Understanding fish-habitat associations using video observations and sonar imaging

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Submitted in fulfilment of the requirements for the degree of

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'Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful' (Box & Draper 1987)

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Abstract

Planning for resilience is now a catch cry of many marine conservation programs and initiatives. These efforts are striving to inform conservation strategies for marine regions to ensure they have inbuilt capacity to retain biological diversity and ecological function in the face of global environmental change – particularly changes in climate and resource exploitation. A fundamental step in these strategies is to understand the distribution of species' (or other biological entities) throughout the focal region. However, in the absence of direct biological and ecological information for many marine species, scientists are increasingly using spatially-explicit predictive modelling approaches. Through the improved access to multibeam echosounder (MBES) data and underwater video technology these models can provide spatial predictions of the most suitable regions for an organism at resolutions previously not possible. This thesis was motivated by the recognition of the potential role of species distribution models in managing marine fish species and their habitats. This thesis sets out to address four interlinked ideas in consecutive chapters, with their justification and outcomes briefly detailed below.

Because of the issues surrounding the detection of species using remotely-sensed video techniques in the marine environment, the application of presence-only techniques are well suited for modelling that habitat suitability of demersal fishes. The geometric mean algorithm within Ecological-Niche Factor Analysis (ENFA) was used to compare models based on seafloor variables derived from 2.5 × 2.5 m cell resolution MBES at three spatial scales;

fine (56.25 m^2), medium (506.25 m^2) and coarse (2756.25 m^2), to determine which spatial scale was most influential in predicting *Notolabrus tetricus* (blue-throat wrasse) habitat suitability. This study was undertaken in a 42 km^2 region that was situated on the western side of Cape Duquesne in Discovery Bay, south-eastern Australia. Of this area 26.3 km^2 is contained within the Discovery Bay Marine National Park (MNP). The coarse scale model was found to have the best predictive capabilities with a Boyce Index of 0.80 ± 0.26. The global marginality and specialisation values indicated that, irrespective of the three spatial scales analysed, *N. tetricus* were associated with seafloor characteristics that are different to the mean available within the study site, but exhibit a relatively wide niche. Although variable importance varied over the three spatial scale models, *N. tetricus* showed a strong association for regions of shallow water, close to reef, with high rugosity and maximum curvature and low HSI-b (backscatter derivative) values. Generally the spatial patterns in habitat suitability were well represented in Discovery Bay MNP compared to the adjacent unprotected region. However, some significant differences in spatial patterns were observed when patch metrics were compared. Unsuitable and highly suitable habitat patches were distributed disproportionally within the MNP (i.e. significantly smaller Interspersion and Juxtaposition Index inside the MNP). Furthermore, unsuitable habitat in the MNP was more regular (i.e. Mean Shape Index of significantly larger).

With the growing number of modelling approaches available, knowledge of the relative performance of different presence-only models in the marine environment is required. Using towed-video-derived observation datasets and MBES-derived seafloor habitat information for the Discovery Bay study site,

habitat suitability of five demersal fish taxa were modelled using 10 presence-only algorithms: BIOCLIM, DOMAIN, ENFA (distance geometric mean [GM], distance harmonic mean [HM], median [M], area-adjusted median [Ma], median + extremum [Me], area-adjusted median + extremum [Mae] and minimum distance [Min]) and MAXENT. Model performance was assessed using kappa and Area Under Curve (AUC) of the Receiver Operator Characteristic (ROC). The influence of spatial range (area of occupancy) and environmental niches (marginality and tolerance) on modelling performance were also tested. The MAXENT generally performed best, followed by ENFA GM, ENFA HM, DOMAIN, BIOCLIM, ENFA M, ENFA Min, ENFA Ma, ENFA Mae and ENFA Me algorithms. Fish with clearly definable niches (i.e. high marginality) were most accurately modelled. Generally, Euclidean distance to nearest reef, HSI-b (backscatter derivative), rugosity and maximum curvature were the most important variables in determining suitable habitat for the five demersal fish taxa investigated. This comparative study encourages ongoing use of presence-only approaches, particularly MAXENT, in modelling suitable habitat for demersal marine fishes.

Accurate estimates of species occurrence are important to any fish biodiversity assessments and distribution models. With increasing emphasis on non-destructive sampling of fishes, underwater video techniques are commonly used without a thorough understanding of their advantages and disadvantages. This study was undertaken in a 25.7 km^2 study region off the coast of Warrnambool, south-eastern Australia. Using baited and towed video systems measures of fish assemblages, functional groups (i.e. pelagic carnivore, epibenthic carnivore/omnivore or herbivore) and observability (i.e.

conspicuous or cryptic) were compared across six biological habitats (mixed brown algae, mixed red and brown algae, mixed red algae, mixed red algae with invertebrates, no-visible macro-biota and seagrass) by means of permutation analysis of variance. To visualise the differences between the two video methods across the six habitats a distance-based Principle Coordinates Analysis was used with the strongest correlated Spearman vectors (i.e. > 0.7) overlaid. It was found that baited and towed video techniques recorded very different assemblages, functional groups and observability categories across structurally complex benthic biological habitats (i.e. algal-dominated habitats). However, as the habitat complexity decreased (e.g. seagrass and areas with no visible macro-biota), both techniques appeared to provide similar fish assemblage information. Results suggests that if a single fish surveying technique is to be used, then the baited-video technique recorded far greater number of species (particularly pelagic and epibenthic carnivores/omnivores) across a broader range of habitats in the study site. However, when combined, the two techniques provided complimentary assemblage information by recording different assemblages compared to each technique used in isolation.

The availability of fine-scale, complete-coverage seafloor variables and video-based occurrence datasets has seen a rapid increase in the use of species distribution models (SDMs) to predict the distributions of marine biological entities (e.g. species, assemblages or habitats) over a variety of spatial scales. However, sensible-looking, well-performing models can provide very different predictions of distribution depending on the survey technique used to obtain occurrence datasets. To examine this, SDMs for nine temperate marine fishes were constructed for the Warrnambool study site. Generalised linear model

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Introduction and overview

1.1 General introduction

Coastal zones constitute only 10% of the marine environment, yet support approximately 90% of all known marine species (Gray 1997). These resource-rich areas are subjected to many adverse anthropogenic activities, including; overexploitation of fisheries, pollution and impacts associated with encroaching coastal urbanisation (Jackson et al. 2001). Consequently, we have seen a rapid decrease in marine biodiversity due to habitat degradation in coastal zones (Sala & Knowlton 2006, Worm et al. 2006). In response, multiple initiatives have been instigated to improve our understanding of coastal marine biodiversity in an effort to identify, prioritise and ultimately preserve areas of importance (e.g. Ward et al. 1999, Campbell & Hewitt 2006, Harris & Whiteway 2009, Last et al. 2010). In the absence of detailed biological and ecological information for many marine organisms, research has focused on predicting the distribution of species or assemblages through the quantification, and subsequent prediction, of species-environment relationships (for a review see Brown et al. 2011). These species-environment relationships are predicated on the assumption that environmental measures reflect ecologically or functionally important factors that, either directly or indirectly, influence species distributions.

There has been substantial research demonstrating the importance of environmental factors in the structuring of marine biological assemblages. For example, numerous researchers have noted the importance of seafloor structure on the distribution and associated measures of habitat suitability for marine demersal fishes (Choat & Ayling 1987, Friedlander & Parrish 1998, Yoklavich

et al. 2000, Willis & Anderson 2003, Cappo et al. 2007, Pittman et al. 2009, Chatfield et al. 2010, Greene et al. 2011). However, these species-environment relationships have typically been limited by the type, coverage and spatial resolution of the data; often relying upon sparsely, co-located occurrences and point descriptors of arbitrarily chosen groupings of continuous physical and biological factors into, for example, 'depth categories' or 'habitat type' (Butler et al. 1991, Friedlander & Parrish 1998, Babcock et al. 1999, Westera et al. 2003). However, this approach is limited as it does not allow the subtle, but important, variation of continuous environmental variables (e.g. depth) on species to be determined. This is because observational and fine-scale continuous environmental data are rarely available for the marine environment.

Over the past decade there has been a rapid increase and application of technology that, when coupled with advances in geographic information systems (GIS) and computational power, make it possible to survey large regions of seafloor with unprecedented detail and accuracy (Hughes Clarke et al. 1996, Nasby-Lucas et al. 2002, Iampietro et al. 2005, Wilson et al. 2007, Ierodiaconou et al. 2011). One such method is the multibeam echosounder (MBES). These MBES datasets are ideal for the application of terrain analysis techniques (historically developed for analogous terrestrial datasets; e.g. topography) that form environmental variable datasets for input into spatially-explicit species-environment models (Wilson et al. 2007). In addition, advances in underwater video systems offer the ability to cost-effectively capture occurrence data beyond the range of traditional methods (e.g. SCUBA; Harvey et al. 2002) and are viable methods for estimating fish population dynamics (for detailed reviews see: Shortis et al. 2009, Murphy & Jenkins

2010). The integration of high-resolution MBES data and occurrence records from underwater video provides an opportunity to develop spatially-explicit models of habitat suitability for temperate marine fishes over large areas of seafloor. However, these underwater video systems are increasingly being used to record occurrence data for spatially-explicit models of habitat suitability without a thorough understanding of their advantages and disadvantages. Understanding the relative detectability of fish species from video survey methods may help to improve the accuracy of models and warrants further investigation.

Another important consideration that should be addressed by any attempt at quantifying and predicting the habitat suitability of marine species is that of spatial scale (Wilson et al. 2007). With seafloor variables, and indeed species distributions, spanning a continuum of scales it is not an easy challenge to meet. Scale is especially important in relation to terrain analysis, since both the initial dataset resolution and the analysis scale can potentially influence the results. For models of species distribution it is important to try and match the data and analysis scales to those relevant to the focal taxa themselves. Previous investigations of habitat suitability of squat lobster suggested that several spatial scales rather than any one scale were relevant (Wilson et al. 2007). By contrast, investigations have also revealed that cold water corals exhibit tendencies to associate with coarse scale features of the terrain such as carbonate mounds (De Mol et al. 2002). The influence of spatial scale of spatially-continuous seafloor variables on fish has received less attention. One study that has investigated the influence of spatial scale of spatially-continuous seafloor variables on demersal fishes concluded that broad-scale variables (i.e.

variables with a 2 × 2 m cell resolution calculated with a kernel radius of 25 m) provided better models (relative to fine-scale models based on a kernel radius of 12.5 m) for seven of the eight models developed (Moore et al. 2009). In addition, based on studies that have used spatially sparse datasets (e.g. diver transects), it is likely that the most relevant spatial scales will vary depending on the focal species, mobility (e.g. sedentary υ mobile) and ontogenetic habitat preferences. For instance, from these spatially sparse studies fine spatial scales (i.e. metres) influence some fish species (e.g. *Dascyllus aruanus*; Holbrook et al. 2000), while other species exhibit tendencies towards variables over coarse spatial scales (i.e. hundreds of metres; e.g. *Scarus iserti*; Tolimieri 1998). Indeed both fine and coarse-scale features may be important contributors to the distribution of some fish species (García-Charton et al. 2004). However, further research is needed to improve our understanding of the influence of spatial scale on habitat suitability models for demersal fishes.

The quest to better characterise a species' response to its environment has seen the proliferation of modelling approaches (Guisan & Zimmermann 2000). Broadly, models can be classified into one of two categories; those that require presence/absence data and those that require presence-only. While presence/absence models (e.g. generalised linear models; GLM, generalised additive models; GAM) remain among the most commonly used methods (for detailed reviews see; Franklin 1995, Guisan & Zimmermann 2000), presence-only approaches have gained popularity in the marine environment (Bryan & Metaxas 2007, Dolan et al. 2008, MacLeod et al. 2008, Skov et al. 2008, Tittensor et al. 2009, Ready et al. 2010). These presence-only techniques were originally created to predict the distributions of organisms that are especially

susceptible to unreliable absences due to an animal's ability to disperse or hide during field surveys (Hirzel et al. 2002). Unreliable absences in the marine environment are common (Bryan & Metaxas 2007, Wilson et al. 2007, Davies et al. 2008). A common cause of uncertainty in absences is attributed to issues in accurately surveying fishes (Mueller et al. 2006). Consider a towed-video survey of a demersal fish species that inhabits a macroalgal dominated reef system (e.g. labrids), inferring an absence because the species is not observed could be very misleading. This is because a '0' observation could represent either an actual absence of the fish, or alternatively may represent a fish hiding within the numerous crevices and macroalgal canopy, but is missed by the limited field of view of the towed-video system employed (i.e. a non-detection of a species that was present). By applying presence-only models to such data it is possible to avoid the inclusion of potentially inaccurate absence data. However, since no single method is universally better than the next, researchers are faced with the difficulty of selecting between numerous modelling approaches. There has been a considerable amount of research devoted to comparing the relative performance of modelling approaches. However, since these models are developed for terrestrial datasets, the majority of these studies have focused on terrestrial, freshwater or simulated datasets (Olden & Jackson 2002, Segurado & Araújo 2004, Elith et al. 2006, Meynard & Quinn 2007, Tsoar et al. 2007). The effective application of modelling methods in the marine environment, however, has received less attention, specifically in relation to demersal fish species. How the results from terrestrial, freshwater and simulated datasets translate into the marine environment remains largely untested.

1.2 Thesis focus, objectives and arrangement

Management agencies are increasingly seeking the provision of accurate, quantitative and spatially-explicit information on patterns of species distributions at scales relevant to the management process (Vanderklift & Ward 2000, Harris & Whiteway 2009, Malcolm et al. 2010a). This is because quantitative and spatially-explicit information is an important initial step in the process of defining the boundaries of proposed marine protected areas (MPAs; Ward et al. 1999, Roberts et al. 2002). This allows areas that are 'representative' and 'distinct' to be given the highest priority for protection (Myers et al. 2000). Increasingly, to support such initiatives, spatially-explicit predictive models are being used to provide this information (Pittman et al. 2007a). For example, Cañadas et al. (2005) used spatially-explicit predictive models to identified regions that were important for a number of cetacean species to define the boundaries of three proposed MPAs. Inevitably, however, a model is only as good as its underlying datasets (Stockwell & Peterson 2002, Zaniewski et al. 2002). For example, Lozier et al. (2009) highlighted the potential issue of incorrect (or incomplete) occurrence data as a source of error that may affect the accuracy of models in predicting sasquatch distributions. Whilst Lozier et al. (2009) used publicly available data (i.e. online repository of sighting localities) to demonstrate that the concept of incomplete or erroneous (i.e. misidentified) occurrence datasets influence models, it is equally applicable for well-designed field surveys in the marine environment. Consequently, understanding the underlying datasets, both the occurrence and the environmental data, as well as their influence on resultant model predictions is important. This thesis used two underwater video methods (i.e.

towed and baited) and high-resolution, spatially-continuous multibeam sonar datasets to examine and interpret the influence of seafloor habitat characteristics on the spatial distribution of temperate marine fishes. To achieve this goal, four separate, but interlinked studies were undertaken. These studies are presented as a series of papers, either published or in review, which form the four research chapters contained within this thesis and the aims of which are detailed below:

Defining and predicting demersal fish distributions and associated measures of habitat suitability are fundamental elements of any planning or management program for coastal subtidal marine environments. Chapter 2 ('*Remotely-sensed hydroacoustics and observation data for predicting fish habitat suitability*') reports the investigation of the potential of towed-video-derived observation and full-coverage MBES datasets to quantify habitat suitability for a marine demersal fish, the blue-throat wrasse (*Notolabrus tetricus*). As a consequence of incomplete detection of mobile demersal fish species using remotely-sensed video techniques, a presence-only approach, Ecological-Niche Factor Analysis (ENFA), was used. The ENFA was conducted using seafloor variables derived from multibeam sonar datasets at three spatial scales; fine (56.25 m^2), medium (506.25 m^2) and coarse (2756.25 m^2), to determine the influence of spatial scale on the prediction of blue-throat wrasse habitat suitability. The best performing model was also used to compare the spatial patterns in habitat suitability in and around Discovery Bay Marine National Park.

Following the demonstrated application of presence-only methods in Chapter 2, and given the growing number of modelling approaches available, closing the knowledge gap of the relative performance of different models in the marine environment was considered important. In this context, in Chapter 3 (*'Comparing presence-only algorithms for predicting habitat suitability for marine demersal fishes'*) MBES and towed-video-derived occurrence datasets are again used to model the habitat suitability of five demersal fish taxa in Discovery Bay, south-eastern Australia. In particular ten presence-only algorithms are contrasted (BIOCLIM, DOMAIN, ENFA; distance geometric mean [GM], distance harmonic mean [HM], median [M], area-adjusted median [Ma], median + extremum [Me], area-adjusted median + extremum [Mae] and minimum distance [Min], and MAXENT) using kappa and Area Under Curve (AUC) of the Receiver Operator Characteristic (ROC). The influences of spatial range (area of occupancy) and environmental niches (marginality and tolerance) on modelling performance were also tested. The best performing model for each taxon was also used to determine the most important variables in predicting suitable habitat for the five demersal fish taxa investigated.

