified according to the size of the study area and depth: random points for sampling were allocated to adequately cover the bathymetric gradient in the bay. In addition, major substrate types (e.g. reef ridge) were particularly targeted based on the skipper's local knowledge of the study area. In addition, distance controls were used in the planning stage to avoid bait plume overlap and reduce the likelihood of fish moving between BV systems, with each pair of stereo systems at least 400 m apart from each other on the day of deployment. Each system comprised two wide-angle Sony CX12 high-definition video cameras that had been baited with approximately 800 g of crushed pilchards (*Sardinops sagax*), and lowered to the bottom for a 60 minute soak time. The 217 video recordings from these deployments were analysed using the software EventMeasure (SeaGIS Pty Ltd). For this study we only included fish within 7 m in front and 2.5 m on each side of the cameras and approximately 3 m into the water column above the system. Additional information on design, calibration (Harvey & Shortis, 1995) and use of the stereo-BRUVs is presented in detail in the literature (e.g. Cappo et al. 2003; Langlois et al. 2012 and references therein).

The TV camera system also consisted of two wide angle Sony CX12 high-definition video cameras mounted 0.7 m apart. The cameras were mounted on a custom cage to protect the system during collisions and provide a secure towing point. The cameras were inwardly converged at eight degrees to gain an optimized field of view with stereo-coverage from 0.5 m to the maximum visibility (Supplement 5.7.1). The same distances for fish inclusion in the video as for the BV were applied for this method. The system was towed immediately behind the boat at speeds 0.5–2 knots at a height approximately 1 m above the seafloor and tilted downward to cover the immediate benthos as well as the water column in the field of view of the cameras. This configuration facilitated an ample field of view to observe demersal fish and allowed safe navigation of the equipment. The video signals were transferred to the surface via an umbilical cable where they were monitored in real-time, time stamped and synchronised with positional data that were recorded at 2 s intervals with handheld GPS. Nine video transects were executed capturing fish assemblage composition along continuous physical and biological gradients within the study area (e.g. substrate and benthic biological habitat) totalling 22 hours of georeferenced underwater towed video footage, covering 83 linear km of seafloor. Subsequently, the video footage of fish species occurrence were visually analysed with the EventMeasure software (www.seagis.com.au).

In both fish occurrence datasets, all fish were identified to the lowest taxonomic level possible and provided a reliable species presence records for future modelling. As prevalence of species can affect modelling outcomes and performance of models (Franklin, 2010), we chose a subset of six focal species that were often observed in both video survey techniques and represent a diversity of demersal fish life histories, size, and mobility in the study region (Table 5.1). To generate pseudo-absences for the BV fish occurrence dataset, we assigned absence to each individual deployment where the particular focal fish taxon was not observed. This method has been previously used in modelling species-environment relationships (Moore et al., 2009; Monk et al., 2012). The final presence-absence BV dataset was partitioned into training (75%) and testing (25%) data for individual focal species.

To generate reliable pseudo-absences for fish observations obtained from constantly moving TV system, we applied kernel density function to the focal species occurrence dataset using ArcGIS 10.2.2. The probability density function relies on assumption that presence is a probabilistic function mainly affected by species abundance and detectability (Silverman, 1986; Brotons et al., 2004). Kernel density function was applied to point data with observed presences of the focal species in order to generate a continuous surface of probabilities of occurrence of the focal species along transect. The neighbourhood search radius for kernel density calculations was set to 400 m to represent similar distance that was used for the BV systems. The results of probability surface were further analysed in PresenceAbsence package (Freeman & Moisen, 2008) using R statistical software version 3.2 (R Core Team, 2014) in order to calculate the optimal threshold for translating a probability surface into presence-absence maps. We selected the optimal threshold based on the maximum values of Kappa, which is a commonly used chance-corrected measure of agreement for presence-absence ecological data (Elith et al., 2006; Freeman & Moisen, 2008). The kernel density values below the optimal threshold were converted to pseudo-absences and true observations of focal species in the video recording from the TV system were kept as presences. The final pseudo-absences for modelling were randomly generated from combination of areas with kernel density below the appointed threshold and with no fish taxa observations from the TV to create a final ratio of 1:1 of true presences and pseudo-absences of a focal species along transects. The final presence-absence TV datasets were partitioned into training (75%) and testing (25%) data for individual modelled species.

Table 5.1 Fish species modelled, with summary of the number of occurrences used in model building based on the two survey methods: baited remote stereo-video (BV) and towed stereo-video (TV).

Scientific name	**Common name**	**Family**	**Method**	**Presence**	**Pseudo-Absence**	**Additional info**
Australabrus maculatus	Black-spotted wrasse	Labridae	BV	97	108	Small size endemic species
			TV	117	117	
Coris auricularis	Western King wrasse	Labridae	BV	140	60	Large size mobile endemic species
			TV	234	234	
Eupetrichthys angustipes	Snakeskin wrasse	Labridae	BV	58	155	Small size endemic species
			TV	59	59	
Notolabrus parilus	Brown-spotted wrasse	Labridae	BV	140	65	Large size endemic species
			TV	70	70	
Ophthalmolepis lineolatus	Southern Maori wrasse	Labridae	BV	150	63	Large size mobile endemic species
			TV	113	113	
Upeneichthys vlamingii	Blue-spotted Goatfish	Mullidae	BV	121	86	Mobile species, bycatch in commercial and recreational fisheries
			TV	85	85	

5.3.3 Habitat data

The bathymetric data was extracted from a mosaic of LiDAR and multibeam surveys collected by Fugro Corporation Pty Ltd gridded to a cell size of 4*4 m. The LiDAR hydrographic survey was performed between April and May 2009 on behalf of the Department of Planning as a part of a national coastal vulnerability assessment. The LiDAR area extended seaward from the coastal waterline to the 20 m marine nautical navigation chart contour and constituted the majority of bathymetric data. For further information on LiDAR collection and processing see www.planning.wa.gov.au, accessed May 2016. In addition to the LiDAR, a small area of deeper water was surveyed during March-April 2006 using Reson 8101 multibeam in the north-west part of the study area as part of the Marine Futures biodiversity surveys (see Radford et al. 2008 and matrix-prod.its.uwa.edu.au/ marinefutures/research/project; accessed July 2016; accessed May 2016 for further details). In addition to bathymetry, we derived nine variables that describe the structure and complexity of the seafloor and were previously shown to influence the distribution of fish using the Spatial Analyst toolkit in ArcGIS 10.2.2 (Moore et al. 2009; Monk et al. 2011; Table 5.2).

5.3.4 Species distribution modelling

To infer the effect of habitat complexity on the probability of occurrence of six fish taxa across the two survey methods, we applied generalised additive models (GAMs) developed for individual study species and the full subsets approach (Zuur et al., 2009). GAMs are the most common and well developed method for modelling fish habitats (Valavanis et al., 2008) and the full subsets method provides an unconstrained approach for fitting ecological responses to the predictor variable (Zuur et al., 2009; Fulton et al., 2014). All models were fitted with binomial error distributions and logit link functions in R version 3.2.0 (R Core Team, 2014). To produce conservative models and to avoid model overfitting, the number of smooths (knots) was restricted to $k = 4$ (Wood, 2006) and the model fits for all possible combinations of variables (total possible model fits =1023) were compared using differences in Akaike Information Criterion corrected (ΔAICc) for finite sample size (Burnham & Anderson, 2003). In addition, to rank the fitted models we computed the Akaike weights (Buckland et al., 1997) to examine the weight of likelihood in favour of a model being the best in the given set of models. Best models were selected based on having lowest AICc value, smallest AICc difference ($\Delta AICc < 2$) and having the highest weight across all possible models (Burnham & Anderson, 2003). To explore the relative importance of each variable, we summed the weighted AICc values across all possible models.

Table 5.2 Description of the seafloor variables used in model building.