Accurate estimates of fish occurrences are important to any species' assessment and distribution model. With increasing emphasis on non-destructive sampling of fishes, underwater video techniques are commonly used without a thorough understanding of their influence on the datasets they produce. Chapter 4 ('*Comparing towed and baited underwater video techniques for assessing temperate marine fishes*') contrasted baited and towed video systems to assess fish assemblages, functional groups (i.e. pelagic carnivore, epibenthic carnivore/omnivore or herbivore) and observability (i.e.

conspicuous or cryptic) across six biological habitats (mixed brown algae, mixed red and brown algae, mixed red algae, mixed red algae with invertebrates, no-visible macro-biota and seagrass).

The availability of fine-scale, complete-coverage seafloor variables and video-based occurrence datasets has seen a rapid increase in the use of species distribution models (SDMs) to predict the distributions of marine biological entities (i.e. species, assemblages or habitats) over a variety of spatial scales. However, sensible-looking, well-performing models can provide very different predictions of distribution depending on which occurrence dataset is used. To bring into focus this potential problem, Chapter 5 ('*Are we predicting the actual or apparent distribution of temperate marine fishes?*') compared predictions of habitat suitability from two presence/absence (generalised linear model and generalised additive model) and one presence-only (MAXENT) techniques. To illustrate the influence of occurrence dataset, models were built using co-located occurrence datasets derived from two underwater video methods (i.e. baited and towed video) and fine-scale multibeam sonar based seafloor habitat variables.

The thesis ends with a summary of key findings (Chapter 6) to link the major outcomes of the research to the objectives defined above in this section (Section 1.2 of Chapter 1) to illustrate the contribution this thesis has made to the field of marine quantitative spatial ecology. This final chapter (Chapter 6) also makes recommendations for future work in this research area.

All of the research chapters represent independent bodies of work that have been published or are under review in peer-reviewed journals. Chapter 2 has

been presented (oral) at the Australian Marine Sciences Association conference held in the Adelaide, Australia (July 2009), and published in *Continental Shelf Research* in 2011 (Monk et al. 2011). Chapter 3 was presented (oral) at the GeoHab Conference held in Wellington, New Zealand (May 2010) and published in *Marine Ecology-Progress Series* in 2010 (Monk et al. 2010). Chapters 4 and 5 have been presented at GeoHab Conference held in Helsinki, Finland (poster; May 2011) and at the Australian Marine Sciences Association conference held in the Fremantle, Australia (oral; July 2011), and are *in review* with *Estuarine, Coastal and Shelf Science* (July 2011) and *PloS ONE* (July 2011), respectively.

Remotely-sensed hydroacoustics and observation data for predicting fish habitat suitability[1]

[1] The research in this chapter has been published as Monk J, Ierodiaconou D, Bellgrove A, Harvey E, Laurenson L (2011) Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability. *Continental Shelf Research* 31: S17-S27

2.1 Introduction

Predictive geographical modelling is increasingly being recognised as an important tool for estimating species' habitat suitability, which is a fundamental step in the planning of conservation and management programs (Franklin 1995, Pearce & Ferrier 2001). These techniques allow the prediction of a species' potential habitat suitability, or distribution, beyond the range of direct observation data alone. Furthermore predictive geographic modelling serves a variety of purposes in applied ecology, including identifying areas of high conservation potential, assessment of suitable habitat representativeness and spatial patterns within protected areas, identifying the best sites for species reintroductions, designing wildlife corridors, predicting sites at risk for disease or exotic species invasions, and predicting how species distributions may change in response to management decisions and climate change (Manel et al. 2001). Although originating and being applied more commonly in terrestrial environments, advances in marine remote sensing technologies and the analytical capabilities of geographic information system (GIS) has seen an increase in marine applications of habitat suitability modelling (Brown et al. 2005, Iampietro et al. 2005, Bryan & Metaxas 2007, Pittman et al. 2007b, Wilson et al. 2007, Galparsoro et al. 2009). Through the utilisation of terrain analysis techniques of high-resolution MBES it is now possible to extract a suite of variable datasets that are ideal for input into predictive models (Wilson et al. 2007).

Advances in remotely operated underwater video systems offer the ability to cost-effectively capture observation data beyond the range of traditional

methods (e.g. SCUBA; Assis et al. 2007) and is a viable method in estimating fish population dynamics (Lauth et al. 2004, Watanabe et al. 2004, Morrison & Carbines 2006). Towed-video techniques have produced similar results to diver transects for estimating fish population dynamics, without being restricted by depth or bottom time (Stobart et al. 2007). This technique also has advantages over capture methods and baited-video systems as it is able to continuously capture data over seafloor transitional zones (Spencer et al. 2005). Morrison and Carbines (2006), for example, compared a large range of commonly used fish survey techniques (i.e. trawls, traps, nets, jigs, long-lining, baited camera and SCUBA diver) to a towed/drift video system to estimate the abundance of *Pagrus auratus* (snapper) during their night-time resting period. They found that the towed-video system appeared to provide better estimates of population abundance because it was not limited by depth, deployment time or size class selectivity. The integration of high-resolution MBES data and presence records from towed-video datasets provides an opportunity to develop models of fish habitat suitability over large areas of seafloor.

Different mathematical techniques have been developed for habitat suitability models (Guisan & Zimmermann 2000); those that require presence/absence data (e.g. generalised linear modelling) and more recently those that involve presence-only data (e.g. ENFA; Hirzel et al. 2002). Although towed-video is well suited to estimating fish occurrences, obtaining reliable absence data for highly mobile demersal fishes that are closely associated with seafloor structures (e.g. kelp beds or overhanging cliff structures) from a remotely-sensed video image can potentially result in an underestimate of a species occurrence. While the application of presence-only approaches negates the

need for reliable absence data, another advantage of these models pertains to species that are not in equilibrium with their environment (e.g. invasive or commercially-exploited species). In this context, an absence of a species may indicate an area has been full-exploited (e.g. fished out), rather than unsuitable habitat. In such circumstances, the inclusion of absence data in SDM could bias predictions of suitable habitat (Cianfrani et al. 2010). Thus, the application of the latter of these two techniques will be the focus of this study.

Spatially-explicit presence-only models utilise some form of environmental envelope or distance approach that compares the environmental niche of a species (defined from occurrence datasets) to the ecological characteristics of the entire study area (stored as GIS layers; Hirzel et al. 2002). While presence-only modelling is commonly used in terrestrial ecology (Hirzel et al. 2001, Brotons et al. 2004, Elith et al. 2006, Phillips et al. 2006, Titeux 2006, Tsoar et al. 2007), recent marine applications have yielded promising results, particularly using ENFA. The ENFA has been applied for modelling coral distribution at local (Dolan et al. 2008), regional (Bryan & Metaxas 2007) and global (Tittensor et al. 2009) scales. It has also been applied to mobile marine species to determine cetacean distribution (Praca et al. 2009), seabird feeding habitats (Skov et al. 2008) and suitable lobster habitat (Wilson et al. 2007, Galparsoro et al. 2009). Furthermore, because presence-only models are comparatively robust to low occurrence sample size, often reaching near optimal performance between 30 and 50 occurrences (Stockwell & Peterson 2002, Hernandez et al. 2006, Wisz et al. 2008), they are ideal for modelling applications where observation data is limited. These characteristics make

presence-only techniques well suited for marine demersal fish habitat suitability modelling.

Species can potentially respond to habitat variables at different spatial scales (Freemark & Merriam 1986, Wilson et al. 2007). Because each species responds to the environment at a unique range of scales (Levin 1992), there is no single correct spatial scale at which to describe species-habitat relationships (Wiens 1989). Thus, assessing species–environment relationships at multiple scales are necessary (Cushman & McGarigal 2003) and are becoming commonplace (Carroll et al. 1999, Thompson & McGarigal 2002, Zabel et al. 2003, Fischer et al. 2004, Wilson et al. 2007). *Notolabrus tetricus* (blue-throat wrasse) are a species common to the inshore waters of southern Australia (Shepherd & Clarkson 2001). Like numerous other wrasse species found along southern Australia, they are protogynous hermaphrodites (Barrett 1995, Shepherd & Clarkson 2001). Exhibiting well-defined home ranges ranging from 400 to 775 m^2 for males and 225 to 725 m^2 for females, they complete their life-cycle in a relatively small area (Barrett 1995). The species has recently become the focus of a rapidly expanding commercial line and trap fishery in Victoria, south-east Australia, with 27 licences across Victoria (Smith et al. 2003). Coupled with likely population structuring at a localised scale and a burgeoning fishing industry, the species has been identified as being highly susceptible to over-exploitation (Smith et al. 2003). Their sedentary and highly territorial nature (Barrett 1995) also means that they may exhibit strong associations with a particular habitat. This combined with their potential susceptibility to over-exploitation makes them an ideal candidate for habitat suitability modelling.

The objectives of this study are threefold. Firstly, ENFA was used to develop a habitat suitability model for *N. tetricus*. Secondly, models were run using MBES sampled at three spatial scales to determine the influence of scale in the prediction of *N. tetricus* habitat suitability. The use of the same occurrence dataset across the different spatial scale models permits a direct comparison of the model outputs. Finally, landscape pattern indices were applied using the best performing model to compare the spatial patterns of habitat suitability classes within the Discovery Bay Marine National Park (MNP) with adjacent waters.

2.2 Materials and methods

2.2.1 Study area

The study site encompassed an area 42 km^2 that was situated on the western side of Cape Duquesne (-38° 22′ S, 141° 21′ E) in Discovery Bay, south-eastern Australia (Figure 1). The site ranged in depth from 12 to 79 m. Vertical basalt reef structures rise some 20 m from the seafloor, reflecting the region's previous dynamic volcanic history (Boutakoff 1963).The tops of these reef structures support diverse assemblages of red algae and kelps (dominated by *Ecklonia radiata, Phyllospora comosa* and *Durvillaea potatorum*), while the deeper regions are covered in sponges, ascidians, bryozoans and gorgonian corals (Ierodiaconou et al. 2007a).

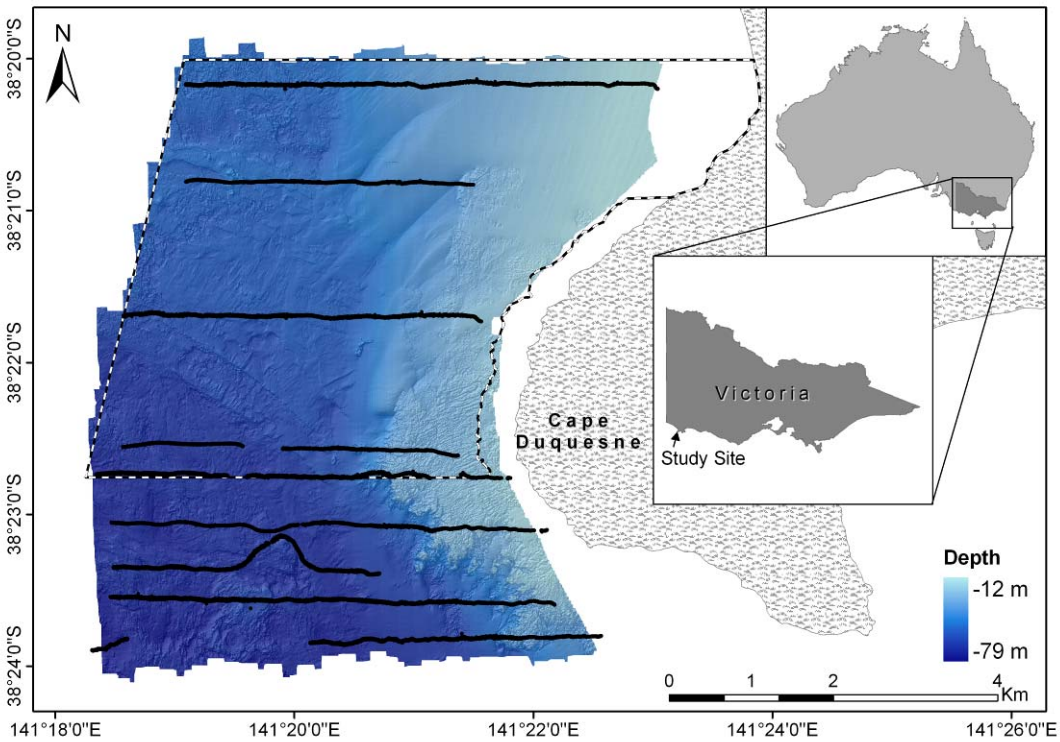

Figure 1. Bathymetric hillshade highlighting the study area used to investigate habitat suitability. Blue shading indicates water depth. Dashed black line shows Discovery Bay Marine National Park Boundary. Solid black lines illustrate towed-video transects positions.

2.2.2 MBES survey and derived seafloor characteristics used in model construction

The MBES derived bathymetry and backscatter variables were gridded to a 2.5 m^2 cell resolution. The MBES data were acquired on the 2nd and 3rd of November 2005 as part of the Victorian Marine Habitat Mapping Project (Ierodiaconou et al. 2007a). The MBES bathymetry and backscatter data were collected using a hull-mounted Reson Seabat 8101 multibeam system with 100 % overlap of run lines to ensure full site coverage. Precise positioning was achieved using Starfix high precision (HP) Differential GPS system (± 0.30 m), integrated with a positioning and orientating system for marine vessels (POS MV) for heave (± 0.05 m or 5%, whichever is greater), pitch, roll and yaw corrections(all ± 0.021° accuracy). Navigation, data logging, real-time quality control, display and post-processing were carried out using the Starfix suite 7.1

(Fugro Survey Pty Ltd.). Sound velocity profiles were taken every 12 hour (h) during survey operations to account for variations in sound speed through the water column. Bathymetry data were corrected to the lowest astronomical tide based on reading from an Aquatec 320 tide gauge that was deployed during the survey. The XYZ data were then used to produce a bathymetric grid at 2.5 m horizontal resolution and a range resolution of ± 12.5 mm. Backscatter data were corrected for gain and time varied gain using the University of New Brunswick (UNB1) algorithm (Starfix suite 7.1). Data were post-processed by trained surveyors to hydrographic standards. Backscatter processing included the correction for transmission loss, the actual area of ensonification on the bathymetric surface, source level, and transmit and receive beam patterns (see Fonseca et al. 2008). Additionally backscatter was corrected for seafloor bathymetric slope from the MBES bathymetry dataset. Final products of the MBES survey constituted cleaned 2.5 m backscatter intensity (dB) and bathymetry (m) grid layers.

The processed 2.5 m gridded backscatter and bathymetry were used to derive 11 additional variables to further characterise local variation within the MBES imagery and delineate analogous regions of morphology and signal scattering (Table 1). These derivatives were selected for their expected influence over distribution of fish as found in previous investigations (e.g. rugosity- Friedlander & Parrish 1998, bathymetric variance- Pittman et al. 2007a, distance to nearest reef- Wedding et al. 2008, slope- Moore et al. 2009). They represent variation in seafloor characteristics in terms of proximity to reef (Euclidean distance to nearest reef), exposure to wave energy and seafloor currents (aspect, benthic position index; BPI, slope), complexity and surface

area of seafloor structure (complexity, rugosity, maximum curvature) and variations in high and low frequency signal scattering properties of the substratum recorded in the backscatter intensity dataset (Hue-Saturation-Intensity). Euclidean distance to nearest reef was calculated using the spatial analyst tool in ArcGIS 9.3 based on an accurately modelled reef class (81 % accuracy) extracted from predicted substrata map (sourced from Ierodiaconou et al. 2007a) of the study area. The analysis was limited to MBES-derived seafloor characteristics because oceanographic variables are not available at the fine-scale resolution of the MBES datasets (2.5 m^2). In addition, because of the relatively small spatial scale of the study area it was expected that there would be little variation in oceanographic characteristics (e.g. temperature).

Variables were calculated at three spatial scales to assess which most influenced wrasse habitat suitability. The spatial scales were chosen to encompass the home range of 225–775 m^2 estimated for *N. tetricus* (Barrett 1995). Consequently, three window sizes of 3 × 3, 9 × 9 and 21 × 21 cells, which equates to ground areas of 56.25, 506.25, and 2756.25 m^2 (hereafter referred to as fine, medium and coarse scale models) were included. These windows represent the finest model possible, a midpoint of the estimated home range and approximately 3.5 times larger than the home range. A correlation tree derived in Biomapper 4.0 was used to assess the correlation between variables at each spatial scale. To avoid incorporating redundant data, a default threshold of 0.5 was chosen in line with previous studies (Hirzel et al. 2002, Galparsoro et al. 2009). For each spatial scale, the same least correlated subset of 8 of the initial 13 variables (Table 1) were used to allow direct comparison of modelling results.

Table 1. Variables used in the ENFA models with biological relevance to *Notolabrus tetricus*. Kernels sizes give the number of cells or scale factor used to calculate fine, medium and coarse models

Model Variables	Variable description	Kernels sizes	Software
Aspect- Eastness	Because aspect is a circular variable (i.e. large values (359º) are very close to small values (1º)) the data were transformed. Aspect was transformed by trigonometric functions (Roberts 1986). Eastness values close to 1 represent east-facing slopes, while those facing west have a value close to -1.	3, 9, 21 cells	Spatial Analyst-ArcGIS 9.3
- Northness	Northness is represented in values close to 1 if the aspect is generally northward, close to -1 if the aspect is southward.	3, 9, 21 cells	Spatial Analyst-ArcGIS 9.3
Backscatter	Backscatter intensity is important in quantifying physical properties of the seafloor (Le Gonidec et al. 2003). Provides a proxy for seafloor hardness and softness.		Fugro Starfix suite 7.1
Bathymetry	Bathymetry provides a measure of depth for the entire site.		Fugro Starfix suite 7.1
Benthic Position Index	Measure of a location relative to the overall benthoscape. Calculated by comparing the elevation of a cell with the mean elevation of surrounding cells by the three analysis extents (scale factors: 56, 506 and 2756). Regions with positive values are higher than their surroundings, where as areas negative values are lower. Flat areas have values closer to zero (Weiss 2001).	8, 22, 52 scale factor	BTM Tool for ArcGIS
Complexity	Complexity provides a measure of the rate of change of the slope and a measure of localised variability in seafloor structure	3, 9, 21 cells	ENVI 4.2
Euclidean distance to reef	The Euclidean distance (in m) to reef was calculated from extracting the reef class from a substratum map that was generated as a part of the Victorian Marine Mapping Project using a decision tree classifier (see Ierodiaconou et al. 2007a).		Spatial Analyst-ArcGIS 9.3
HSI-blue -green	A Synthetic Colour Image transformation was applied to the backscatter. This transforms backscatter from a gray scale image into a synthetic colour image by		ENVI 4.2

Table 1. Continued…

-red	applying high pass and low pass filters. Low pass data are assigned to hue, while high pass is assigned to intensity, and a fixed saturation level is used. These hue, saturation and intensity data are transformed into red, green, and blue (RGB) spectrum, producing a three band colour image. This transformation is commonly used with radar data to improve the display of subtle large-scale features while retaining fine detail (Daily 1983).		
Maximum Curvature	Maximum Curvature provides the greatest curve, relative to its neighbors, of either the profile (i.e. the curvature in the direction of maximum downwards slope) or plan (i.e. the shape of the surface viewed as if a horizontal plane) convexity (Gallant & Wilson 1996).	3, 9, 21 cells	ENVI 4.2
Rugosity	Rugosity, or vertical relief, is the ratio of surface area to planar area within analysis window and is to represent a measure of structural complexity (Lundblad et al. 2006).	3, 9, 21 cells	BTM Tool for ArcGIS
Slope	Slope is the rate of change in bathymetry over the analysis window (Wilson et al. 2007).	3, 9, 21 cells	Spatial Analyst-ArcGIS 9.3

2.2.3 Towed-video fish surveys

Towed-video transects, which were initially collected for benthic habitat mapping, were used to provide fish occurrence data for model training and testing (Ierodiaconou et al. 2007a). Nine transects, aligned perpendicular to the coast were selected to encompass the main physical gradients (e.g. depth, topographic variation, exposure). These nine transects covered 56 linear km of the study area (Figure 1). Over four days (24th, 25th March and 26th, 27th April 2006) a micro remotely-operated vehicle (VideoRay Pro 3) was towed along the transects at 0.5-1 ms^{-1} (1-2 knots) to collect video data. The oblique angled camera was maintained approximately 2 m from the bottom using a vessel-mounted winch system. A text overlay containing a time stamp and transect ID were recorded with the video using a Sony MiniDV recorder. The video footage was interrogated to identify fish to the lowest possible taxonomic resolution. The exact spatial position (± 5 m accuracy) of each fish taxon was then determined by matching the time stamp of the video with the corresponding survey positional data. The survey positional data were recorded through the integration of vessel location (Omnistar satellite dGPS), motion sensor (KVH) and acoustic camera positioning (Tracklink Ultra Short Baseline). Transects were analysed by the same observer to decrease any between operator bias. Video footage was only excluded from the analysis when the video quality was too poor to identify fish or view the seafloor. To minimise erroneously positioned fish, individuals were only counted if they were observed in the foreground (within 5 m of the camera) of the video footage.

2.2.4 Model formulation and evaluation

The ENFA was used to develop the habitat suitability models using Biomapper 4 software (Hirzel et al. 2007). For each spatial scale, rasters of the least correlated subset of variables were imported into the Biomapper program along with a grid identifying which cells were classified as 'presence' for *N. tetricus*. A Box–Cox transformation was used to improve the normality of the variables (Hirzel et al. 2002). The ENFA then reduces original variables to a subset of uncorrelated factors. MacArthur's broken-stick rule (MacArthur 1957) was used to determine how many of these factors were retained in the habitat suitability calculation. The 'broken-stick' concept of MacArthur (1957) describes how species partition a resource pool in multi-dimensional space into non-overlapping niches. Based on this concept, the 'Mac Arthurs broken-stick' rule compares the Eigen value distribution of the factors to ensure that there is no overlap and that only those which are necessary are retained (i.e. with Eigen values > 1). Thus, the retained factors explain most of the information related to the distributions of the original variables and constitute the dimensions of the environmental-space for the calculation of habitat suitability. The important difference between ENFA, and other data reduction techniques such as principal components analysis, is that rather than only accounting for the variance among factors the ENFA factors have ecological relevance (Hirzel et al. 2002). Marginality of the species (i.e. how species' habitat differs from the mean available conditions) is represented in the first factor, while specialisation (breadth of the ecological niche) is maximised in the subsequent factors (Hirzel et al. 2001). The factor coefficients give the importance of each variable to the different factors and the relative range of the variables preferred

by the species (positive coefficients indicate associations with areas above mean for that variable and the inverse for negative coefficients). They are also used to compute a global marginality (varying between 0 and 1, with higher values indicating greater differences) and specialisation (indicating some degree of specialisation when greater than 1). The distance geometric mean algorithm was used to generate habitat suitability maps. This algorithm computes a smooth set of habitat suitability envelopes by relating each observation cell in such a way that the denser these are in the environmental-space, the higher the habitat suitability (Hirzel et al. 2007). A cell with a habitat suitability value of zero would have the least suitable combination of values for all variables, while a cell with a value of 100 would have the most suitable combination. To determine which spatial scale model performed best, habitat suitability models were evaluated in Biomapper 4 using the predicted-to-expected ratio curve(p/e curve) and the continuous Boyce Index(*B*; Boyce et al. 2002, Hirzel et al. 2006). A perfect model would exhibit a straight increasing line p/e curve. The *B* is a Spearman rank correlation coefficient between the p/e ratio and the habitat suitability values. It varies from -1 to 1, a perfect model having a $B = 1$. Hirzel et al. (2006), however, compared the accuracy of different validation methods and found a $B \sim 0.6$ corresponds to an AUC > 0.9 (AUC evaluates the proportion of correctly and in correctly classified predictions over a continuous range of presence–absence thresholds. The closer AUC is to 1, the better the model). In practice, the occurrence data is partitioned into *k* independent subsets, and *k*-1 partitions are used as a calibration dataset, leaving the last partition for validation. A $k = 10$, together with 1 random seed, was used for each spatial scale model. To generate the p/e

curve for each model, three equal-width habitat suitability windows (0 – 33, 34 – 67, and 68 – 100) were used. If a model properly predicts the suitable areas, the p/e ratio should be < 1 for unsuitable habitat, > 1 for moderately suitable habitat and >> 1 for highly suitable habitat. The p/e ratio should also exhibit a monotonic increase from unsuitable to highly suitable. *B* is then computed between the p/e ratio and the mean values of habitat suitability window. The p/e curve and B are then produced *k* (in this case 10) times, each time leaving out another validation partition, allowing the assessment of their central trend and variance (presented here as mean ± SD). Using the p/e curve, thresholds were estimated following Hirzel et al. (2006), which are the points where the curve is < 1, > 1 and >> 1. This permits reclassification of predicted maps into meaningful habitat suitability classes, which can then be used to analyse spatial patterns.

2.2.5 Spatial patterns of *Notolabrus tetricus* habitat suitability

Using the best performing model, the spatial arrangement and representation of the three habitat suitability classes (determined by p/e curve) were compared inside Discovery Bay MNP with adjacent waters. Patch Grid Analyst 4 extension in ArcGIS 9.3 was used to generate six measures of landscape pattern indices. Twenty-two non-overlapping landscape analysis windows were randomly positioned in-and outside the MNP. The size of the landscape analysis window was selected following recommendations by O'Neill et al. (1996), suggesting that the landscape analysis window be 2-5 times larger than the largest patch of interest. A 550 × 550 m^2 landscape analysis window was selected because it was large enough to contain the 98th percentile of habitat

suitability patches. For each landscape analysis window, interspersion and juxtaposition index (IJI), largest patch index (LPI), landscape shape index (LSI), mean patch size (MPS), mean shape index (MSI) and patch size coefficient of deviation (PSCV) were calculated (see footnotes in Table 5 for descriptions). While there are numerous landscape pattern indices available (McGarigal & Marks 1994), these were selected based on the findings by Teixido et al. (2002), who identified them as an adequate subset of indices to describe marine benthoscape patterns (akin to landscape patterns in terrestrial systems). The differences in these indices between the Discovery Bay MNP and adjacent waters were compared to assess the representativeness of the MNP for habitat suitability of *N. tetricus*. A non-parametric Kruskal–Wallis test was used for comparisons as the raw and transformed data did not conform to parametric assumptions.

2.3 Results

2.3.1 Ecological-Niche Factor Analysis modelling and scale selection

A total of 83 *N. tetricus* individuals were identified from the video analysis, as some frames included multiple individuals this equated to 61 occurrences records. To determine which variable spatial scale most influenced the habitat suitability of *N. tetricus*, three ENFA models were generated. The models were based on three different spatial scales (fine: 56.25 m^2, medium: 506.25 m^2, and coarse: 2756.25 m^2) and were constructed using the same occurrence dataset to enable direct comparison between outputs (Figures 2; 3). For each scale model, ENFA reduced the least correlated subset of variables (bathymetry, benthic position index, eastness, Euclidean distance to nearest reef, hue-saturation-

intensity-blue, maximum curvature, northness and rugosity) to five explanatory factors (selected by comparison with the broken-stick distribution; MacArthur 1957, Hirzel et al. 2002). These five explanatory factors were fitted using the distance geometric mean algorithm to define habitat suitability of *N. tetricus* at each spatial scale.

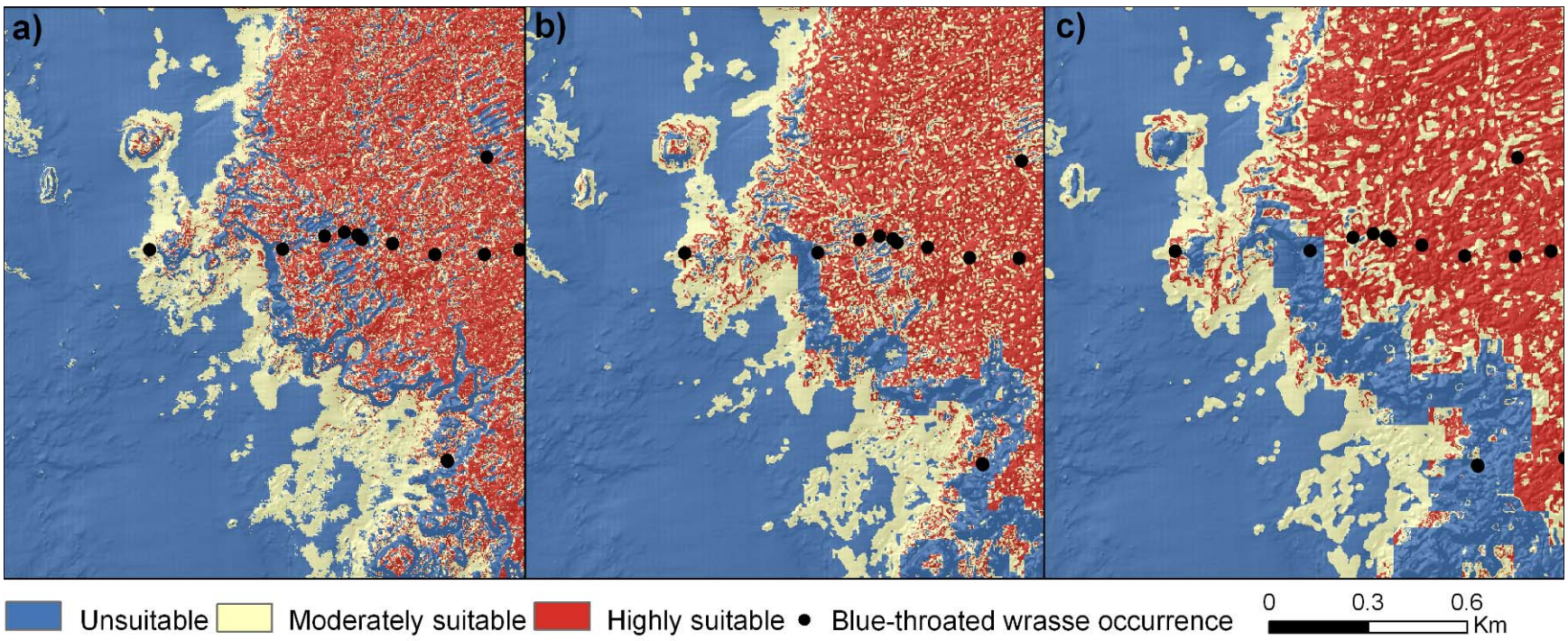

Figure 2. Predicted habitat suitability of *Notolabrus tetricus* for the different spatial scale models and occurrences: (a) fine spatial scale model: area 56.25 m^2, (b) medium spatial scale model: area 506.25 m^2, and (c) coarse spatial scale model: area 2756.25 m^2. Habitat suitability models generated using the geometric mean algorithm within ENFA.

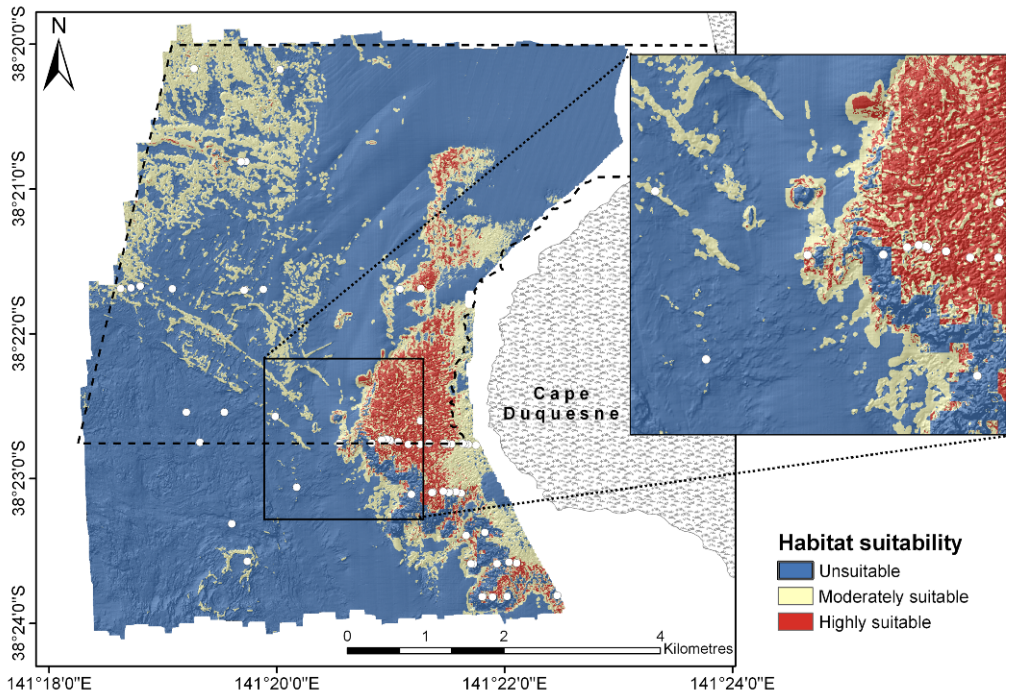

Figure 3. Predicted habitat suitability for *Notolabrus tetricus* over the whole study area using the coarse scale model. Inset map shows how presence cells (white dots) mainly fall within pixels with high habitat suitability. A few observations are in pixels with moderate-unsuitable habitat reflecting the fact that *N. tetricus* may not always occur in optimal habitat as indicated by the specialisation value. Heavy dashed black line delineates the Discovery Bay Marine National Park boundary.