Environmental Predictor	**Description**
Bathymetry	Elevation in metres relative to the Australian Height Datum.
Eastness	Trigonometric transformation of a circular azimuthal direction of the slope (*sin* (aspect)). Values close to 1 represent east-facing slope, close to -1 if the aspect is westward.
Northness	Trigonometric transformation of a circular azimuthal direction of the slope (*cos* (aspect)). Values close to 1 represent north-facing slope, close to -1 if the aspect is southward.
Slope	First derivative of elevation. Average change in elevation, steepness of the terrain, % rise.
Range 2, 5, 10	Maximum minus the minimum elevation in the local neighbourhood (local relief). Calculated at window sizes of 2*2, 5*5, 10*10 cells respectively, which equates to ground area of 64, 400 and 1600 m2 (i.e. fine, medium and coarse scale local relief).
Plan curvature	Secondary derivative of elevation. Measure of concave/convexity perpendicular to the slope.
Profile curvature	Secondary derivative of elevation. Measure of concave/convexity parallel to the slope.
Curvature	Combined index of profile and plan curvature.

5.3.5 Model evaluation and predictions

The test dataset was used to evaluate the discrimination and accuracy of the best developed models for all species across two methods. We used threshold independent Receiver Operating Characteristic (ROC) and the area under the curve (AUC) as graphical means to test the sensitivity (true positive rate) and specificity (false positive rate) of a model output (Fielding & Bell, 1997; Pearce & Ferrier, 2000). The area under the ROC curve is a measure of overall fit and commonly varies between 0.5 (no predictive ability) and 1 (perfect fit; Elith et al. 2006). In addition, we calculated a threshold dependent Kappa statistics which is commonly used in ecological studies with presence-absence data and provides an index that considers both omission and commission errors (Cohen, 1960; Elith et al., 2006). P_{fair} was chosen as the threshold to convert predicted probabilities of occurrence to presence/absence values as it minimises the difference between sensitivity and specificity and provides a measure of how well the model predicts both presences and absences (Moore et al., 2009; Chatfield et al., 2010). P_{fair} was also found to be better at selecting a threshold value when the prevalence of species was not close to 50% (Liu et al., 2005), as in the case of this study. Final comparison for model predictive performance across two survey methods were done by comparing the AUC values of best model fits developed for individual species.

Semivariograms were used to assess the level of spatial autocorrelation in the residuals of all models using Automap package in R (Hiemstra et al., 2009). Low levels of spatial autocorrelation (semi-variance 0.18 – 0.28) were found in TV datasets, which can be attributed to the initial method of generating pseudo-absences for this dataset. The kernel density function is relying on point observation of presences in order to generate continuous surfaces of probabilities of occurrence, which in turn were used to generate pseudo-absences. Furthermore, we plotted model residuals and final model predictions against the spatial coordinates to examine systematic spatial patterns in fitted models and distribution of correct/incorrect classifications. After evaluation, the best models for individual species were predicted on 4*4 grid using both train and test datasets across two sampling methods. Binary presence-absence maps were then constructed using the P_{fair} probability thresholds.

5.3.6 Costs

Accurate time budgets were maintained for all activities associated with each methodology and were expressed in staff time (number of hours per person devoted to each activity; Langlois et al., 2010; Holmes et al., 2013). We also included direct costs associated with general logistics (e.g. vessel and camera systems cost) for each survey method. Time not directly associated with the actual survey task (e.g. travel time to and from survey sites, accommodation costs) was excluded as it was similar for both methods. Time budgets were divided into three categories: Pre-Field Time (e.g. equipment calibration: 10*stereo-BRUV systems, one towed stereo video system), In-Field Time (e.g. data collection, video download), and Post-Field Time (e.g. video analysis). To make comparison possible, all estimates of In-Field costs were standardised to 40 * 60 minutes stereo-BRUV deployments (10 stereo-BRUV systems rotated four times within an eight hour day) and 8 hour-long video recording from the towed stereo video system.

5.4 Results

5.4.1 Model selection and variable contributions

The best models for explaining probabilities of occurrence differed between methods for all six fish species (Table 5.3). Occasionally there were a number of candidate models tied for best for data analysis with none or only marginal differences in Akaike weights for evidence support (i.e. candidate models for *Eupetrichthys angustipes* BV in Table 5.3). The explanatory power of the best models did not differ greatly between methods for the same species. Notable exceptions were models using BV data had higher adjusted R^2 values than models using TV data for *Coris auricularis* and vice versa for *Eupetrichthys angustipes* (Table 5.3).

The most important variables for explaining the probability of occurrence of the study species across two survey methods was bathymetry followed by the range variable, which is indicative of structural complexity of relief (Figure 5.2 and Table 5.3). The bathymetry variable was consistently identified as important with exception being models fitted for *Notolabrus parilus* when using the TV method and *Upeneichthys vlamingii* when using the BV method. Indeed all models for *U. vlamingii* presence derived from BV data were generally poor accounting for ≤ 2% variance in data. Range was also consistently included in models, though the spatial scale at which relief was considered important varied among species and methods. When using TV data, finer scale relief (range 2) was often considered more important than broader spatial measures of relief (range 10). Conversely, models using BV data consistently included range 10 as an important variable (Figure 5.2, Table 5.3).

There were linear and non-linear correlations between the environmental variables and probability of occurrence of all study species identified by the GAMs of best fit (Figure 5.). Nine out of twelve models of best fit had bathymetry as important environmental variable. The probability of occurrence of all species was typically higher in deeper water with exception to *Notolabrus parilus* when using the BV method. Range 10 and slope had a positive correlation with probabilities of species' occurrence, while range 5 had mixed effect on probabilities of occurrence. Range 2, profile (concavity/convexity of the slope) and easting (azimuthal slope direction) all had linear negative correlations with probabilities of occurrence of the study species (Figure 5.).

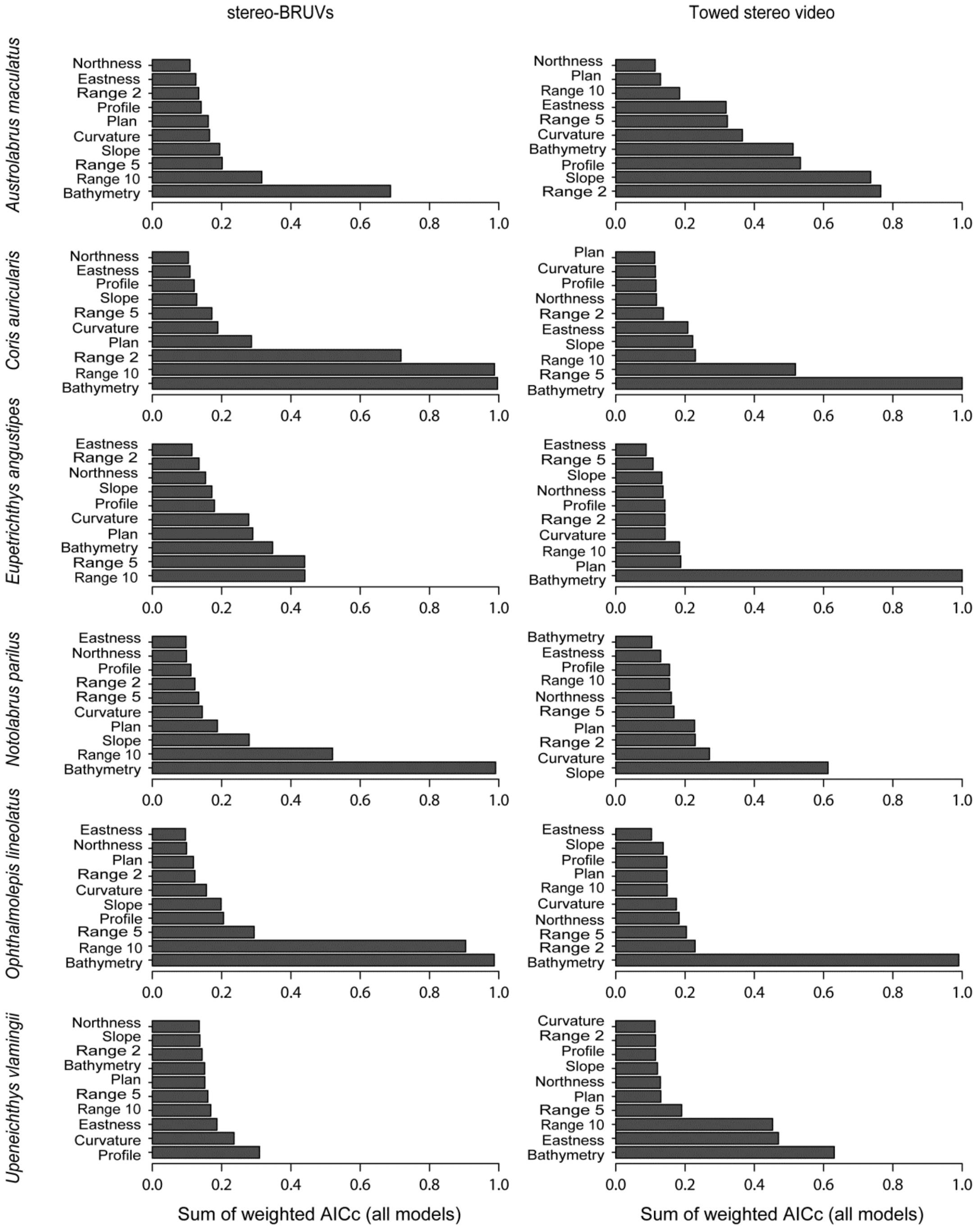


Figure 5.2 Relative importance of all fitted environmental variables as indicated by the sum of weighted AICc for each variable across all fitted models.