Global marginality, specialisation and Boyce Index values for each spatial scale investigated are presented in Table 2. Although all models performed well, the Boyce Index indicated that the coarse scale model (0.80 ± 0.26; Figure 4) performed better than both fine and medium scale models, 0.75 ± 0.33 and 0.60 ± 0.42, respectively. The p/e curves for all models showed a positive monotonic trend as habitat suitability for *N. tetricus* increased; Figure 4). As the spatial scale increased, global marginality was found to decrease from 1.03 to 0.95, but global specialisation values stayed the same (1.54). These global marginality and specialisation values indicate that, irrespective of the spatial scale analysed, *N. tetricus* were associated with regions that are different to the mean available but exhibit a relatively wide niche.

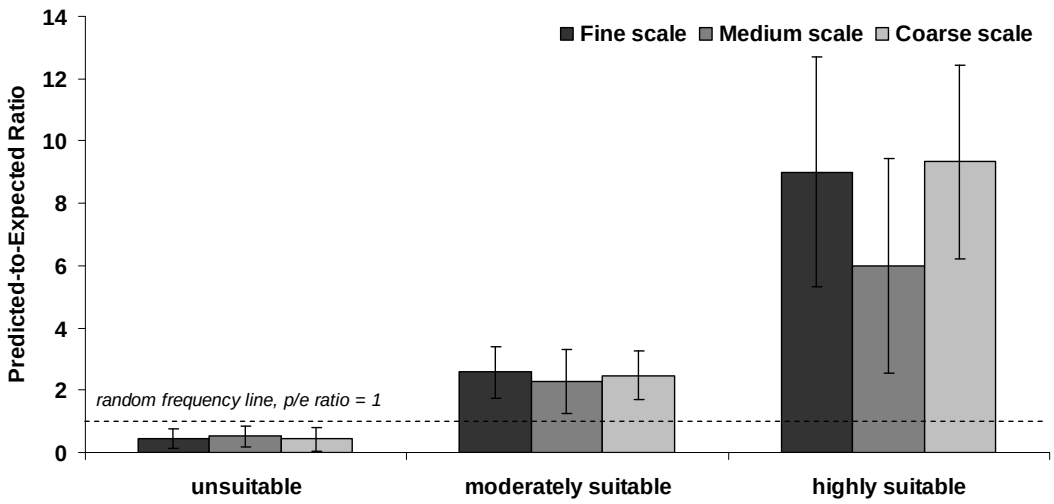

Figure 4. Cross-validation results for habitat suitability models for *Notolabrus tetricus* produced using the geometric mean in ENFA. Predicted-to-expected ration indicates the number of species occurrence cells encountered between cross-validation runs (k = 10).

Table 2. Continuous Boyce Index (B, varying between -1 and 1), global marginality (***M***, varying generally between 0 and 1) and global specialisation (***S***, indicating some degree of specialisation when superior to 1) for the fine, medium and coarse scale models.

Scale	***B*** **(mean ± SD)**	***M***	***S***
Fine	0.7 ± 0.33	1.03	1.54
Medium	0.6 ± 0.42	0.93	1.54
Coarse	0.8 ± 0.26	0.92	1.54

2.3.1.1 Fine scale model

The marginality factor indicated a strong relationship for areas close to reef (-0.61) and high rugosity (0.61; Table 3). This factor also showed the importance of higher HSI-b values (0.31), shallow water (bathymetry: 0.30) and high maximum curvature (0.25). Specialisation coefficients highlighted that *N. tetricus* are restricted to regions that are shallow water (bathymetry: 0.79), low HSI-b (-0.69), east facing (eastness: 0.66), depressions (BPI: -0.59), close proximity to reef (0.55) and lower maximum curvature (-0.43). Northness at this scale did not appear to be important (Table 3).

2.3.1.2 Medium scale model

The marginality factor showed a similar trend to the fine scale model, with a strong association for areas close to reef (-0.67), whereas maximum curvature had a greater influence (0.39). High rugosity (0.39), higher HSI-b values (0.33), shallow water (bathymetry: 0.32) were also found to be important. Specialisation coefficients highlighted that all eight variables were important. *N. tetricus* were restricted to areas that had low HSI-b (-0.92), north-west facing (eastness: -0.85, northness: 0.47), shallow water (-0.80) and high rugosity (0.24; Table 3).

2.3.1.3 Coarse scale model

The marginality factor showed the same trend as that of the fine scale model. A strong association was evident with areas close to reef (-0.68), high rugosity (0.47), high HSI-b values (0.34), shallow water (0.33) and high maximum curvature (0.29; Table 3). Specialisation coefficients indicated that *N. tetricus* were restricted to areas that were north-east facing (northness: 0.86, eastness: 0.78), high HSI-b (0.85), close to reef (-0.53), on top of crests (0.22) and in shallow water (0.33; Table 3).

Table 3. Contribution of the variables to the factors generated by ENFA used to build the three different spatial scale models of habitat suitability for *Notolabrus tetricus*. Coefficients are sorted by decreasing value of coefficients on the marginality factor (***M***). Specialisation values for each factor are represented (in brackets) by ***S***. Variables that make the largest contribution (<-0.1 or >0.1) to each factor are highlighted in bold.

Fine scale Variables	**Factor 1** ***M*** **(100%)** ***S*** **(43%)**	**Factor 2** ***S*** **(24%)**	**Factor 3** ***S*** **(15%)**	**Factor 4** ***S*** **(6%)**	**Factor 5** ***S*** **(4%)**
Distance to nearest reef	**-0.61**	**0.55**	-0.10	**0.39**	0.02
Rugosity	**0.61**	0.00	0.05	0.04	0.02
HSI-b	**0.31**	**0.34**	**-0.69**	0.41	-0.17
Bathymetry	**0.30**	**0.76**	**0.36**	-0.01	**0.27**
Maximum curvature	**0.25**	0.01	0.10	**0.26**	**-0.43**
Eastness	0.09	0.00	0.15	**0.49**	**0.66**
BPI	0.03	0.07	**-0.59**	**-0.59**	**0.52**
Northness	-0.01	-0.03	-0.04	-0.10	0.09

Medium scale Variables	**Factor 1** ***M*** **(100%)** ***S*** **(46%)**	**Factor 2** ***S*** **(27%)**	**Factor 3** ***S*** **(10%)**	**Factor 4** ***S*** **(6%)**	**Factor 5** ***S*** **(6%)**
Distance to nearest reef	**-0.67**	**-0.54**	**-0.26**	**-0.27**	0.17
Maximum curvature	**0.39**	-0.02	0.09	-0.07	0.01
Rugosity	**0.39**	-0.02	0.03	-0.14	**0.24**
HSI-b	**0.33**	**-0.25**	**-0.92**	0.15	0.07
Bathymetry	**0.32**	**-0.80**	**0.26**	**-0.25**	-0.01
BPI	-0.14	-0.01	-0.05	-0.09	**0.47**
Eastness	0.11	0.06	-0.06	**-0.85**	**0.24**
Northness	0.05	0.03	-0.01	**0.29**	**0.79**

Coarse scale Variables	**Factor 1** ***M*** **(100%)** ***S*** **(44%)**	**Factor 2** ***S*** **(28%)**	**Factor 3** ***S*** **(11%)**	**Factor 4** ***S*** **(7%)**	**Factor 5** ***S*** **(5%)**
Distance to nearest reef	**-0.68**	**-0.53**	0.12	**0.44**	**0.22**
Rugosity	**0.47**	0.04	-0.14	0.18	0.13
HSI-b	**0.34**	**0.22**	**0.85**	**0.27**	0.05
Bathymetry	**0.33**	**0.81**	**-0.33**	0.19	0.11
Maximum curvature	**0.29**	0.01	-0.02	0.05	0.10
BPI	-0.07	-0.01	0.03	0.04	**0.22**
Eastness	0.06	-0.05	**-0.33**	**0.78**	**0.35**
Northness	0.00	-0.09	0.14	-0.24	**0.86**

2.3.2 Spatial patterns of *Notolabrus tetricus* habitat suitability

Only minimal differences were observed when total predicted area of the three habitat suitability classes (i.e. unsuitable, moderately and highly suitable) were compared (Table 4). To compare the spatial patterns in habitat suitability classes within the Discovery Bay MNP with adjacent waters six landscape pattern indices were applied to the best performing coarse-scale ENFA model. The IJI exhibited significantly lower values in the MNP compared to adjacent waters for unsuitable (H = 13.20, df = 1, $p < 0.001$) and highly suitable (H = 10.24, df = 1, $p < 0.001$) habitat classes indicating that they are both unevenly distributed (Table 5). Although statistically non-significant in- and outside the MNP, IJI for moderately suitable habitat exhibited much greater values compared to unsuitable and highly suitable habitats, indicating a more even arrangement of patches. In contrast, the mean shape index (MSI) for unsuitable habitat was significantly larger (H = 4.88, df = 1, $p < 0.05$) in the MNP. All habitat suitability classes exhibited mean MSI values greater than one, indicating that they all exhibit noncircular patch shapes. Largest patch index (LPI) and mean patch size (MPS) showed similar trends with high values being recorded for unsuitable habitat monotonically decreasing to highly suitable habitat but were statistically non-significant between regions. Low LPI and MPS values for highly suitable habitat indicate that the largest and mean patches are smaller than other suitability classes presented. Landscape shape index (LSI) and patch size coefficient of deviation (PSCV) exhibited higher values for moderately suitable habitat compared to unsuitable and highly suitable but were not significantly different (Table 5).

Table 4. Comparison of predicted habitat suitability class areas inside Discovery Bay Marine National Park compared to the adjacent unprotected region. Areas are given in km^2 with % contained within each region in brackets.

Habitat suitability	Inside MNP	Outside MNP
Unsuitable	22.3 (84.8)	13.0 (82.8)
Moderately	3.1 (11.8)	2.0 (12.7)
Highly	0.9 (3.4)	0.7 (4.5)
Total	26.3 (100)	15.7 (100)

Table 5. Landscape indices used to assess the spatial arrangement and configuration of habitat suitability for *Notolabrus tetricus* inside and out of Discovery Bay Marine National Park (MNP). Significant difference between the Marine National Park and adjacent region are shown in bold and denoted by * $p < 0.05$. ** $p < 0.001$. Descriptions of indices are given in footnote. Descriptions modified from McGarigal and Marks (1994).[2]

Landscape pattern index	Region	Suitability Class	Mean ± SD
LPI	Inside MNP	Unsuitable	64.04 ± 37.32
		Moderately	23.79 ± 23.98
		Highly	11.05 ± 22.44
	Outside MNP	Unsuitable	78.73 ± 30.71
		Moderately	11.95 ± 17.78
		Highly	6.44 ± 13.13
LSI	Inside MNP	Unsuitable	3.11 ± 1.96
		Moderately	6.38 ± 3.72
		Highly	4.21 ± 4.18
	Outside MNP	Unsuitable	2.50 ± 1.76
		Moderately	4.81 ± 4.28
		Highly	4.77 ± 3.14
IJI	Inside MNP	Unsuitable	**0.48 ± 0.51****
		Moderately	42.13 ± 33.37
		Highly	**0.17 ± 0.43****
	Outside MNP	Unsuitable	**7.35 ± 12.30****
		Moderately	39.06 ± 45.04
		Highly	**17.51 ± 18.21****
MSI	Inside MNP	Unsuitable	**1.39 ± 0.32***
		Moderately	1.47 ± 0.25
		Highly	1.56 ± 0.16
	Outside MNP	Unsuitable	**1.19 ± 0.16***
		Moderately	1.42 ± 0.25
MPS	Inside MNP	Unsuitable	10.42 ± 13.57
		Moderately	0.52 ± 1.04
		Highly	0.14 ± 0.41
	Outside MNP	Unsuitable	15.03 ± 14.53
		Moderately	0.10 ± 0.08
		Highly	0.05 ± 0.07
PSCV	Inside MNP	Unsuitable	277.58 ± 330.84
		Moderately	471.87 ± 374.69
		Highly	342.56 ± 325.53
	Outside MNP	Unsuitable	226.65 ± 238.20
		Moderately	354.81 ± 330.58
		Highly	308.51 ± 224.32

[2] Largest Patch Index (LPI) is the percentage of the landscape window comprised by the largest patch. With low values indicating the largest patch in the landscape is increasingly small. Landscape Shape Index (LSI) is the sum of the all edge segments (m) within the landscape boundary involving the corresponding patch type, divided by the square root of the total landscape area (m^2), and adjusted by a constant for square raster cell edges. The larger the LSI the more irregular the patch shape. Mean Shape Index (MSI) is the patch perimeter (m) divided by the square root of patch area (m^2) for each corresponding patch type, adjusted by a constant for a square raster cell edge, divided by the number of patches of the same type. When MSI equals one all patches of the corresponding patch type are circular. Mean Patch Size (MPS) is the total landscape area (m^2), divided by the total number of patches, divided by 10000 (to convert to hectares). Interspersion and Juxtaposition Index (IJI) is the observed interspersion (%) over the maximum possible interspersion for the given number of patch types. When IJI approaches 100% all patches are equally and maximally adjacent to all other patch types. Patch Size Coefficient of Deviation (PSCV) is the variability in patch size relative to the mean patch size (Note, this is the population mean, not the sample mean).

2.4 Discussion

Models were based on high-resolution MBES-derived variables and towed-video observations at three spatial scales. The coarse-scale ENFA model provided the best prediction of habitat suitability for *N. tetricus*. Using this coarse-scale prediction, the spatial patterns of habitat suitability classes were compared. It was found that both unsuitable and highly suitable habitat classes were more unevenly distributed inside the MNP, while unsuitable patches exhibited more complex shapes inside the MNP. Based on the results, four main points will be discussed: (i) issues surrounding the use of presence-only models on remotely-sensed datasets; (ii) the importance of spatial scale for predicting habitat suitability of *N. tetricus*; (iii) importance of habitat parameters identified by the models; and, (iv) spatial patterns in habitat suitability classes.

2.4.1 Predictive ability of models

All three variable scales yielded model performances that were comparable with other good performing ENFA models in the literature (e.g. Hirzel & Arlettaz 2003, Wilson et al. 2007). While these models exhibit variability among cross-validation results, even the lower end of these ranges produced adequate p/e ratio values and good separation between suitability windows. This supports the idea that the ENFA technique appears to be well matched to modelling habitat requirements of marine demersal fish based on remotely-sensed datasets. A presence-only modelling approach was chosen over presence/absence methods because there are difficulties in obtaining reliable absence data from remotely-sensed video datasets. While it is acknowledge

that to attain ‘perfect detection’ (i.e. probability of 1) is unrealistic, obtaining ‘true’ absence data (when animals are actually absent) is problematic for mobile or inconspicuous species, such as demersal fishes. Kéry (2002), for example, estimated that 12-34 visits to a site are needed before assuming a 95 % probability that a site is unoccupied. ‘False’ absence data, when animals are present but not detected, can significantly bias the generated model. This shortcoming can be avoided using presence-only methods, such as ENFA (Hirzel et al. 2002). Because of the use of presence-only data, however, such methods tend to overestimate the area of suitable habitat (Zaniewski et al. 2002). Overestimating, however, might be more preferable to underestimating their existence, particularly when considering a commercially or ecologically important species that is likely to be targeted by management (Fielding & Bell 1997). Indeed, presence-only methods predict the potential distribution (fundamental niche; i.e. the total range of environmental conditions that are suitable for a species existence without the effects of interspecific competition and predation from other organisms), whereas presence/absence methods reflect the present distribution (realised niche; i.e. the part of the fundamental niche that a species actually occupies) of the species (Zaniewski et al. 2002, Brotons et al. 2004). Even though presence-only methods have limitations, they are increasingly being shown to be a useful approach for predictive habitat modelling in marine environments. Another important factor that influences the predictive performance of these models is variable selection (Araújo & Guisan 2006). The models were generated based on seafloor variables because of availability of data (MBES data) and the known ecology of the species (strong seafloor associations; Johnson & Gillingham 2005). While the models

performed well, the addition of other variables may further improve their predictive capabilities. For a detailed discussion of additional variables see Chapter 6 section 6.2.1

2.4.2 Spatial scale

By comparing the three different scale models in this study, the results indicated that the coarse model (2756.25 m^2) produced better suitability results compared to fine and medium. The value of 2756.25 m^2 is substantially larger than the home range estimates of 400–775 m^2 for males and 225–725 m^2 for females (Barrett 1995). The results, however, support the suggestion that habitat selection of space-demanding species may be dominated by variables operating above the home-range scale (Carroll et al. 1999). While the coarse-scale model performed better overall, variable importance differed at the three spatial scales analysed. Maximum curvature, for example, was found to have a stronger influence at the medium scale compared to fine and coarse scales. This is in agreement with the idea that species respond to their environment at multiple spatial scales. Similar scale-dependence of single habitat variables has been found for both terrestrial and marine species. For example, Fisher et al. (2004) found that the distribution of some reptile species were influenced by habitat structure at one, but not all, spatial scales. Similarly, Moore et al. (2009) found that the distributions of the four demersal fish species were better represented by the coarse-scale variables (i.e. variables with a 2 × 2 m cell resolution calculated with a kernel radius of 25 m), with only one model providing a better fit with the fine-scale environmental variables (i.e. variables with a 2 × 2 m cell resolution calculated with a kernel radius of 12.5 m).

2.4.3 Variables selected by the models

The results confirmed that benthoscape-scale variables derived from MBES data can explain a large proportion of the variability describing the habitat suitability of *N. tetricus* . They also support the idea that factors operating at the benthoscape-scale could explain the variance of species occurrence that may not be explained by fine-scale habitat associations (Storch 2002). Although varying slightly over the three scale models, *N. tetricus* showed a strong association with regions of shallow water, close to reef, with high rugosity and maximum curvature and low HSI-b values. Mature *N. tetricus* preferably live on relatively deep and exposed reef-dominated habitats, while juveniles occur in large numbers on shallow seaweed-dominated reefs (Shepherd & Clarkson 2001). This general habitat association is reflected by the strong correlations with low values of Euclidean distance to nearest reef and bathymetry, and high values of rugosity and maximum curvature in the models. As expected, it was found that models predicted the largest areas of highly suitable habitat to be shallow reef areas. These regions are dominated by large stands of kelp (mainly *Ecklonia radiata*; Ierodiaconou et al. 2007a), and perhaps reflect the habitat use of juveniles. Models also predicted smaller patches of highly suitable habitat in deeper regions at the northern end of the site, and may reflect more isolated adult populations (Figure 3). This is only speculative as models did not take into account different size-class fish. This is because the towed-video system utilised here is not capable of providing accurate length measurements. However, given adequate data, building similar models based on different size-class fish may enable the detection of differences in habitat uses throughout the life history of *N. tetricus.*

2.4.4 Spatial patterns of *Notolabrus tetricus* habitat suitability

The decline of many species has been linked directly to habitat loss and fragmentation (Fahrig 2003). Conservation strategies now frequently consider not only the amounts of habitat that must be retained, but also the spatial configurations of habitat across landscapes of concern (Pulliam et al. 1992, O'Neill et al. 1996). By generating spatially-continuous models of habitat suitability and applying a suite of landscape pattern indices, the research presented here is able to provide management agencies with accurate information that not only indicates where habitat suitability patches are located, but also an indication of size, variability, isolation, position, spatial arrangement and boundary characteristics (McGarigal & Marks 1994). It was found that there were minimal differences in predicted areas of the habitat suitability classes represented inside the MNP compared to the adjacent unprotected region. However, when the spatial patterns of habitat suitability classes were compared a few significant differences were observed. Unsuitable patches exhibited more complex shapes inside the MNP, while both unsuitable and highly suitable habitat classes were more unevenly distributed inside the MNP. It is not surprising that only a few differences were observed in the spatial characteristics in habitat suitability classes between the two regions. Recent habitat mapping studies along the Victorian coastline have revealed complex, spatially heterogeneous reef systems that support a diversity of benthic habitats (Ierodiaconou et al. 2007b, Holmes et al. 2008, Rattray et al. 2009). Intuitively, with *N. tetricus* showing such strong associations with seafloor structure, it is likely that the adjacent seafloor regions that exhibit

similar heterogeneous seafloor characteristics reflect this in terms of habitat suitability.

2.5 Conclusions

The present research highlighted the benefits of having spatially-continuous layers of environmental data rather than the sparsely-located categorical or linear descriptors relied on by earlier studies (Friedlander & Parrish 1998, Babcock et al. 1999, Westera et al. 2003). By providing spatially-continuous coverage across an entire site this research enabled the prediction of habitat suitability based on video occurrence records and variables derived from MBES over large regions of seafloor. Through these models, the importance of spatially-continuous variables and the influence of spatial scale on the prediction of habitat suitability for *N. tetricus* were determined. Furthermore, the research enabled the quantification of spatial arrangement and representation of habitat suitability to provide marine managers with a level of information that has historically been limited to coarse spatial resolutions. Practitioners should remember, however, that these models predict a species potential habitat suitability, or distribution, and should not replace but compliment empirical research.

Comparing presence-only algorithms for predicting habitat suitability for marine demersal fishes[3]

[3] The research in this chapter has been published as Monk, J. Ierodiaconou, D. Versace, V. L., Bellgrove, A., Harvey, E., Rattray, A., Laurenson, L., and Quinn G.P. (2010). Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. *Marine Ecology Progress Series.* **420**: 157-174.

3.1 Introduction

Understanding species' distribution and associated measures of habitat suitability are fundamental elements of any planning or management program (Franklin 1995, Pearce & Ferrier 2001). In the terrestrial context, models of species distribution have long been recognised as cost-effective and powerful tools to estimate species' occurrence across a landscape where limited direct observations exist (Pearce & Ferrier 2001, Ferrier et al. 2002a, Ferrier et al. 2002b, Zaniewski et al. 2002, Elith et al. 2006, Guisan et al. 2006, Hirzel et al. 2006, Braunisch et al. 2008). These models are predicated on the assumption that the spatial variation in environmental factors (e.g. topography) used by a species influence (either directly or indirectly) its geographic distribution (Guisan & Zimmermann 2000). It is only recently that predictive species distribution models have been used to predict species' occurrence in management of the marine environment. These include applications to identify high conservation priority areas (Cañadas et al. 2005), assess the spatial patterns of suitable habitat within protected areas (Chapter 2), predict sites at risk of invasion by exotic species (Compton et al. 2010) and investigate the distribution of coral disease (Williams et al. 2010a).

Parallel to the development and application of species distribution modelling in the marine environment, is the increasing access to MBES technology and underwater video systems. As mentioned in Chapter 2 section 2.1, these technological developments make it possible to apply a variety of terrain-analysis techniques that form predictor variable datasets for input into models (see Wilson et al. 2007).

While traditionally used for assessing sessile species, underwater video systems such as drop video, towed/drift video and remotely operated vehicles (ROV) are increasingly being used as cost-effective, non-destructive, methods for assessing marine fish species distributions (Morrison & Carbines 2006, Anderson & Yoklavich 2007, Williams et al. 2010b). These video-based survey methods have significant advantages over traditional methods (e.g. SCUBA divers) in collecting fish occurrence data. They are capable of being deployed at depths and times that are dangerous for divers (Assis et al. 2007), provide a permanent record of survey (Watson et al. 2005), afford accurate positioning when coupled with differential GPS and acoustic positioning, enable high replication and, in the case of drift/towed and ROV, capture transitions between different habitat types (Spencer et al. 2005). However, video-based survey methods also have a number of disadvantages, including restricted field of view and the need for high water clarity that result issues surrounding accurate detection and species identification (Murphy & Jenkins 2010). Mueller et al. (2006), for example, estimated that a stationary underwater video camera was able to detect around 45-75 % of large (i.e. 30-50 cm) trout in water with turbidity levels equivalent to those encountered in shallow temperate marine waters (i.e. 0-4 Nephelometric Turbidity Units; NTU). Additionally, towed-video systems are constantly moving (i.e. up, down and side-to-side) and are often 'flown' over highly rugose reef systems covered in a dense canopy forming macroalgae. These factors combined have the potential to underestimate species' distributions because fish may simply be hiding under or camouflaged within the canopy and reef. Consequently, observations of demersal fishes derived from such towed-video techniques may

lead to the inclusion of 'false absences' (i.e. a failure of the survey to detect the species when it is actually present). Incorporation of such 'false absences' has the potential to bias model predictions (Hirzel et al. 2001).

Integrating towed-video data capture methods and MBES in a presence-only predictive modelling framework has the potential to improve our understanding of the fine-scale spatial ecology and distribution of many marine fish species, while avoiding issues of 'false' absences. Presence-only models have two unique attributes that make them potentially more useful than presence/absence models for estimating habitat suitability for marine demersal fishes based on towed-video observations. First, presence-only models do not require the explicit constraints indicated by absence data. Considering the issues surrounding accurately surveying fish assemblages using towed-video, it would be inappropriate to treat localities without an observed presence as unsuitable. Instead, presence-only approaches are based on constructing a model of a species' niche from locational records. This modelled niche/habitat signature can then be used to predict distribution, or suitability, within the available environment. Second, most presence-only models are designed to function well even when limited to very small occurrence datasets (Engler et al. 2004, Hernandez et al. 2006), meaning that useful models of habitat suitability can often be developed from very few presence locations (i.e. ~ 30 observations). This feature is particularly important because of the often small sample sizes obtained from marine fish surveys (Langlois et al. 2010).

There is a broad array of quantitative approaches available to model species' habitat suitability based on presence-only datasets (e.g. Nix 1986, Stockwell &

Noble 1992, Robertson et al. 2001, Hirzel et al. 2002, Phillips et al. 2006, Li & Hilbert 2008). Consequently, researchers are faced with the difficulty of selecting between numerous presence-only modelling approaches. Relatively few studies have compared more than three different methods on the same data, and the majority of these have focused on terrestrial, freshwater or simulated datasets (Elith & Burgman 2002, Ferrier et al. 2002b, Olden & Jackson 2002, Farber & Kadmon 2003, Loiselle et al. 2003, Brotons et al. 2004, Segurado & Araújo 2004, Elith et al. 2006, Tsoar et al. 2007). The effective application of presence-only modelling methods in the marine environment, however, has received less attention, specifically in relation to demersal fish species. Only two studies exist that have compared presence-only algorithms for marine organisms (MacLeod et al. 2008, Tittensor et al. 2009). Macleod et al. (2008) used data on the occurrence of harbour porpoises to compare the predictive abilities of one presence/absence approach (generalised linear modelling) and three presence-only approaches (principal component analysis-based approach, genetic algorithm for rule-set prediction and ENFA). They concluded that presence-only approaches can produce models of habitat suitability of marine species that are significantly better than random and exhibit comparable performances to presence/absence modelling approaches (MacLeod et al. 2008). Similarly, Tittensor et al. (2009) compared MAXENT and ENFA to model the global distribution of suitable habitat for scleractinia stony corals on seamounts. They concluded that MAXENT consistently outperformed ENFA.

In the marine environment, studies have predominantly focused on how variations in predictor variables (e.g. seafloor characteristics such as

bathymetry or rugosity) affect the ability of the models to predict species distributions (e.g. Pittman et al. 2009). In the terrestrial context, in addition to the predictor variables, the influence of response variables (i.e. the ecological characteristics of the species' occurrence data) has been more widely investigated (e.g. Araújo & Williams 2000, Pearce & Ferrier 2000, Manel et al. 2001, Pearce et al. 2001, Segurado & Araújo 2004, Sérgio et al. 2007). An organism with a narrow range of environmental requirements (i.e. clearly definable niche) is likely to return a better performing model in terms of model diagnostics (e.g. model performance measures such as kappa and AUC; Pearce & Ferrier 2001, Brotons et al. 2004, Segurado & Araújo 2004, Elith et al. 2006). In contrast, it may be more difficult to define the habitat characteristics of an organism with a much wider range of environmental tolerances as there are more combinations of biophysical factors that could potentially be used as habitat.

In this study, the relative performance of presence-only modelling approaches to predict habitat suitability of marine fish taxa using remotely-sensed occurrence and high-resolution MBES-derived seafloor datasets was compared. Specifically, data on five demersal fish taxa and two measures of model performance were used to compare 10 different modelling algorithms: BIOCLIM, DOMAIN, ENFA (using the seven available algorithms in the software) and MAXENT. Previous evidence indicates differences in model performance may depend on the species range and environmental niches (Pearce & Ferrier 2000, Brotons et al. 2004, Segurado & Araújo 2004, Elith et al. 2006). How variation in these factors influence model performance was also investigated. Finally, the key seafloor variables that influence the spatial

distribution were identified and discussed in terms of the known ecology of each taxon investigated.

3.2 Materials and methods

3.2.1 Study site

The research presented in this chapter was undertaken at the Discovery Bay study site. Details of this study location are presented in Chapter 2 section 2.2.1.

3.2.2 Fish occurrence data for model training and testing

The fish occurrence datasets used in this chapter are derived from the same demersal fish surveying program (i.e. towed-video) outlined in Chapter 2 section 2.3.3.

More than 7300 individual fish, representing 40 species, were observed (Appendix 1). Some video frames included multiple individuals of the same species resulting in a total of 1648 observational events. From these observations, occurrence data for the five most commonly observed demersal fish taxa were used (Table 6). For each taxon, 10 random partitions of the occurrence localities were made. Each partition was created by randomly selecting 75 % of the occurrence localities as training data, with the remaining 25 % reserved for testing the resulting models (Table 6). Ten random partitions were used to assess the average performance of the algorithms, and to allow for statistical testing of observed differences in performance for each taxon.

Table 6. Partitioning of occurrence data into training and test localities.

Taxon	Common Name	Training	Testing	Total
Caesioperca spp.	Perch	710	237	946
Cheilodactylus nigripes	Magpie morwong	25	8	33
Notolabrus tetricus	Blue-throat wrasse	47	16	62
Pempheris multiradiata	Common bullseye	38	13	50
Pseudolabrus psittaculus	Rosy wrasse	283	94	377

3.2.3 MBES survey and derived seafloor characteristics used in model construction

This chapter used the same processed MBES bathymetry and backscatter datasets as detailed in Chapter 2 section 2.3.2. However, to simplify comparisons between models across the five focal fish taxa only fine-scale MBES-derived variables (i.e. variables calculated based using 3 × 3 cell-analysis window) were used (Table 1; Chapter 2 section 2.3.2). As in Chapter 2, to reduce the likelihood of model over-fitting, a covariance matrix and correlation tree, using a correlation coefficient threshold of 0.5 (Hirzel et al. 2002, Galparsoro et al. 2009), were used to reduce the 13 variables to the eight least correlated (Table 7). Consequently, bathymetry, benthic position index (BPI), eastness, Euclidean distance to nearest reef, hue-saturation-intensity-blue (HSB-b; backscatter derivative), maximum curvature, northness and rugosity were retained for model construction (Figure 5; Table 1; Chapter 2 section 2.3.2). These variables were chosen as they captured the main seafloor characteristics and many of them are known to be important determinants of demersal fish habitat (e.g. rugosity- Friedlander & Parrish 1998, bathymetric variance- Pittman et al. 2007a, distance to nearest reef- Wedding et al. 2008, slope- Moore et al. 2009). Again, the analysis was limited to MBES-derived seafloor characteristics because oceanographic variables are not available at the fine-scale resolution of the MBES datasets (2.5 × 2.5 m). In addition, because

of the relatively small spatial scale of the study area it was expected that there would be little variation in oceanographic characteristics (e.g. temperature).

Table 7. Correlation matrix used to assess independence between seafloor variables. A 0.5 threshold was applied to determine the least correlated variables that were retained for model construction (shown in bold).