5.4.2 Predictive performance

The predictive performance of models of best fit developed for the six species, was good for one model (AUC 0.8-0.9), fair for two models (AUC 0.7-0.8), and poor for nine models (0.5< AUC < 0.7; Table 5.4). Models developed for the TV method had consistently better predictive performance, the exception being for *Ophthalmolepis lineolatus* models where the BV method had a slightly higher AUC. Similar general trends were evident for Kappa statistics, with models developed for the TV method having greater Kappa values except the *O. lineolatus* BV model (Table 5.4). Sensitivity values (correct presences) ranged from 0.41 to 0.75 and specificity ranged from 0.48 to 0.78 (correct absences). The total proportion of correct predictions (presence and absence) ranged from 0.44 for *Upeneichthys vlamingii* BV to 0.77 for *Coris auricularis* TV (Table 5.4). These results indicated that data from the TV method better predict the likely distributions than BV for all except one species. However, poor model fits suggest that all fitted models could benefit from additional environmental information.

5.4.3 Mapping species distributions

Presence absence maps provided a detailed representation of continuous predicted distributions of the six species using the two survey methods (Figure 5.4 and Figure 5.3 for partial response plots as result of GAMs of best fit). The distribution of *Austrolabrus maculatus*, *Coris auricularis* and *Ophthalmolepis lineolatus*, all reef associated species, were predicted to be in close proximity to the reef ridge by both survey methods (Figure 5.4a-d, i-j). In contrast, the ecological niche predictions for *Eupetrichthys angustipes*, *Notolabrus parilus* and *Upeneichthys vlamingii* differed between the two survey methods. The best fit GAM for *E. angustipes* from the BV data predicted this species to be spread across the bay and associated with flat protected areas. Whereas habitat associations predicted by the TV data for this species were mainly in deeper protected waters (Figure 5.4e-f). The distribution of *Notolabrus parilus* using the BV data predicted high probability of detection along the shallow reef ridge. Whereas the distribution based on the TV data, predicted this species to more closely associate with steep terrain and maps show an even distribution across much of the bay with high probability of detection in the more exposed western part of the bay (Figure 5.4g-h). Models for explaining variation in *Upeneichthys vlamingii* presence using BV data had weak explanatory power (Table 5.3) and there was no particular area of the bay that was recognised unsuitable for the *Upeneichthys vlamingii* based on BV data. Predictions from the TV data however mapped intermediate to deep water areas as most suitable for this species (Figure 5.4k-l).

Table 5.3 Best descriptor variables (+) and the summary of candidate models (ΔAICc < 2) for predicting probability of occurrence of the six study species across two survey methods: stereo-BRUVs (BV) and towed stereo-video (TV). GAMs of best fit identified by ΔAIC = 0 and highest Akaike weights for evidence support.

Species/method	**Intercept**	**Bathymetry**	**Slope**	**Curvature**	**Plan**	**Profile**	**Range10**	**Range2**	**Range5**	**Eastness**	**Adjusted R2**	**df**	**AICc**	**ΔAICc**	**Akaike weight**
Austrolabrus maculatus BV	0.026	+									0.06	3	199.43	0	0.12
Austrolabrus maculatus BV	0.033	+					+				0.08	5	200.70	1.27	0.06
Austrolabrus maculatus TV	-0.018	+	+			+		+			0.15	9	242.38	0	0.06
Austrolabrus maculatus TV	-0.018		+			+		+			0.12	7	242.74	0.36	0.05
Austrolabrus maculatus TV	-0.016	+	+	+				+			0.14	9	243.19	0.80	0.04
Austrolabrus maculatus TV	-0.019		+			+		+		+	0.14	9	243.61	1.23	0.03
Austrolabrus maculatus TV	-0.014		+	+				+			0.11	7	243.70	1.32	0.03
Austrolabrus maculatus TV	-0.021	+	+			+		+		+	0.17	11	243.80	1.42	0.03
Austrolabrus maculatus TV	-0.016	+	+			+		+	+		0.17	11	243.86	1.48	0.03
Coris auricularis BV	1.132	+					+	+			0.29	7	155.27	0	0.22
Coris auricularis BV	1.169	+			+		+	+			0.32	9	156.58	1.31	0.11
Coris auricularis TV	0.016	+							+		0.11	5	465.88	0	0.13
Coris auricularis TV	0.015	+									0.1	3	466.33	0.45	0.11
Coris auricularis TV	0.016	+					+				0.11	5	467.29	1.41	0.07
Coris auricularis TV	0.018	+	+						+		0.12	7	467.40	1.52	0.06
Eupetrichthys angustipes BV	-0.938								+		0.06	3	180.93	0	0.05
Eupetrichthys angustipes BV	-0.930						+				0.06	3	181.04	0.11	0.05
Eupetrichthys angustipes BV	-0.981			+					+		0.09	5	181.61	0.68	0.04

Eupetrichthys angustipes BV	-0.964				+				+		0.09	5	181.65	0.72	0.03
Eupetrichthys angustipes BV	-0.961				+		+				0.09	5	181.66	0.73	0.03
Eupetrichthys angustipes BV	-0.971			+			+				0.09	5	181.77	0.84	0.03
Eupetrichthys angustipes BV	-1.004	+							+		0.08	5	182.21	1.27	0.03
Eupetrichthys angustipes BV	-0.999	+					+				0.08	5	182.30	1.37	0.03
Eupetrichthys angustipes BV	-1.038	+			+		+				0.12	7	182.63	1.70	0.02
Eupetrichthys angustipes BV	-1.036	+			+				+		0.12	7	182.70	1.77	0.02
Eupetrichthys angustipes BV	-1.047	+		+					+		0.12	7	182.83	1.90	0.02
Eupetrichthys angustipes BV	-0.975					+			+		0.08	5	182.86	1.93	0.02
Eupetrichthys angustipes TV	-0.433	+									0.43	3	94.54	0	0.26
Notolabrus parilus BV	0.670	+									0.13	3	176.57	0	0.14
Notolabrus parilus BV	0.729	+					+				0.16	5	176.87	0.30	0.12
Notolabrus parilus BV	0.865	+	+				+				0.2	7	177.39	0.82	0.09
Notolabrus parilus TV	0.153		+								0.11	3	142.67	0	0.12
Notolabrus parilus TV	0.203		+	+							0.15	5	143.96	1.28	0.06
Notolabrus parilus TV	0.194		+		+						0.14	5	144.23	1.56	0.05
Ophthalmolepis lineolatus BV	1.154	+					+				0.22	5	164.41	0	0.20
Ophthalmolepis lineolatus BV	1.191	+					+		+		0.25	7	165.79	1.38	0.10
Ophthalmolepis lineolatus TV	-0.219	+									0.09	3	226.77	0	0.16
Ophthalmolepis lineolatus TV	-0.232	+						+			0.11	5	228.35	1.58	0.07
Ophthalmolepis lineolatus TV	-0.223	+							+		0.11	5	228.59	1.82	0.06
Upeneichthys vlamingii BV	0.268					+					0.02	3	202.32	0	0.10
Upeneichthys vlamingii BV	0.267			+							0.02	3	203.04	0.73	0.07
Upeneichthys vlamingii BV	0.265									+	0.01	3	203.76	1.44	0.05

Upeneichthys vlamingii BV	0.264		+			0.01	3	204.02	1.70	0.04
Upeneichthys vlamingii BV	0.264			+		0.01	3	204.05	1.73	0.04
Upeneichthys vlamingii TV	-0.067	+			+	0.1	5	177.95	0	0.11
Upeneichthys vlamingii TV	-0.066	+				0.05	3	178.77	0.82	0.07
Upeneichthys vlamingii TV	-0.076		+			0.04	3	179.23	1.28	0.06

5.4.4 Costs

The main difference in the costs associated with the two methods relate to general logistics and pre-field preparations. Surveys using BV method require a vessel large enough to deploy 10 video systems and accommodate an additional crew member compared to the smaller boat and crew required to deploy a single towed video system.