	Backscatter	Bathymetry	BPI	Complexity	Eastness	Euclidean distance to nearest reef	HSI-b	HSI-g	HSI-r	Maximum curvature	Northness	Rugosity
Bathymetry	-0.894											
BPI	-0.022	0.043										
Complexity	0.223	-0.168	0.134									
Eastness	0.289	-0.279	0.06	0.296								
Euclidean distance to nearest reef	-0.015	-0.125	-0.138	-0.607	-0.262							
HSI-b	0.152	0.036	0.048	0.186	0.138	-0.363						
HSI-g	-0.769	0.749	0.043	-0.114	-0.208	-0.143	-0.205					
HSI-r	0.59	-0.622	-0.049	0.027	0.131	0.246	-0.319	-0.683				
Maximum curvature	-0.023	0.057	0.279	0.331	0.089	-0.254	0.089	0.038	-0.091			
Northness	-0.058	0.06	0.008	-0.034	-0.089	-0.025	-0.083	0.04	0.035	-0.014		
Rugosity	-0.038	0.086	0.128	0.341	0.071	-0.266	0.111	0.051	-0.127	0.461	-0.023	
Slope	0.115	-0.049	0.106	0.679	0.141	-0.515	0.221	-0.038	-0.094	0.345	-0.025	0.375

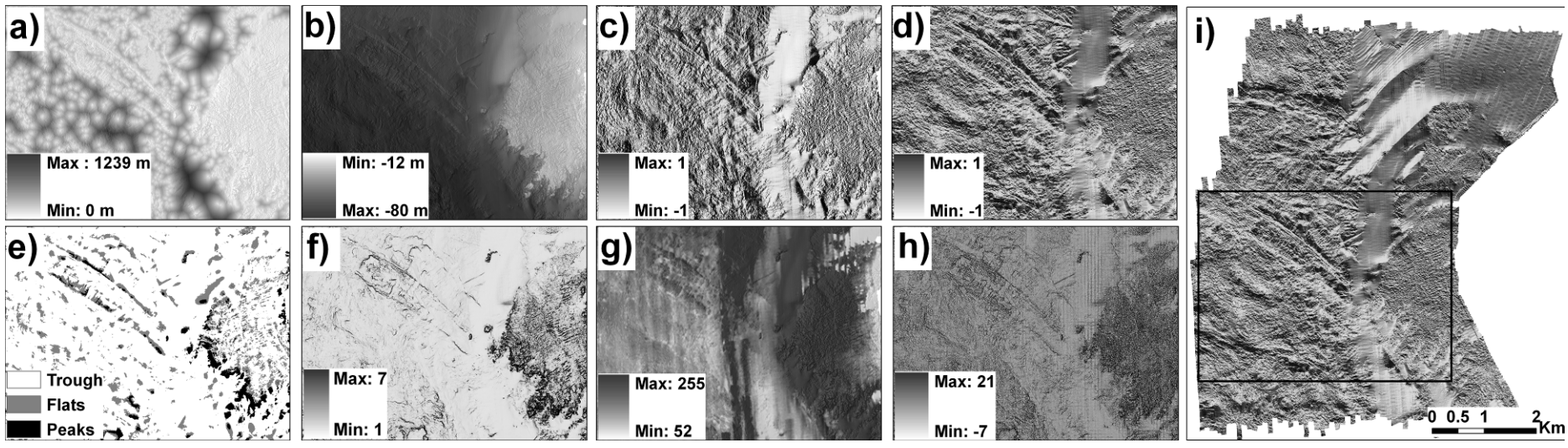

Figure 5. Zoomed examples of the eight variables used in model construction. Darker shading indicates high values. a) Euclidean distance to nearest reef. b) bathymetry. c) eastness. d) northness. e) benthic position index. f) rugosity. g) hue-saturation-intensity-blue. h) maximum curvature. i) hillshade of study area showing extent of zoomed examples.

3.2.4 Modelling approaches

Four distinct modelling approaches were used; however ENFA outcomes were converted into geographic-space using all seven available algorithms, resulting in 10 different models for each of the five fish taxa. Each algorithm was run on each of the 10 fish-occurrence data partitions, resulting in 500 model runs. Predictive models used were; BIOCLIM (Busby 1986, Nix 1986), DOMAIN (Carpenter et al. 1993), ENFA (using all seven available algorithms; Hirzel et al. 2002, Braunisch et al. 2008), and MAXENT (Phillips et al. 2006). All of these methods are based on the concept of the ecological niche (Hutchinson 1957). Each method uses mathematical algorithms to define the ecological niche of the focal taxon based on the distribution of the occurrence records in multidimensional environmental-space. Once this niche is defined, it is projected into geographic-space to produce a predictive map of suitable habitat.

Both BIOCLIM and DOMAIN were run through DIVA-GIS (Hijmans et al. 2005, Hijmans & Graham 2006). The BIOCLIM predicts suitable conditions in a 'bioclimatic envelope', consisting of a rectilinear region in environmental-space representing the range (or some percentage thereof) of observed presence values in each environmental dimension. This envelope specifies the model in terms of percentiles or upper and lower tolerances of variables, and does not allow for regions of absence (i.e. 'holes') within the envelope. In this study a percentile range of 95 % (excluding 2.5 % of the values either side of the rectilinear box in environmental-space) was used. Similarly, DOMAIN (Carpenter et al. 1993) uses the Gower metric, a distance measure that standardises each variable by its range over all occurrence observations to

equalise the contribution of all variables. A predicted suitability index is given by computing the minimum distance in environmental-space to any occurrence record.

The ENFA was conducted through Biomapper 4 software (Hirzel et al. 2007). It is similar to principal components analysis, involving a linear transformation of the environmental-space into orthogonal 'marginality' and 'specialisation' factors. Environmental suitability is then modelled by seven different distance-based algorithms in the transformed-space (distance geometric mean, distance harmonic mean, medians, area-adjusted median, median + extremum, area-adjusted median + extremum and minimum distance). These algorithms make the assumptions that, on all ENFA factors, either the geometric mean, harmonic mean, median, or minimum distance of the species distribution offers the optimal habitat conditions, taking into account the density of observations in environmental-space. By contrast, the area-adjusted median algorithm (Ma) assumes that, for all ENFA factors, the optimal habitat is the median of the habitat use to habitat availability ratio (Braunisch et al. 2008). The median + extremum algorithm (Me) assumes that the optimal habitat suitability on the marginality factor is either the lowest or highest value, whereas on all specialisation factors it is the median (as in the M algorithm; Braunisch et al. 2008). Finally, the area-adjusted median + extremum algorithm (Mae) is a combination of the Ma and Me algorithms. For all ENFA algorithms, across the five fish taxa, three factors were retained based on 'MacArthurs broken-stick' rule (MacArthur 1957) that was explained in Chapter 2, section 2.4.4.

MAXENT uses the maximum entropy method for modelling species geographic distributions with presence-only data (Phillips et al. 2006). The MAXENT is a general-purpose, machine-learning method with a simple and precise mathematical formulation, and it has a number of aspects that make it well-suited for species distribution modelling (see Phillips et al. 2006). Models were trained using default settings; convergence threshold (0.00001), maximum iterations (1000), auto features, regularisation multiplier (r = 1) and background points (10 000).

3.2.5 Model testing

Using the occurrence datasets that were set aside for model testing, model performance was evaluated using two methods: the threshold-independent AUC of the ROC (Receiver Operating Characteristic; Fielding & Bell 1997) and threshold-dependent kappa statistic (Cohen 1960).

The ROC plots sensitivity (the fraction of occurrence records that are classified as presence) against 1 - specificity (the portion of absences points that are classified as absent) for all possible thresholds. A curve that maximises sensitivity for low values of the false-positive fraction is considered a good model and is quantified by calculating the AUC. An AUC value of 0.5 implies the model predicts species occurrence no better than random and a value of 1.0 implies perfect prediction (Fielding & Bell 1997). While this technique was initially applied to presence/absence methods, it can be adapted to evaluate presence-only models (Wiley et al. 2003, Phillips et al. 2006). Plotting sensitivity against a random sample of background locations is sufficient to define an ROC curve (Wiley et al. 2003, Phillips et al. 2006). The ROC plot

method has an advantage over confusion matrix-derived evaluation methods (for examples see; Fielding & Bell 1997) because it does not require the arbitrary selection of a threshold above which a prediction is considered positive; a procedure that can bias evaluations (Fielding & Bell 1997). A 1:1 ratio of presence/background point was used (i.e. if there were 237 occurrences, then 237 background points were randomly generated). For each individual taxon, these background points were randomly generated along transects where no fish taxa were observed. The AUC derived from the ROC plot of this study can be interpreted as a measure of the ability of the algorithm to discriminate between a suitable environmental condition and a random analysis pixel (background), rather than between suitable and unsuitable conditions, as an AUC developed with measured absences is interpreted (Phillips et al. 2006). The ROC curves and the AUC values were calculated in DIVA-GIS.

Although the continuous map of the probability of presence produced by distribution models is itself useful for many conservation applications (e.g. Wilson et al. 2005) it is often converted into a presence/absence map. Despite threshold-independent measures of model performance being widely preferred, such as the AUC, the reliability of these methods has recently been questioned (Lobo et al. 2008). Therefore, to enable a thorough evaluation of the models the threshold-dependent kappa statistic was also selected (Cohen 1960). The kappa statistic assesses the extent to which a model predicts occurrence at a rate higher than expected by chance. The results vary between 1.0 for perfect agreement and 0 for random agreement. The kappa-maximised threshold was run in DIVA-GIS. This threshold method calculates kappa scores for 100

threshold values (in 0.01 increments) and the one which provides maximum kappa is accepted as the threshold (Thuiller 2003). When multiple thresholds had the same kappa value, the mean threshold value was selected.

To compare the influence of the modelling algorithm on model performance (as measured by AUC and kappa), a permutational multivariate analysis of variance (PERMANOVA) was used (Anderson 2001). PERMANOVA was run with 999 permutations of the residuals under a reduced model. Post-hoc pairwise tests (t-tests) were conducted, again using 9999 permutations. All analyses were tested at $\alpha = 0.05$. PERMANOVA was conducted using PERMANOVA+ add-on in the statistical package PRIMER-E (Clarke & Gorley 2006, Anderson et al. 2008).

3.2.6 Influence of species' spatial range and environmental niches on modelling performance

When examining model outputs of marine species distribution much of the emphasis is on the influence of explanatory variables (e.g. Moore et al. 2009). However, the influence of species' spatial range and environmental niches is less often considered in the marine environment. To address this imbalance a series of orthogonal contrasts were carried out on the modelled distributions of habitat suitability generated in this study. The rationale of these analyses was the assumption that the modelled distributions of habitat suitability of taxa with wider spatial range and environmental niches would be characterised by lower performance (in terms of kappa and AUC) relative to taxa that exhibit a narrower range and niche. The spatial range and environmental niches were determined using three measures: area of occupancy (AOO), marginality and

tolerance. AOO is an estimate of geographic-range size that is actually occupied by a taxon (Gaston 1996). It was calculated by summing the number of 2.5 × 2.5 m grid cells where a fish taxon was observed. Marginality is the difference between the species optimum habitat and the mean environmental conditions in the study area. This is therefore representative of the species' ecological niche position. Tolerance describes the species' niche breadth by comparing the variability in the environmental conditions where the species occurs to the range of environmental conditions in the study area. These characteristics were calculated using BIOMAPPER (Hirzel et al. 2007).

Six sets of Helmert contrasts (Field 2000) were used to test: (1) the influence of marginality on mean kappa; (2) the influence of marginality on mean AUC; (3) the influence of tolerance on mean kappa; (4) influence of tolerance on mean AUC; (5) the influence of AOO on mean kappa; and (6) the influence of AOO on mean AUC. For the design of these contrasts the five fish taxa were used to provide the measures of AOO, marginality and tolerance, while model diagnostics of the ten algorithms were used to provide measures of mean kappa and mean AUC. Using a series of t-tests, orthogonal contrasts provide an efficient way to test specific hypothesis while maintaining strict control over Type I error rate by reducing the amount of pairwise comparisons when compared to *post-hoc* testing (Field 2000). Homogeneity of variance in the dependent variables was assessed using Levene's test and normal distribution was assessed using Kolmogorov-Smirnov test (Field 2000).

3.2.7 The most important variables for characterisation of suitable habitat for demersal fishes

Using the best model run (i.e. MAXENT) for each fish taxon, a jackknife analysis of the regularised gain (a statistic that measures how well a variable distinguishes localities where taxa occur from the total area under study) with the training occurrence data was used. The variables with regularised gains ≥ 0.1 were considered important. To assess how the variation in these variables influenced suitable habitat, response curves (log contribution to prediction) were used. These curves show how prediction of suitable habitat changes as each seafloor variable is varied, keeping the remaining seven variables at their average sample value. Predictor variable values with positive log contribution (i.e. > 0) indicate higher habitat suitability.

3.3 Results

3.3.1 Comparison of model performances

Generally, MAXENT was found to be the best performing model (Figure 6). Subtle differences between each fish taxon, however, were observed (Figure 6). Pairwise comparisons based on kappa and AUC indicated that MAXENT was significantly better than all other algorithms for *N. tetricus* and *P. psittaculus* (pairwise tests: $P < 0.05$). Similarly, pairwise comparisons based on kappa and AUC indicated that MAXENT was significantly better than all other algorithms with the exception of DOMAIN for *Caesioperca* spp. and *C. nigripes*; where MAXENT was better but not significantly so. Results for *P. multiradiata* were less defined. Pairwise comparisons based on AUC indicated that MAXENT was significantly better than ENFA-Min, but was not significantly different to all other algorithms (Figure 6h). Pairwise results from

kappa indicated, however, that MAXENT was significantly better than all other algorithms with exception to ENFA-GM (Figure 6g). In addition to differences in model performance, considerable variation in the spatial distributions projected by the different algorithms was observed (Figure 7 shows examples of the highest and lowest performing algorithms for the five demersal fishes investigated).

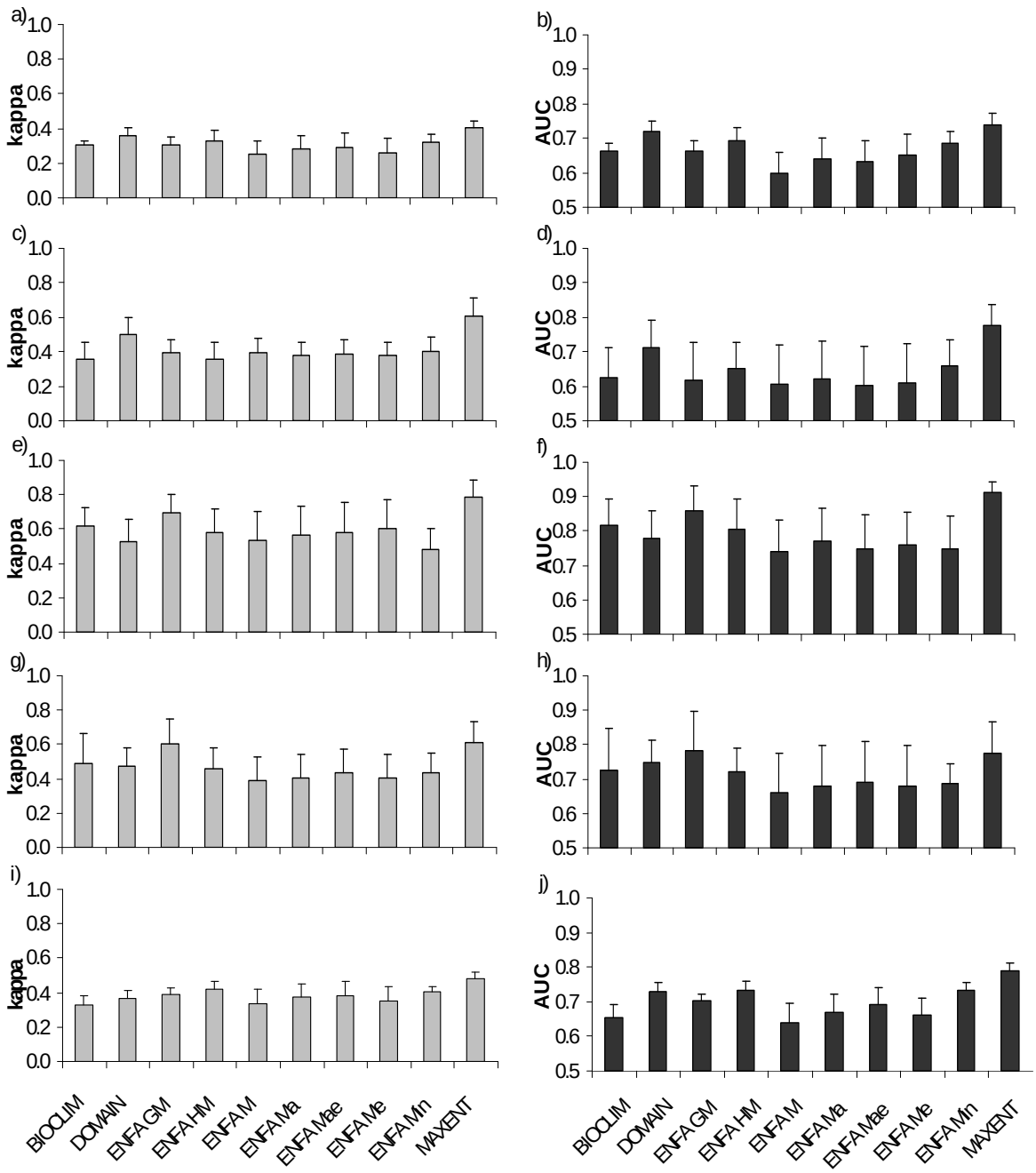

Figure 6. Model performance for *Caesioperca* spp.: a) kappa; pseudo-$F_{9,81}$ = 8.95, $P < 0.001$, b) AUC; pseudo-$F_{9,81}$ = 13.93, $P < 0.001$, *Cheilodactylus nigripes*: c) kappa; pseudo-$F_{9,81}$ = 7.64, $P < 0.001$, d) AUC; pseudo-$F_{9,81}$ = 4.57, $P < 0.001$, *Notolabrus tetricus*: e) kappa; pseudo-$F_{9,81}$ = 6.85, $P < 0.001$, f) AUC; pseudo-$F_{9,81}$ = 6.07, $P < 0.001$, *Pempheris multiradiata*: g) kappa; pseudo-$F_{9,81}$ = 6.63, $P < 0.001$, h) AUC; pseudo-$F_{9,81}$ = 3.41, $P < 0.001$, and *Pseudolabrus psittaculus*: i) kappa; pseudo-$F_{9,81}$ = 9.74, $P < 0.001$, j) AUC; pseudo-$F_{9,81}$ = 17.10, $P < 0.001$ produced with BIOCLIM, DOMAIN, ENFA-M, ENFA-Ma, ENFA-Mae, ENFA-Me, ENFA-GM, ENFA-HM, ENFA-Min and MAXENT. Kappa is shown in the left column represented by the light grey bars, while AUC of ROC is presented in the right column by the dark grey bars. Error bars indicate Standard Deviation.

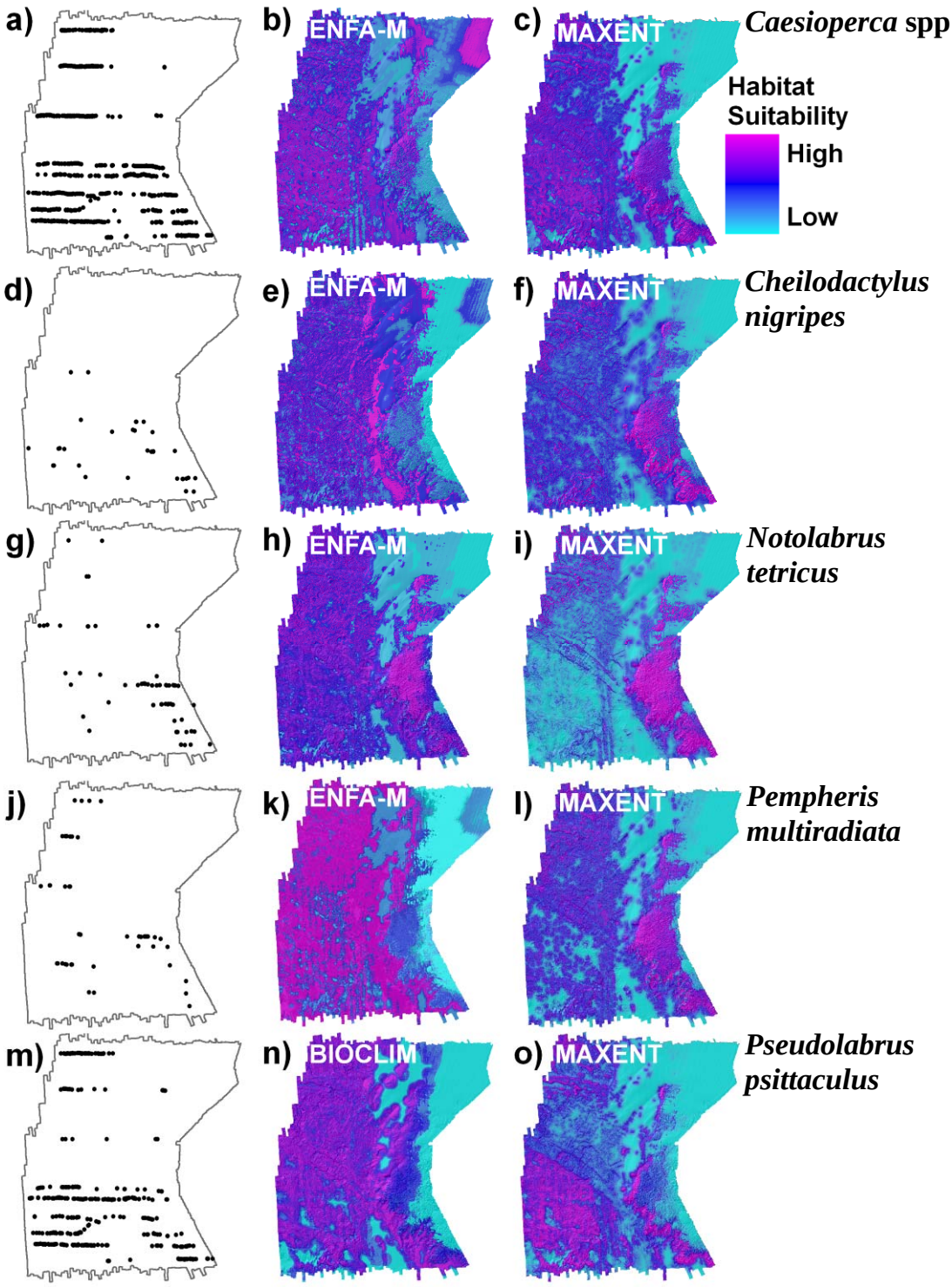

Figure 7. Examples of the predicted habitat suitability for the lowest (middle column) and highest (right column) performing models. Left column shows spatial arrangement of occurrences for each taxon.

3.3.2 Influence of species spatial range and environmental niches on modelling performance

Helmert contrasts indicated that as marginality increased, there was a trend of increasing mean kappa and AUC (Table 8). There were no discernable trends when examining the influence of niche breadth (tolerance) or species spatial range (AOO) on mean AUC and mean kappa (Table 8).

Table 8. Summary of Helmert contrasts used in determining influence of species range and environmental niches on model performance. Significant contrasts are shown in bold.

Contrast Description	Contrast	*t*-statistic (45 *df*)	Significance (1-tailed)
Marginality influence on mean kappa	1	**6.298**	**<0.001**
	2	**4.320**	**<0.001**
	3	1.292	0.105
	4	**5.818**	**<0.001**
Marginality influence on mean AUC	1	**2.844**	**0.004**
	2	1.174	0.123
	3	0.455	0.326
	4	**6.630**	**<0.001**
Tolerance influence on mean kappa	1	1.041	0.152
	2	-1.579	0.061
	3	**-9.209**	**<0.001**
	4	**-2.333**	**0.012**
Tolerance influence on mean AUC	1	**3.944**	**<0.001**
	2	0.322	0.375
	3	**-5.969**	**<0.001**
	4	-1.530	0.067
AOO influence on mean kappa	1	1.041	0.152
	2	-1.579	0.061
	3	**-9.209**	**<0.001**
	4	**-2.333**	**0.012**
AOO influence on mean AUC	1	**3.994**	**<0.001**
	2	0.322	0.375
	3	**-5.969**	**<0.001**
	4	-1.530	0.065

3.3.3 The most important variables for characterisation of suitable habitat for demersal fishes

Variable importance varied for the five fish taxa based on the best performing MAXENT model run (Table 9). It is acknowledged that the fitted response curves (log contribution to prediction; Figure 8) are graphical descriptions of how the different variables influence habitat suitability and do not describe the environmental limits of the taxa (Ysebaert et al. 2002).

For *Caesioperca* spp., the areas surrounding sheer drop-offs along the south-eastern region of the study area were predicted to be the most suitable habitat (Figure 7b). Areas of fragmented highly suitable habitat were also predicted throughout the deeper (> 30 m) regions of the study area (Figure 7b). The jackknife test of variable importance showed that bathymetry, Euclidean distance to nearest reef, HSI-b and rugosity were important for determining suitable habitat for *Caesioperca* spp. (Table 9). Response curves of these variables indicated that suitable habitat for *Caesioperca* spp. decreased with the increase in distance from reef (Figure 8d). Similar patterns were observed for bathymetry and HSI-b variables (Figures 8a and 8e). The response curves showed that as these values increased so did habitat suitability of *Caesioperca* spp. However, the curves showed this trend up to a certain point (~ 32 m depth and ~ 80 HSI-b) and beyond that the habitat suitability plateaued. Variation in rugosity, however, had only a small influence on suitability; with high values (~ 2) being most important (Figure 8h).

Regions of highest habitat suitability for *Cheilodactylus nigripes* were predicted to be the deeper (> 30 m) fringing reefs at the base of the drop-offs

(Figure 7d). The most important seafloor variables for defining suitable habitat were rugosity, Euclidean distance to nearest reef, HSI-b and maximum curvature (Table 9). Examination of the response curves for these variables showed that areas delineated by depths around 40 m, close to reef, with low rugosity, intermediate maximum curvature and high HSI-b values were the most suitable habitats for this species (Figure 8).

The shallow (< 20 m) highly complex reef structures in the eastern region of the study site were found to have the highest habitat suitability for *Notolabrus tetricus* (Figure 7f). Some fragmented highly suitable habitat was also predicted throughout the deeper (> 50 m) regions in the north-west of the study site. Among seafloor variables, Euclidean distance to nearest reef, rugosity, bathymetry, HSI-b, BPI and maximum curvature were selected as important variables for defining habitat suitability for this species (Table 9). Examination of the response curves for these variables highlighted regions that were delineated by close proximity to reef, high rugosity, high HSI-b, either highly positive or negative BPI (i.e. peaks or troughs), intermediate maximum curvature, around 20 m water depth was the most suitable habitat for *N. tetricus* (Figure 8).

The predicted distribution of suitable habitat for *Pempheris multiradiata* showed similar patterns to that of *N. tetricus*, albeit more widespread in the deeper regions of the study area (Figure 7h). Several seafloor variables defined the predicted distribution of suitable habitat for *P. multiradiata*; Euclidean distance to nearest reef, maximum curvature, rugosity, HSI-b, northness and eastness (Table 9). Response curves of these variables indicated that, in

general, south-east facing (i.e. northness values ~ - 0.8 and eastness values ~ 0.8) regions close to reef, with low rugosity, moderate maximum curvature and high HSI-b values were the best indicators for suitable habitat for this species (Figure 8).

Pseudolabrus psittaculus was predicted by MAXENT to have similar patterns to *C. nigripes*, with highly suitable habitat being confined to the deeper regions of the study area (Figure 7j). The jackknife test of variable importance showed that bathymetry, rugosity, HSI-b, maximum curvature, Euclidean distance to nearest reef and BPI were the primary determinants in characterising the habitat suitability for this species (Table 9). Response curves of these seafloor variables indicated that the highest habitat suitability for *P. psittaculus* was observed with the increase in depth (Figure 8a). However, the curves showed this trend up to certain point (~ 31 m depth) and beyond that the habitat suitability plateaued until 73 m after-which there was a sharp decline. The response curve for rugosity (Figure 8h) showed a similar trend to that of *Caesioperca* spp. with only a slight increase in habitat suitability of *P. psittaculus* around high rugosity values (~ 2). Lower values of HSI-b were associated with most suitable habitat for *P. psittaculus* (Figure 8e). Increased maximum curvature decreased habitat suitability (Figure 8f). Euclidean distance to nearest reef showed the same trend as all other taxa, with diminishing suitability increasing with distance from reef (Figure 8d). Albeit more pronounced than for *N. tetricus,* BPI showed a decrease in suitable habitat around BPI values of 0 for *P. psittaculus* (Figure 8b).

Table 9. Relative variable importance as measured by regularised gain for each fish taxon. Variables contributing most to predictions are shown in bold.

Taxon	Variable	Regularised gain
Caesioperca spp.	Bathymetry	**0.16**
	BPI	0.06
	Eastness	0.05
	Euclidean distance to nearest reef	**0.13**
	HSI-b	**0.13**
	Max. curvature	0.08
	Northness	0.03
	Rugosity	0**.11**
Cheilodactylus nigripes	Bathymetry	0.06
	BPI	0.09
	Eastness	**0.10**
	Euclidean distance to nearest reef	**0.27**
	HSI-b	**0.13**
	Max. curvature	**0.10**
	Northness	0.05
	Rugosity	**0.39**
Notolabrus tetricus	Bathymetry	**0.39**
	BPI	**0.15**
	Eastness	0.03
	Euclidean distance to nearest reef	**1.00**
	HSI-b	**0.29**
	Max. curvature	**0.11**
	Northness	0.03
	Rugosity	**0.89**
Pempheris multiradiata	Bathymetry	0.05
	BPI	0.02
	Eastness	**0.10**
	Euclidean distance to nearest reef	**0.35**
	HSI-b	**0.14**
	Max. curvature	**0.19**
	Northness	**0.13**
	Rugosity	**0.17**
Pseudolabrus psittaculus	Bathymetry	**0.24**
	BPI	**0.11**
	Eastness	0.05
	Euclidean distance to nearest reef	**0.14**
	HSI-b	**0.17**
	Max. curvature	**0.15**
	Northness	0.03
	Rugosity	**0.17**

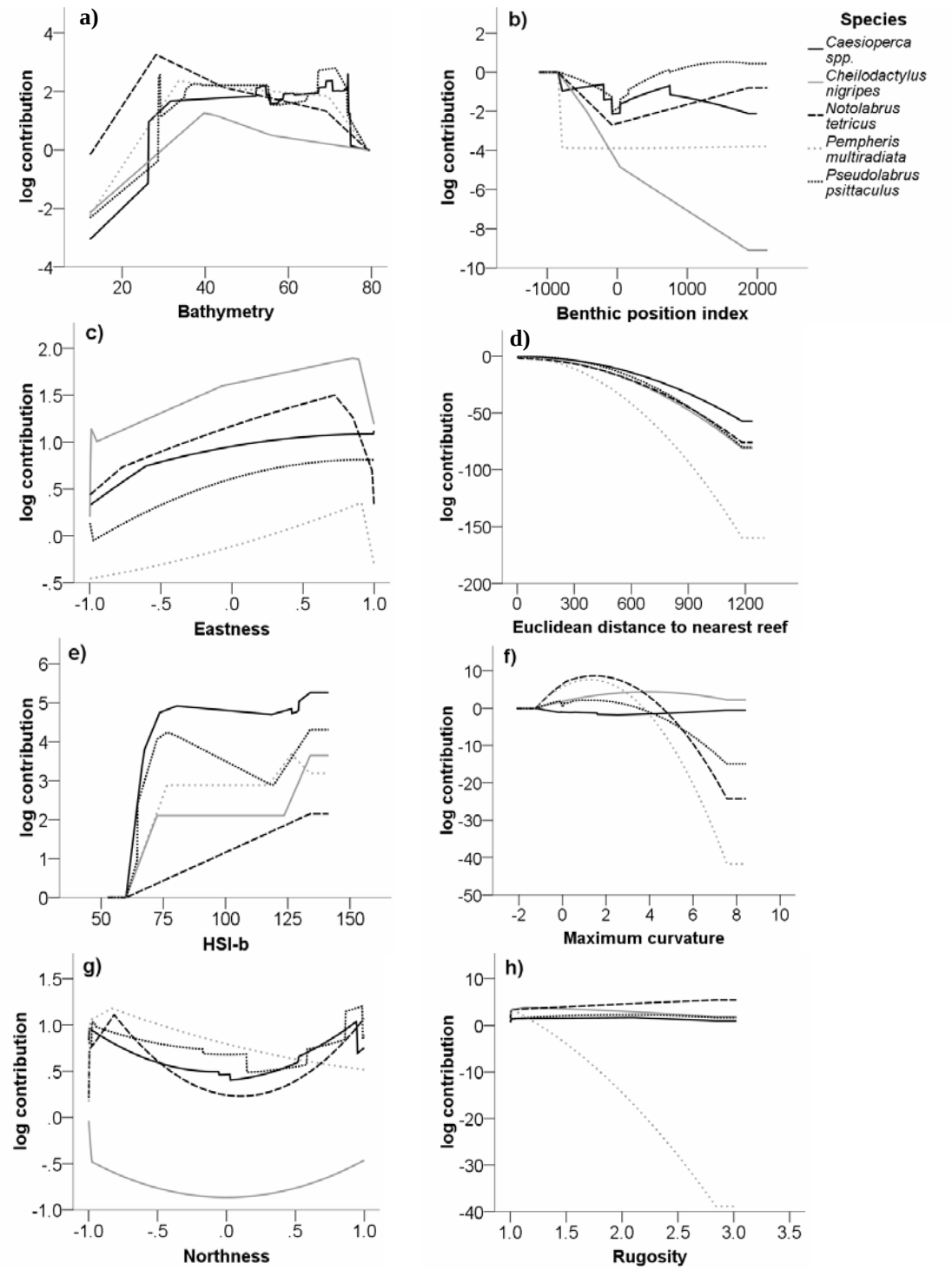

Figure 8. Response curves (log contribution to prediction) for each predictor variable as generated by the best MAXENT model run for the five demersal fish taxa investigated. Lines indicate difference taxa; Caesioperca spp. solid black, Cheilodactylus nigripes solid light grey, Notolabrus tetricus large black dashed, Pempheris multiradiata small light grey dashed and Pseudolabrus psittaculus small black dashed.