Table 5.4 Summary of model predictive performance for each fish species across two survey methods: stereo-BRUVs (BV) and towed stereo-video (TV). Presences and absences for assessing sensitivity and specificity were determined using P_{fair} as threshold.

Species/method	P_{fair} threshold for presence	Proportion Correctly Classified	Sensitivity	Specificity	Kappa	AUC
Austrolabrus maculatus BV	0.54	0.62	0.65	0.61	0.24	0.64
Austrolabrus maculatus TV	0.5	0.67	0.67	0.68	0.34	0.66
Coris auricularis BV	0.6	0.7	0.7	0.71	0.35	0.74
Coris auricularis TV	0.48	0.77	0.75	0.78	0.54	0.82
Eupetrichthys angustipes BV	0.33	0.5	0.5	0.5	0	0.61
Eupetrichthys angustipes TV	0.52	0.69	0.68	0.7	0.36	0.68
Notolabrus parilus BV	0.71	0.51	0.51	0.5	0.01	0.51
Notolabrus parilus TV	0.48	0.54	0.56	0.53	0.09	0.6
Ophthalmolepis lineolatus BV	0.66	0.7	0.7	0.7	0.37	0.76
Ophthalmolepis lineolatus TV	0.5	0.58	0.58	0.57	0.15	0.62
Upeneichthys vlamingii BV	0.57	0.44	0.41	0.48	-0.1	0.57
Upeneichthys vlamingii TV	0.54	0.52	0.52	0.53	0.05	0.62

Consequently, the vessel and camera systems associated costs could be as much as 6 to 7 times higher for surveys performed with stereo-BRUVs. In addition, pre-field system calibrations took an extra five hours for the BV method (Table 5.5).

5.5 Discussion

TV is a robust, non-intrusive, low cost method that can be useful to examine fine-scale species-environment associations, which are typically overlooked by the BV. In combination with precise habitat data from remote sensing systems, TV may allow rapid identification of sensitive or ecologically important areas which are important for marine conservation. We found that bathymetry was a good predictor of occurrence patterns of endemic fish species, though the relative importance of depth differed among species and with survey methods. Depth has been recorded as a strong driver in assemblage pattern of fishes on oceanic islands (Luiz et al., 2015). Depth can also be a proxy for other environmental variables, such as light penetration, which influences the distribution and species composition of seagrass and algae (Kendrick et al., 2002). Canopy-forming seaweeds can drive distribution patterns of fish species that rely on these habitats for food (Lim et al., 2016), shelter (Gillanders & Kingsford, 1998; Wilson et al., 2014) or nesting (Azevedo et al., 1999).

The spatial scale at which structural complexity was measured was also an important predictor of fish occurrence and differed among species. This may relate to different sized species requiring different sized refuges (Friedlander & Parrish, 1998; Wilson et al., 2007; Nash et al., 2013), or interspecific variation in motility and home range (Nash et al., 2015), or the extent of habitat specialisation (Munday, 2004; Pratchett et al., 2012). However, the regular inclusion of large-scale structural complexity of habitat from the BV most probably related to fish being attracted from surrounding habitats to a single focus point by the bait. Conversely, models based on the TV data often incorporated complexity measured across a smaller scale, reflecting the movement of the system across the seascape and recording fish presence in areas they inherently occupy and use as refuge within their normal home range. Clearly, depth and structural complexity are good predictors of fish distributions, and as these metrics are also indicative of key processes that relate to resilience in other systems (Graham et al., 2015) they are important variables for spatial planning of marine reserves. Moreover, maintaining connectivity between habitat patches with different levels of complexity across seascape maintains the structure of fish communities and ecosystem function (Olds et al., 2014; Nagelkerken et al., 2015).

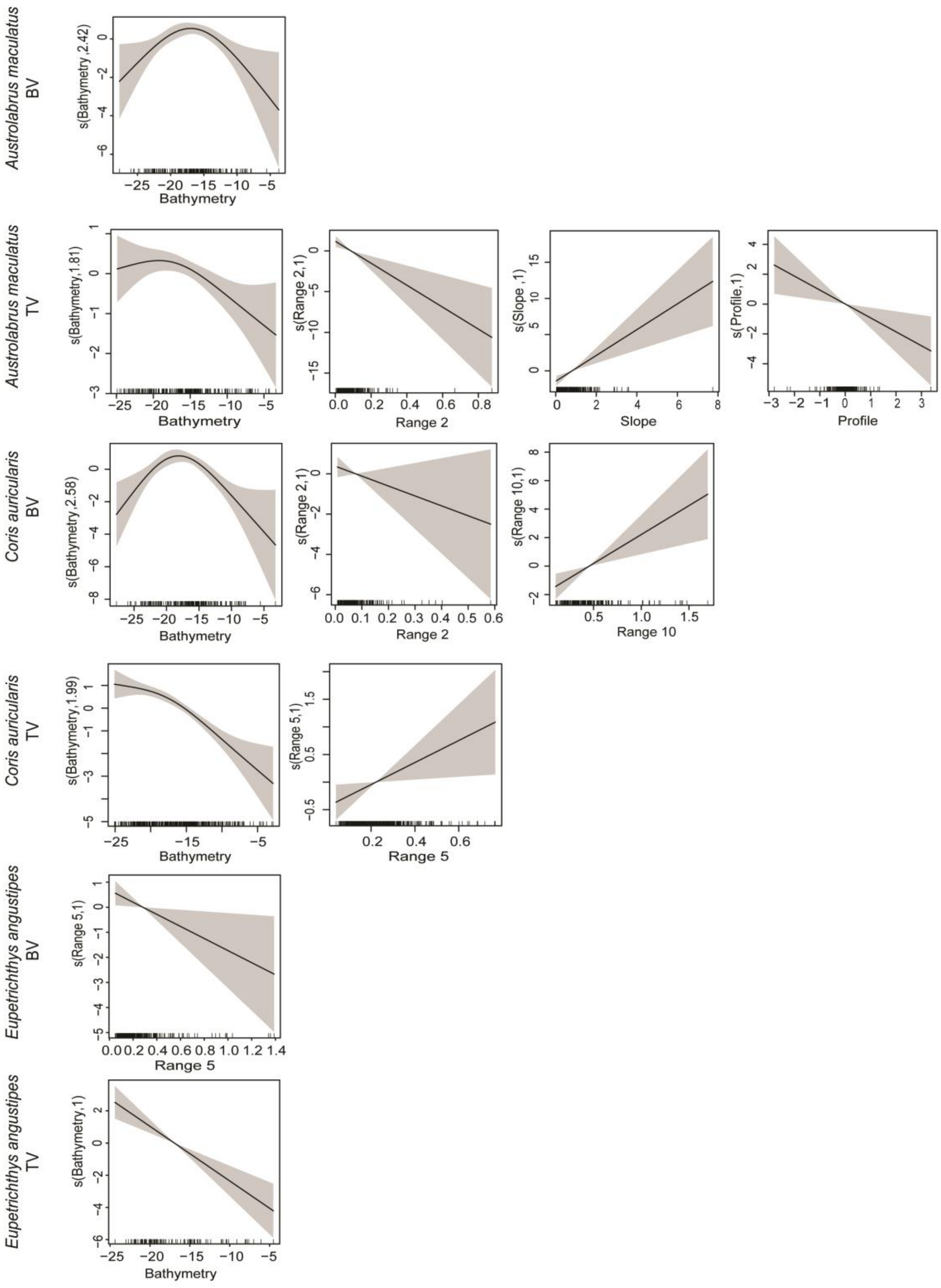


Figure 5.3 Smoother estimates (solid line) for the environmental predictors as obtained by generalised additive models for six study fish species across two survey methods: stereo-BRUVs (BV) and towed stereo-video (TV). The approximate 95% confidence envelopes are indicated (grey shading), marks along the x-axis are sampled data points. All explanatory variables were fitted with model smooths (knots) k = 4. Summary of the environmental predictors is provided in Table 5.2.

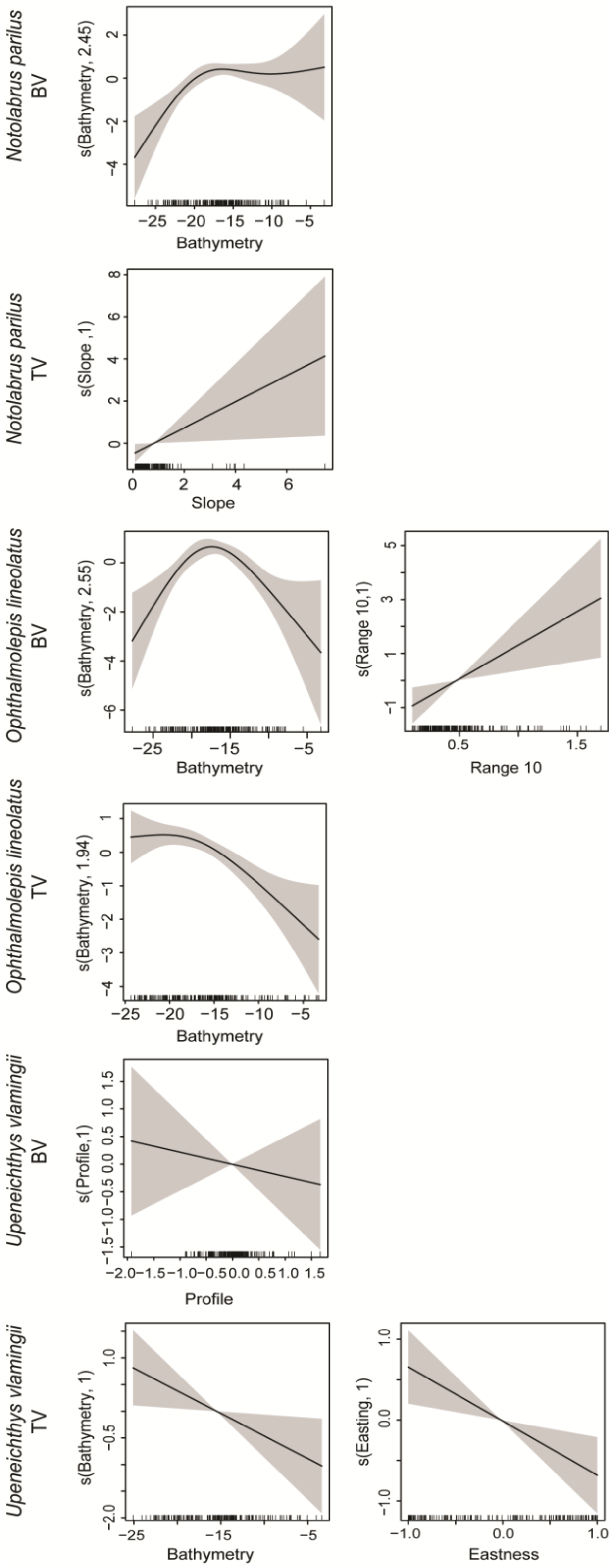


Figure 5.3 continued Smoother estimates (solid line) for the environmental predictors as obtained by generalised additive models for six study fish species across two survey methods: stereo-BRUVs (BV) and towed stereo-video (TV). The approximate 95% confidence envelopes are indicated (grey shading), marks along the x-axis are sampled data points. All explanatory variables were fitted with model smooths (knots) k = 4. Summary of the environmental predictors is provided in Table 5.2.

Our results indicate that the choice of data collection method is important for fitting and performance of species distribution models. All fitted models for the TV method, except for the Southern Maori wrasse *Ophthalmolepis lineolatus*, provided a better model fit and had higher AUC values. This is probably due to TV introducing less variation in datasets by sampling fish in their natural habitat. In contrast, BV may lure fish from their natural habitat, thus introducing more variation into observed species-habitat relationships (e. g. Moore et al. 2009). It is clear, however, that all model fits would benefit from incorporation of additional biotic variables, such as extent of canopy cover of macrophytes or occurrence of sessile invertebrates. For example, previously fitted GAMs for probability of occurrence of the Brown-spotted wrasse *Notolabrus parilus* and *O. lineolatus* using macroalgal type and presence of sessile biota among other substrate associated explanatory variables, were characterised by good model fits and AUC > 0.8 for data collected with BV (Chatfield et al., 2010). In addition, Monk et al. (2012) produced a much lower AUC value for the TV method than that reported here for Blue-spotted Goatfish *Upeneichthys vlamingii* when using only seafloor variables and a similar number of occurrences. However, the AUC value for GAM fitted for *U. vlamingii* from the BV method was much higher in the study by Monk et al. (2012). One possible explanation for this dissimilarity with our findings could be differences in prevalence of modelled species between the two studies. Prevalence of species is known to affect modelling outcomes and performance of models (Franklin, 2010). The overall sample sizes in both studies were similar, however the prevalence of *U. vlamingii* in our study was four times higher than that reported by Monk et al. (2012).

While the predictive performance of models varied between methods, the predicted distributions of species across the bay and the extent of the ecological niches predicted by both methods were similar for four of the study species. For the remaining two species (*Eupetrichthys angustipes* and *Upeneichthys vlamingii*), the distribution patterns were more clearly defined by the TV method. The similarity in niche predictions between the two datasets could be attributed to choice of the modelled species, which are mostly narrow distributional range and/or small size species. Small sized fish tend to have smaller home ranges and are less likely to move as far as larger bodied counterparts (Nash et al., 2015). Furthermore, narrowly distributed species exhibit minimal niche variation, and are more reliably modelled when extrapolating to unsurveyed areas (Segurado & Araujo, 2004; Monk et al., 2010). While the TV may provide more refined distribution models than BV, the applicability of higher resolution information to spatial management will most certainly vary among species in question.

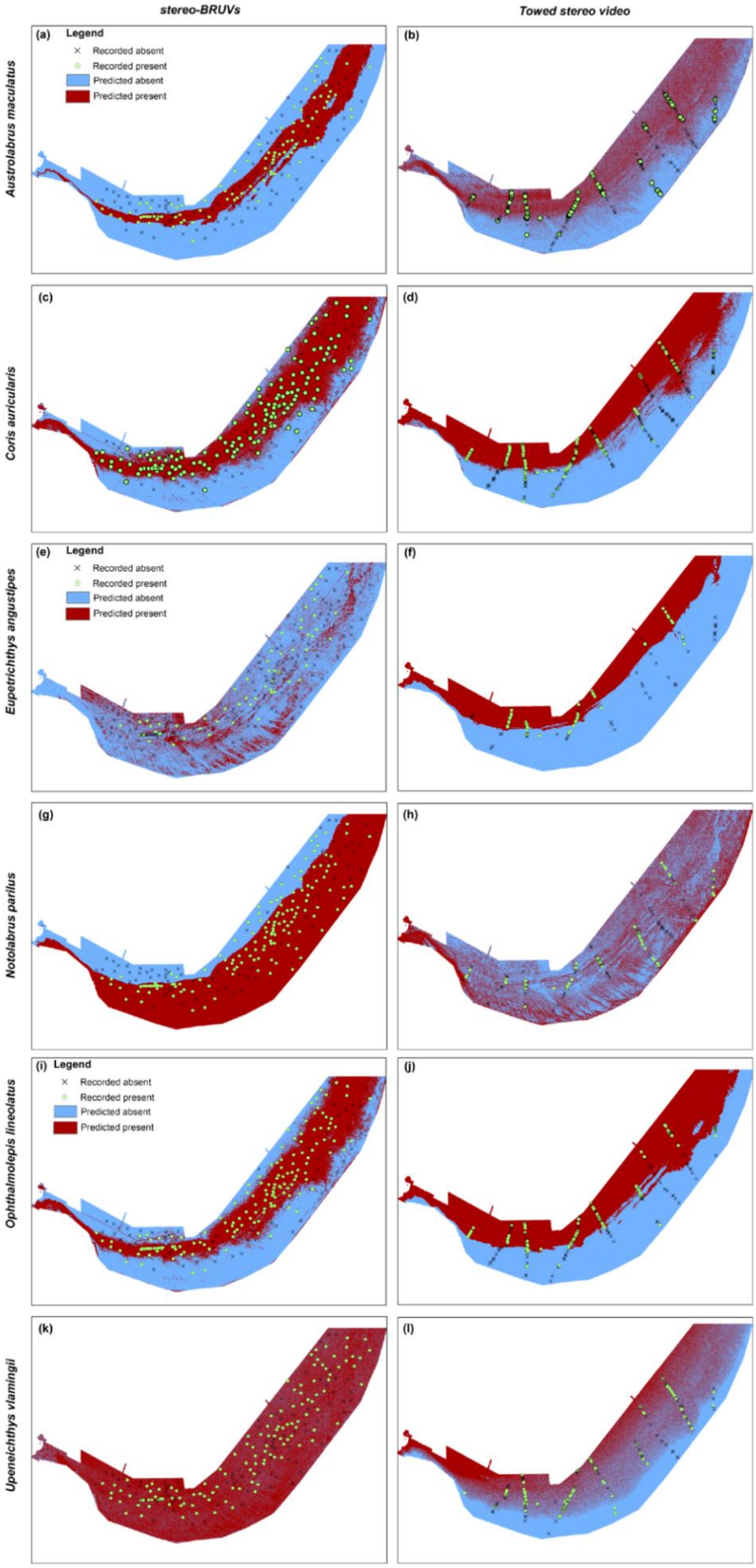


Figure 5.4 Predicted niche distributions in Geographe Bay as defined by the GAMs of best fit for individual study species across two sampling methods.

For example, large mobile carnivores would be better surveyed using BV, where bait is necessary for attracting these rarely occurring species in to the field of view of the camera system (Cappo et al., 2004), or they are scared by the camera system moving through the water. In addition, fish species associated with structurally complex habitats or cave-dwelling species may be more effectively surveyed using methods that can effectively search caves and overhangs (Watson et al., 2005; Holmes et al., 2013; Goetze et al., 2015). However, where there is extensive low-relief habitat, such as the seagrass meadows surveyed by this study, the TV appears to perform better than the BV in terms of examining the natural relationships between fish and their habitat. Moreover, models based on TV datasets, where boundaries of a surveyed area can be defined and absolute species abundance or density can be calculated, will be a significant step towards improving the biological appeal of spatial modelling in the marine environment (Hobbs & Hanley, 1990; Pearce & Ferrier, 2001; Moore et al., 2011).

Table 5.5 General costs and staff time budgets (total hours devoted to each activity) associated with data collection by each of the survey methods.

	stereo-BRUV	Towed stereo-video
General logistics		
Vessel costs ($AU/day)	2000[a]	350[a]
Camera system costs($AU/day)	2000[b]	400[b]
Pre-Field		
Equipment calibration and processing (staff hours)	8	3
In-Field		
Data collection (total)	132[c]	136[c]
Video download	2	0.5
Post-field		
Video processing total	1 h video recording= 3 h processing	1 h video recording= 3 h processing

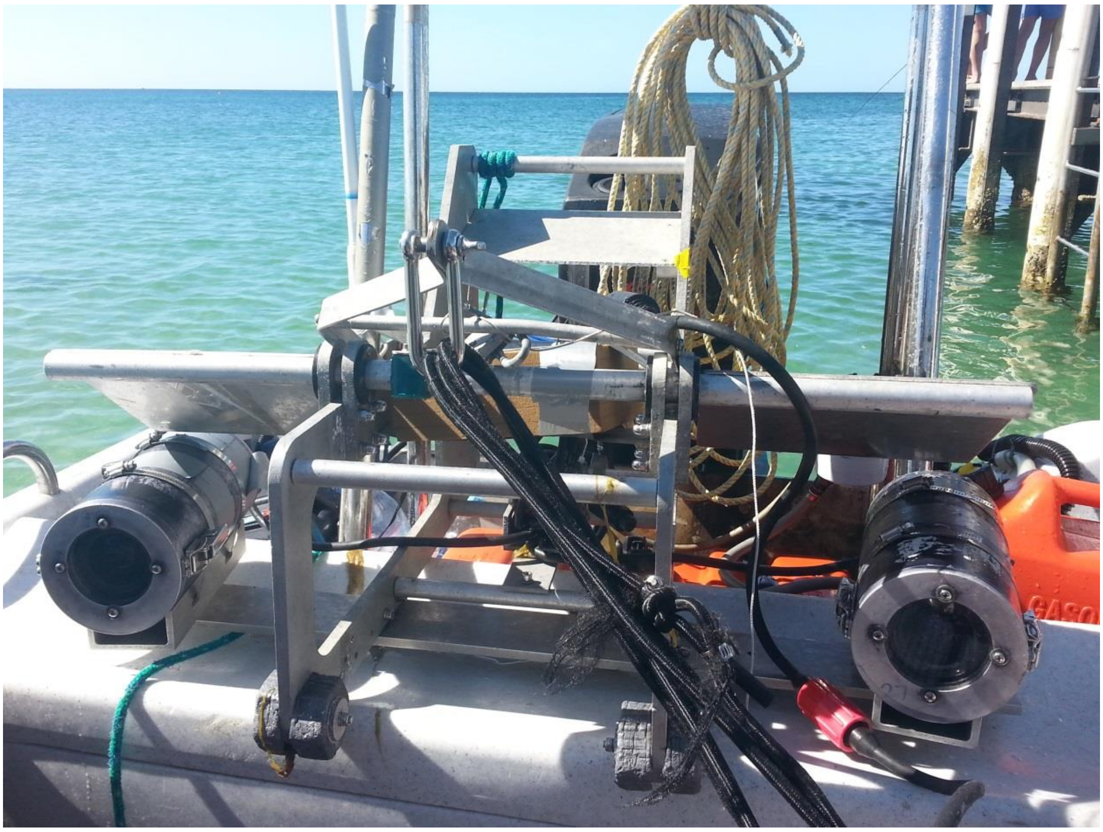
[a] large vessel carrying 4 crew and staff deploying 10 stereo-BRUVs; small vessel carrying 3 crew and staff deploying one towed stereo-video
[b] calculations based on 10 stereo-BRUVs and one towed stereo-video
[c] stereo-BRUVS = 3staff * 5.5days * 8h /day; towed stereo-video = 2staff * 8.5days * 8h /day

The lower survey cost associated with the use of TV compared to the BV provides additional support for considering this method for marine spatial management purposes. The level of expertise and time required for collecting and processing data from the two methods is virtually identical, the major difference being costs associated with vessel hire and the purchase of camera systems. The initial outlay of purchasing equipment is also five times greater when using BV, though repeated use of the same cameras would reduce the long term differences. The daily costs associated with needing a larger vessel and extra crew will, however, become more relevant on longer field trips.

5.6 Conclusions

Research programs must choose survey techniques and indicators applicable to their research questions (Cappo et al., 2004; Watson et al., 2005). While stereo-BRUVs are a well-established method for surveying fish assemblages, their usefulness for species distribution modelling should be revised due to the biases that may be introduced with respect to habitat associations of fish. Other methods for surveying fine-scale species-habitat associations typically involve divers (stereo-DOVs, underwater visual census) and are limited by diving depths and times. Video from towed or autonomous underwater vehicles are, however, less constrained by depth and could become an effective method that combines the benefits of a remote video and a fine spatial scale observations of species-habitat associations. Our study provides evidence that towed stereo-video is a robust, non-intrusive, low cost method for fine-scale data collection that can be useful for spatial ecological modelling. In combination with precise habitat data from remote sensing systems, developments in towed video methods can map demersal species distributions and may allow rapid identification of sensitive or ecologically important areas which are important for marine conservation.

5.7 Supplementary material

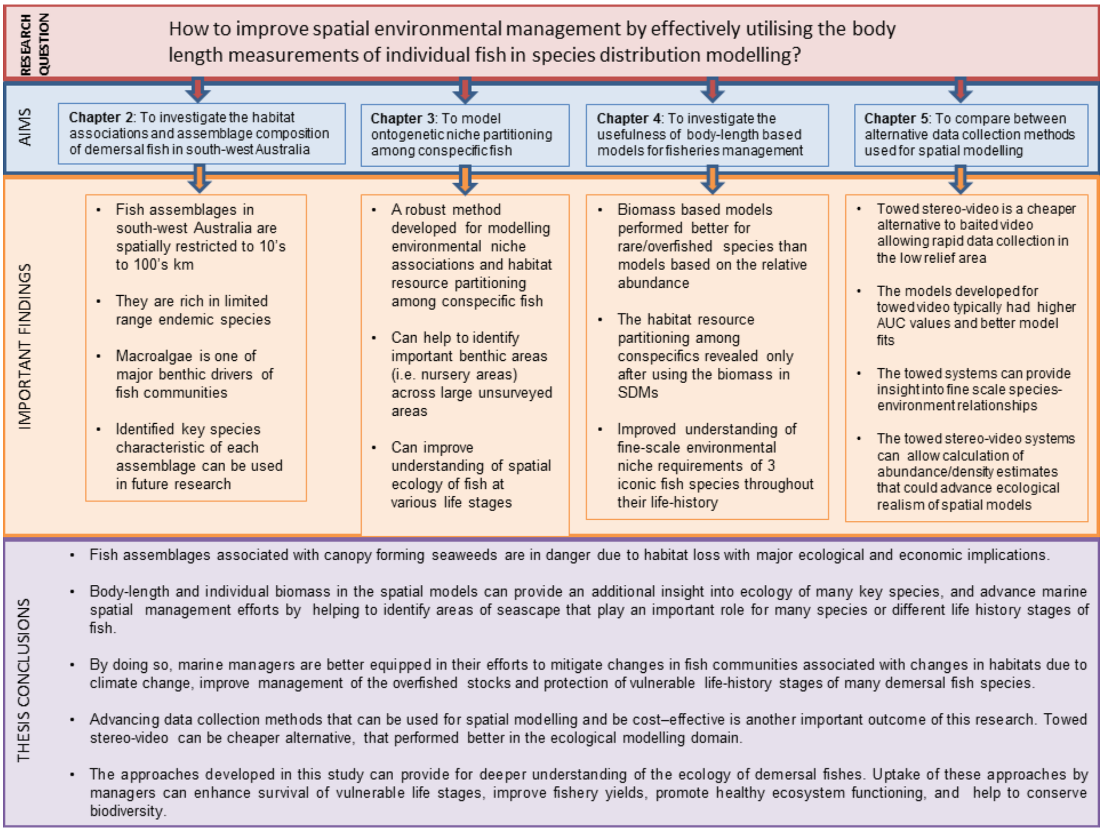


Supplement 5.7.1 Picture of the towed stereo-video system ready for deployment.

Chapter 6 General Discussion

6.1 Summary of findings

This thesis critically assesses how incorporating individual body length measurements into species distribution models can be used to examine the species-environment relationships of demersal fishes at different life stages. This is a useful approach for effective fisheries and marine spatial management in the face of global environmental change. In this general discussion I summarise my main findings and evaluate the strengths and limitations of the approach I tested and its usefulness for marine spatial management (Figure 6.1).



How to improve spatial environmental management by effectively utilising the body length measurements of individual fish in species distribution modelling?

Chapter 2: To investigate the habitat associations and assemblage composition of demersal fish in south-west Australia

Chapter 3: To model ontogenetic niche partitioning among conspecific fish

Chapter 4: To investigate the usefulness of body-length based models for fisheries management

Chapter 5: To compare between alternative data collection methods used for spatial modelling

- Fish assemblages in south-west Australia are spatially restricted to 10's to 100's km
- They are rich in limited range endemic species
- Macroalgae is one of major benthic drivers of fish communities
- Identified key species characteristic of each assemblage can be used in future research

- A robust method developed for modelling environmental niche associations and habitat resource partitioning among conspecific fish
- Can help to identify important benthic areas (i.e. nursery areas) across large unsurveyed areas
- Can improve understanding of spatial ecology of fish at various life stages

- Biomass based models performed better for rare/overfished species than models based on the relative abundance
- The habitat resource partitioning among conspecifics revealed only after using the biomass in SDMs
- Improved understanding of fine-scale environmental niche requirements of 3 iconic fish species throughout their life-history

- Towed stereo-video is a cheaper alternative to baited video allowing rapid data collection in the low relief area
- The models developed for towed video typically had higher AUC values and better model fits
- The towed systems can provide insight into fine scale species-environment relationships
- The towed stereo-video systems can allow calculation of abundance/density estimates that could advance ecological realism of spatial models

- Fish assemblages associated with canopy forming seaweeds are in danger due to habitat loss with major ecological and economic implications.
- Body-length and individual biomass in the spatial models can provide an additional insight into ecology of many key species, and advance marine spatial management efforts by helping to identify areas of seascape that play an important role for many species or different life history stages of fish.
- By doing so, marine managers are better equipped in their efforts to mitigate changes in fish communities associated with changes in habitats due to climate change, improve management of the overfished stocks and protection of vulnerable life-history stages of many demersal fish species.
- Advancing data collection methods that can be used for spatial modelling and be cost–effective is another important outcome of this research. Towed stereo-video can be cheaper alternative, that performed better in the ecological modelling domain.
- The approaches developed in this study can provide for deeper understanding of the ecology of demersal fishes. Uptake of these approaches by managers can enhance survival of vulnerable life stages, improve fishery yields, promote healthy ecosystem functioning, and help to conserve biodiversity.

Figure 6.1 Flow diagram outlining the important findings and major conclusions from the thesis.

My research provides further evidence that the environmental niche requirements of conspecific individuals of many demersal fish species can change as the individual grows. Understanding the habitat requirements of fishes of different sizes and at different life stages will greatly improve our knowledge of the dynamics of demersal fish communities and the habitats they rely on. The statistical approach I have used can help fisheries and conservation managers identify and manage essential fish habitat ensuring the connectivity of populations across a mosaic of habitats.

My results indicate that community structure and assemblage composition of demersal fishes in south-western Australia is closely associated with features of benthic habitat complexity and biological cover (chapter 2). This close association is not surprising as many fish communities in this SST hotspot region are limited range endemic species (Fox & Beckley, 2005). Species that are habitat specialists are inherently more susceptible to change in habitat quality and cover as a result of climate change or other anthropogenic stressors, such as sedimentation and eutrophication (Munday, 2004). As result of this biogeographic scale analyses, I was able to identify key indicator species characteristic of individual assemblages, which I later use as model species in the following chapters. Ecological or fisheries indicator species are commonly used to monitor overall ecosystem health (Garcia et al., 2000) when monitoring of the whole assemblages is not feasible (Smale et al., 2011; D'Amen et al., 2015). For demersal fish in Western Australia, most of the indicators were derived to monitor the effects of fishing and fisheries management of targeted species (Smale et al., 2011). However, to ensure overall ecosystem health, it is essential to recognise the importance of non-targeted species as indicators, particularly those that could be under immediate threat of climate associated changes, such as limited range endemic species. The key indicator species identified in my thesis could be used by managers and spatial ecologists as surrogates for assessing the health and stress responses of the assemblages they represent and for identifying significant changes in existing patterns of species richness and assemblage composition in the south-western Australia.

My results indicate that both ecological indicator fish species (chapter 3) and fisheries indicator species (chapter 4) undergo changes in their ecological niche requirements which reflects on the choice of habitat throughout their life. This is particularly relevant for species that are dependent on a specific habitat for juvenile recruitment (Jones et al., 2004) where the spatial distribution patterns of adult populations are dependent on the distribution and the productivity of nursery areas, where areas close to nurseries replenish more isolated areas (Huijbers et al., 2013). Ontogenetic habitat shifts are identified as one of the mechanisms that connect fish populations between nursery areas and hotspots of animal abundance within a habitat mosaic (Huijbers et al., 2013; Nagelkerken et al., 2015). Inability to move between habitats is likely to adversely impact survivorship. Furthermore, identifying key areas of the seascape that are crucial for different life-history stages of the same species or for multiple species (i.e. spawning grounds, fisheries refugia or nursery areas) may preserve critical spawning stock biomass of exploited species and result in lower losses and higher survival of vulnerable life stages (Dugan & Davis, 1993). Preserving functional seascape connectivity patterns between nursery areas and adult populations can enhance the abundance of target species as well as other fish species relying on healthy ecosystem functioning (Olds et al., 2014) which in turn can support the overarching goal of preserving biodiversity.

As a fisheries management tool, the ability to monitor juvenile recruitment variability in areas of critical juvenile habitat using GAMs and individual body length would allow for early predictions (up to eight years in case of *Glaucosoma hebraicum*) of future strength of cohorts to be made before they enter the fishery (Lewis et al., 2012). Furthermore, by creating temporary closures of adult breeding grounds during spawning season, it is possible to enhance the reproductive dynamics of the entire population of the target species. For example, protecting the crucial areas of seascape for large sexually mature females can further enhance the abundance and biomass of depleted stocks (Polacheck, 1990; Denny et al., 2003).

6.2 Implications for management and conservation

Management and conservation efforts are often constrained by economic considerations, which raise questions for decisions about where scarce conservation and fisheries management resources should be directed, and what areas are most worthy of protection (Ferrier, 2002). Similarly, the decision about where to locate marine reserves and closed areas to maximise biodiversity conservation and sustainable fisheries management outcomes is challenging, as designated areas may not encompass the essential habitat requirements of different life stages of a range of targeted and ecologically important fishes (Schmiing et al., 2013). The spatial hotspots that I have identified can address this knowledge gap by spatially establishing the location of new benthic areas that are important for numerous species and/or for different life stages for a wide variety of species (e.g. fish nurseries). The very same approach could be used to identify entire areas that may not require future in-depth surveys, thus optimising limited management resources. It is well recognised that to optimise the design and placement of reserves (e.g. Possingham et al. 2000) and closed areas it is important to take into account patterns of population connectivity across mosaic of habitats (e.g. Nagelkerken et al. 2015; Olds et al. 2016) for multiple species. Hotspot areas should be considered in zoning schemes and become priority areas for marine spatial monitoring and management (Schmiing et al., 2013). In addition, any future re-zoning efforts should consider including hotspot areas to increase their efficiency thus reducing the risk of compromising effective conservation of marine biodiversity (Stewart et al., 2003).

6.3 Alternative survey methods

Despite stereo-BRUVs being a well-established survey method for surveying fish assemblages, I have demonstrated in chapter 5 that stereo-BRUVs data may mask the fine scale species-environment interactions that could be crucial for spatial ecology of less mobile species. I have also demonstrated that it is possible to use a towed stereo-video method for a rapid survey of low complexity marine seascapes. Towed stereo-video has similar advantages to stereo-BRUVs in that it is non-destructive and it can sample across a broad range of habitats and depths, but can record fine spatial scale observations of species-habitat associations. The low cost associated with data collection using the towed video in combination with improved model performance provides evidence that this method can be useful for mapping demersal fish species distributions and may allow rapid identification of sensitive or ecologically important areas. My findings highlight the usefulness of this alternative survey method which has the potential to enhanced marine conservation and management efforts.

6.4 Limitation from this thesis

The strategic choice of Geographe Bay for data collection to compare the performance of models based on stereo-BRUVs and towed stereo-video (chapter 5) was driven by logistics of funding, vessel availability and local weather conditions. The bay is characterised by an extremely marginal environmental gradient, making this area a challenging place for comparison of the applied methods. I believe that if sampling was performed in an area with more distinct differences between various habitat patches, the modelling results could have been even more pronounced for the two data collection methods.

The modelling approaches that I have utilised throughout my thesis are currently lacking the ability to implement zero inflated GAMs with negative binomial error distribution, or a two-stage (hurdle) GAMs with gamma error distribution in R statistical software. This limitation has consequences for models developed for overfished or rare species where a high proportion of zeroes in datasets could result in poor model fits and consequentially low explanatory power. At this stage, only Generalised Linear Models (GLMs) have the capacity to predict the response of various species to environmental predictors utilising the aforementioned types of error distributions. However, as most of the biological responses in the marine environment are not linear (Leathwick et al., 2006), GAMs are more appealing method for describing these relationships. GAMs have become widely used in ecological, spatial and management oriented marine studies (Pittman et al., 2007; Valavanis et al., 2008;

Schmiing et al., 2013). In addition, my results for comparison between the biomass and abundance models (chapter 4) indicated that the biomass model fits had notably higher explanatory power in comparison to the abundance models, thus identifying this modelling approach as particularly beneficial for models developed for overfished and/or rare species. At this stage, only one package compatible with R statistical software is still under development that will allow fitting zero inflated GAMs with negative binomial error distribution that could provide a potential solution for modelling non-linear relationships between rarely recorded marine species and their environment (VGAM; Yee 2015). In the meantime, I suggest using biomass and abundance models as complementary to each other such as has been done in this thesis. Such approach could be extremely useful for spatial management when mapping distribution patterns in fish diversity and for understanding of population dynamics of endangered species.

The multiple species hotpots that I have identified in chapters 3 and 4 for adults/large size individuals and juveniles/small size fish, are perhaps quite small-sized and not always applicable to all modelled species. My intention was to demonstrate that the technique for size-specific hotspot extraction could be applied to any species with varying habitat requirements and biological characteristics. I believe that when applied to fish species with similar habitat requirements and demographic processes this approach could be highly beneficial for identifying the hotspot areas for different life-history stages of multiple species.

6.5 New research avenues

Towed stereo-video systems can capture accurate and precise measurements of fish length and provide measurements of sampling area. Most importantly it can continuously capture the fine scale spatial data over seascape transition zones (Spencer et al., 2005) which is a major advantage in comparison to the baited systems. The ability to combine the fine-scale density and/or abundance estimates of surveyed species with precise habitat data from remote sensing systems can help to rapidly map demersal fish distributions across large areas of seascape and allow identification of ecologically important areas which are important for marine conservation. However, a current major limitation of the towed stereo-video systems is associated with movement of the system through the water column which can affect quality of the video image and deter or attract certain fish species (McIlwain et al., 2011; Warnock et al., 2016). Future developments in the towed systems should aim to miniaturize and stabilise the camera system in order to reduce its effects and improve the recoded imagery.

To effectively deal with rapid global change, conservation managers need to utilise multiscalar statistical analysis tools for compilation of integrated local, regional, and global datasets to produce standardized, relevant, and interpretable outputs (Edgar et al., 2016). Novel methods for conducting large scale underwater surveys are being developed based on availability of autonomous and remotely operated sampling platforms (e.g. gliders, AUVs, ROVs), which could provide the necessary hydroacoustic, biological cover and fish density datasets without limitations posed by commonly used methods such as stereo-BRUVs (Seiler et al., 2012). These large, complex datasets necessitate concurrent development of algorithms and software to efficiently extract useful information that quantify species patterns and improve our understanding of consequences of associated environmental and socioeconomic threats to biodiversity and individual species (Cooke et al., 2016).

6.6 Thesis conclusions

Robust predictive modelling can improve our knowledge of the spatial ecology of demersal fishes at various life-history stages, which can directly enhance management and conservation efforts of regions and demersal fish communities affected by the climate change, fisheries and other anthropogenic impacts. Temperate and subtropical West Australian demersal fish assemblages are dominated by limited range endemic species which are closely associated with biotic and abiotic environmental factors (such as canopy forming seaweeds and structural complexity of habitat at varying spatial scales). However, limited ranges of species are also recognised as indicators of vulnerability to climate driven extinction (Bender et al., 2013; Harvey et al., 2013). Most recent studies in this region demonstrate northern range contraction of kelp-dominated temperate reefs, which is currently resulting in ecosystem shifts to marine communities associated with tropical waters (Bennett et al., 2015; Wernberg et al., 2016). Together, these changes can cause ecological phase shifts between the alternative macroalgae or coral dominated communities and bear dire consequences to the endemics reach demersal fish communities. Understanding of hierarchy and scale of influence of various processes, while paying special attention to demographic processes at species or community levels, can help successful management of these vulnerable assemblages and can be a key to a deeper understanding of marine ecology. In addition, higher survival of vulnerable life stages of targeted and non-targeted species can enhance fishery yields, promote healthy ecosystem functioning and preserve worldwide decreasing biodiversity.

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