3.4 Discussion

3.4.1 Predictive performance

This study compared 10 presence-only algorithms to predict the habitat suitability of five demersal fish taxa in Discovery Bay, Australia. To the best of my knowledge this is the first time that towed-video-derived fish occurrence and detailed spatially-explicit seafloor datasets have been used to compare presence-only modelling approaches. Overall, it was found that the range in kappa and AUC values from the models were comparable with other marine and terrestrial presence-only modelling studies (e.g. Elith et al. 2006, Tsoar et al. 2007, Tittensor et al. 2009). Statistically significant differences in values of kappa and AUC were observed between the modelling algorithms. Generally, MAXENT significantly outperformed the other algorithms, similar with findings from previous studies. Tittensor et al. (2009) used MAXENT and ENFA GM to predict global habitat suitability of stony corals on seamounts and found that MAXENT consistently outperformed ENFA GM. Similarly, Elith et al. (2006), who compared sixteen modelling approaches using a variety of terrestrial flora and fauna from six different regions of the world, found that MAXENT significantly outperformed BIOCLIM and DOMAIN. No significant difference between the more recently developed ENFA Ma, ENFA Mae, ENFA Me approaches and the original ENFA M algorithm was also found. This is in contrast to findings by Braunisch et al. (2008), who found that the more recent ENFA algorithms provided better models of habitat suitability for large forest grouse (*Tetrao urogallus*) than the original ENFA M algorithm.

There are numerous reasons for the observed differences in predictive model performances in this study. Differences could potentially be due to the modelling algorithms ability to fit the complex species-environment relationships. Pearce and Ferrier (2000) suggested that algorithms used to fit species distribution models can be ranked in accordance to their 'function complexity'. The models examined in this study differed considerably from each other in their complexity. The BIOCLIM is conceptually the simplest model tested, assuming a rectilinear environmental envelope around occurrence data in environmental-space. Consequently, only the outer records along each environmental variable are used to define the boundaries of the ecological niche and it cannot deal with correlations or interactions between the environmental variables (Hijmans et al. 2005). The DOMAIN differs from BIOCLIM in its ability to cope with discontinuity of the species occurrence datasets in environmental-space (Hijmans et al. 2005). Its main restraint is that, for each potential site, only a single record (the nearest neighbour in environmental-space) is used to determine suitable habitat. The original ENFA-related algorithms (geometric mean, harmonic mean, median and minimum distance) take into account the distribution of all the occurrence records in environmental-space and create elliptic envelopes that are consistent with the assumption of unimodal responses to environmental gradients. The more recent ENFA algorithms (area-adjusted median, median + extremum, area-adjusted median + extremum) are slightly more complex than the original ENFA algorithms, taking into account marginality and specialisation (see Braunisch et al. 2008). Because of MAXENTs ability to iteratively evaluate and improve the rules used for generating predictions, it is the most complex algorithm among

the methods examined in this study. The results indicated that the 10 modelling algorithms can be generalised into three groups based on their kappa and AUC scores: (1) MAXENT consistently performed best; (2) ENFA GM, ENFA HM and DOMAIN had intermediate levels of performance, and (3) BIOCLIM, ENFA M, ENFA Min and the more recent ENFA algorithms performed lowest. Consequently, with the exception of the relatively poor performance obtained for the more recent ENFA algorithms, the results are consistent with the hypothesis that increasing model complexity may provide a better fit for complex species-environment relationships, resulting in better model performance.

3.4.2 Influence of species range and environmental niches on modelling performance

Niche position (expressed by marginality) was the only descriptor to be significantly associated with model performance (i.e. kappa). Higher performing models were obtained based on occurrence data from fish taxa with niche positions that were greatly different from the mean conditions of the study area. However, no discernable association was achieved from the other environmental niche (i.e. tolerance) and species range (i.e. AOO) descriptors examined. In relation to marginality, this association with model performance (kappa) coincides with observations made by Hernandez et al. (2006), who found that predictive performance of organisms with clearly definable environmental niches (i.e. high marginality) can be modelled with higher performance than those of more generalist species (i.e. low marginality). The lack of association between model performance and the remaining descriptors contrasts with previous terrestrial studies. Tsoar et al. (2007) found that

tolerance had a negative effect on predictive performance as measured by kappa. A possible explanation for these discrepancies between these findings and previous studies could relate to the spatial scale at which the variables are generated and fitted. Brotons et al. (2004) proposed that species inhabiting a wide range of habitats in a certain area might not be limited by any of the measured variables at the scale at which the models are fitted and may therefore perform lower. Because this study was primarily concerned with assessing model performance between algorithms, the same variables were used across all taxa and were generated at the finest possible spatial scale (3 x 3 cell analysis window). It is acknowledged that there is no universally correct spatial scale at which to describe species-habitat relationships (Wiens 1989) and that better models may be achieved if variables were generated at multiple spatial scales as noted in Chapter 2.

3.4.3 The most important variables for characterisation of suitable habitat for demersal fishes

The integration of occurrence data from towed-video and MBES-derived seafloor variables in a presence-only modelling framework were useful for explaining the characteristics that define suitable habitat for the five demersal fish taxa investigated. It was found that MAXENT models consistently delineated areas of suitable habitat to be regions of seafloor that relate to the known ecology of these focal taxa. For example, adult *Caesioperca* spp. is known to school on top of deeper (> 30 m) rocky outcrops, feeding on plankton, while juveniles remain close to the rocky substrata (Edgar 2000, Williams & Bax 2001). Its distribution of suitable habitat was defined with seafloor variables that express these deeper reef drop-offs. Similarly,

Cheilodactylus nigripes is a common species that inhabits reefs, over a range of depths, feeding on benthic invertebrates (Cappo 1980, Cappo 1995). Highly suitable habitat identified as the less complex intermediate to deep reef systems, which are known to be densely covered in a variety of sponges, ascidians and bryozoans (Ierodiaconou et al. 2007a). *Pempheris multiradiata* are generally observed near over-hangs and caves near the edges of reefs (Annese & Kingsford 2005). Consistent with this, the MAXENT model highlighted areas of highly suitable habitat were the protected south-east facing reefs (the predominant swell direction is from the south-west) with low seafloor complexity.

The MAXENT models highlighted an important difference in the ecological requirements of two wrasse species (Labridae). While both *Notolabrus tetricus* and *Pseudolabrus psittaculus* are benthic carnivores that consume a variety of mobile and sessile invertebrates (Barrett 1995, Shepherd & Clarkson 2001, Edgar et al. 2004), differences in seafloor variables that influence their habitat suitability were observed. *N. tetricus* juveniles and small females are commonly observed in kelp and seagrass dominated shallow waters (< 20 m), while larger fish inhabit deeper invertebrate dominated rocky reefs (Edgar et al. 2004). Males of this species are fiercely territorial and maintain a harem of females over home ranges of 400-775 m^2 (Barrett 1995). By contrast, *P. psittaculus* were commonly observed in pairs, or small schools, in and around sessile invertebrate and thallose-red-algal-dominated reef systems that are greater than 30 m. Examining the predicted habitat suitability and response curves of these two species indicated that highly suitable habitat for *N. tetricus* was predicted as present in shallow areas of reef with high seafloor complexity

(i.e. high rugosity and either positive or negative BPI); whilst *P. psittaculus* was predicted to be mainly confined to the less complex deeper reefs.

Many studies have identified the influence of seafloor characteristics on the distributions of suitable habitat for demersal fishes because they are either direct or indirect proxies that represent important physiological or ecological limitations; including the availability of territory, food, shelter or the existence of predation or competition (Choat & Ayling 1987, Friedlander & Parrish 1998, Priede & Merrett 1998, García-Charton et al. 2004, Moore et al. 2009, Chatfield et al. 2010). This study, however, highlights the importance of having detailed spatially-explicit (i.e. full-coverage) seafloor data rather than the point-located descriptors relied on by earlier studies (Friedlander & Parrish 1998, Babcock et al. 1999, Westera et al. 2003, Willis & Anderson 2003). These spatially-continuous measures of seafloor data reflect subtle, but important, differences in habitat suitability which provide end users (e.g. management agencies or research scientists) with accurate and detailed spatially-explicit information about demersal fishes. Consequently, the spatially-explicit model predictions generated in this study should be viewed as a framework upon which targeted empirical research can be based.

3.5 Conclusions

The comparison of 10 algorithms provided a comprehensive evaluation of which presence-only techniques are most suited to modelling suitable habitat of demersal fishes. Generally, MAXENT produced the best performing models for the taxa and study area examined. It was also found that fish with clearly definable environmental niches can be modelled with higher performance than

those of more generalist species. The continued use of these presence-only models for mobile demersal fish taxa in marine environment, particularly MAXENT, is encouraged. The MAXENT models clearly demonstrated the value of remotely-sensed occurrence and detailed, spatially-explicit, seafloor datasets in determining the importance of variables that influence suitable habitat of demersal fishes. While the models are still only describing associations and not necessarily demonstrating causal relationships, it is their ability to develop realistic response curves and to provide spatially-explicit predictions of suitable habitat that makes these approaches a useful management tool.

Comparing towed and baited underwater video techniques for assessing temperate marine fishes[4]

[4] The research in this chapter is in review as Monk J, Ierodiaconou D, Versace VL, Rattray A, Stagnitti F, Harvey ES (*In Review*) Comparing towed and baited underwater video techniques for assessing temperate marine fishes. Estuarine, Coastal and Shelf Science

4.1 Introduction

When non-destructively surveying fish it is important to consider the technique that provides the most accurate results for the question posed. This is because the choice of technique has the potential to influence the assemblages recorded by the survey method (Rotherham et al. 2007, Watson et al. 2010). Such examples include the inability of fish traps to effectively sample herbivorous species (Munro 1974) or fish attraction to SCUBA divers (Cole 1994, Cole et al. 2007). Traditionally, scientists have critically examined the biases and limitations of different non-destructive fish surveying techniques with the over-arching goal of identifying at least one technique that can provide the most accurate description of the focal fish assemblage (Lincoln-Smith 1989, Trenkel et al. 2004, Morrison & Carbines 2006). These studies have focused their comparisons on a single habitat (e.g. sediment dominated habitat; Morrison & Carbines 2006) or do not explicitly account for the influence of habitat structure on survey method (e.g. Willis et al. 2000). The physical structure of the habitat (e.g. high profile reef systems vs. low profile seagrass habitat) has the potential to influence the results obtained from non-destructive fish survey techniques. Consequently, it is important to determine how differences in habitat structure influences non-destructive fish survey methods.

There are many different non-destructive surveying techniques available to assess fish populations. SCUBA diver-derived Underwater Visual Census (UVC) has been the most widely used fish surveying technique (Bell 1983, Pyle 2000, Samoilys & Carlos 2000, Harvey et al. 2002, Cole et al. 2007). This technique, however, is limited by depth (usually < 20 m because of

decompression limits), has issues surrounding intra/inter-observer bias (Thompson & Mapstone 1997, Harvey et al. 2001a, b), can over or underestimate the area surveyed (Kulbicki 1998, Harvey et al. 2004) and is limited by the small number of dives that can be achieved in a day (Harvey et al. 2002). More recently, the increase in affordability of underwater video technology has seen more studies beginning to use video-based survey methods to assess fish populations (for detailed reviews see; Shortis et al. 2009, Murphy & Jenkins 2010). Williams et al. (2010b), for instance, described two stereo camera systems (one still and the other video) to survey untrawlable regions of the seafloor (i.e. areas of seafloor that have complex reef systems). They found that both towed systems provided accurate quantification of fish occurrences for these regions (Williams et al. 2010b). Similar to UVC, underwater video provides information on fish assemblages as well as the associated benthic biological habitats. Carbines and Cole (2009) highlighted the effectiveness of a drift video method in estimating densities of demersal fish and making qualitative measures of benthic habitat. This makes it a particularly attractive tool for assessing fish species whilst negating some of the issues associated with SCUBA-based diver surveys.

Whilst different underwater video techniques are available (Murphy & Jenkins 2010), there are two in particular that are becoming popular for assessing fish assemblages and associated habitats. Baited-video systems are popular and widely noted as particularly effective at recording a diverse assemblage of fish species (Willis & Babcock 2000, Harvey et al. 2007, Malcolm et al. 2007, Langlois et al. 2010, Watson et al. 2010). Like other video-based platforms, baited-video are not limited by depth and provide permanent records (Harvey

& Shortis 1996, Harvey et al. 2002). However, static nature of deployments, dietary preferences of fish species and issues associated with bait attraction (and intra/inter-specific competition around the bait) have the potential to influence the species assemblages observed by these baited camera systems (Willis & Babcock 2000).

Towed/drift video surveys are another video technique that are increasingly being used to assess fish populations (Assis et al. 2007, Williams et al. 2010b). This is because towed-video systems are not restricted by depth, provide a permanent record for further analysis and, when coupled with acoustic positioning and GPS, offer precisely georeferenced frames allowing accurate integration with seafloor structure information across habitat transition zones (Spencer et al. 2005). However, towed-video systems are limited by their field of view, the need for high water clarity and are in constant motion (i.e. moving up, down and side-to-side). In shallow (i.e. < 30 m) temperate marine ecosystems, they are also often 'flown' over highly complex reef systems (e.g. Williams et al. 2010b) covered in dense canopy forming macroalgae. These issues combined have the potential to underestimate species' occurrences because fish may simply be hiding under or camouflaged within the canopy and reef.

Towed/drift and baited video have been compared elsewhere. For example, Morrison and Carbines (2006) compared a drift video system to eight other fish survey methods (including baited-video) to estimate the relative abundance of *Pagrus auratus* (snapper). They found that drift video detected a wider range of snapper sizes compared to baited systems. Their study however, focused on

a sheltered harbor that exhibited relatively low seafloor complexity (i.e. predominately sediment dominated habitat). Since towed-video systems potentially underestimate the occurrence of fish simply because they may be hiding under or camouflaged within the canopy and reef, how drift video compares to baited methods across varying benthic biological habitat types (especially over more complex seafloor regions) remains largely untested. Consequently, the objective of this study is to provide a comparison of the type of information that can be extracted from baited and towed-video techniques in terms of fish assemblages, functional groups (i.e. pelagic carnivores, epibenthic carnivore/omnivore and herbivore) and degrees of observability (conspicuous or cryptic natured) across six different benthic biological habitats. Knowledge of this type will be of benefit to scientists and managers of marine resources when considering what survey method best suits their aspirations.

4.2 Materials and methods

4.2.1 Study site

The study site encompassed a 25.7 km^2 area that was situated offshore from the city of Warrnambool (-38° 43′ S, 142° 43′ E), south-eastern Australia (Figure 9). The site ranged in depth from 12 to 50 m (based on MBES data coverage for the study area; relative to lowest astronomical tide datum). Canopy-forming kelp, *Ecklonia radiata* and *Phyllospora comosa*, dominated the large shallow limestone reef structure (Hopkins Bank) that was situated across the northern section of the study site. A large sandy area in the north-western region of the study site also supported a sparse cover of seagrass (*Zosteraceae* sp.), while the deeper regions consisted of a mixture of low (< 1 m) profile limestone reef and sandy sediments with assemblages dominated by mixed red algae, sponges,

ascidians, bryozoans and gorgonian corals (Ierodiaconou et al. 2007b). These assemblages can be qualitatively classified into six broad habitat types, including: seagrass, mixed brown algae, mixed red and brown algae, mixed red algae, mixed red algae and invertebrates, and no visible macro-biota (Table 10). Density thresholds and details about how these habitats are defined can be found in Ierodiaconou et al. (2007b).

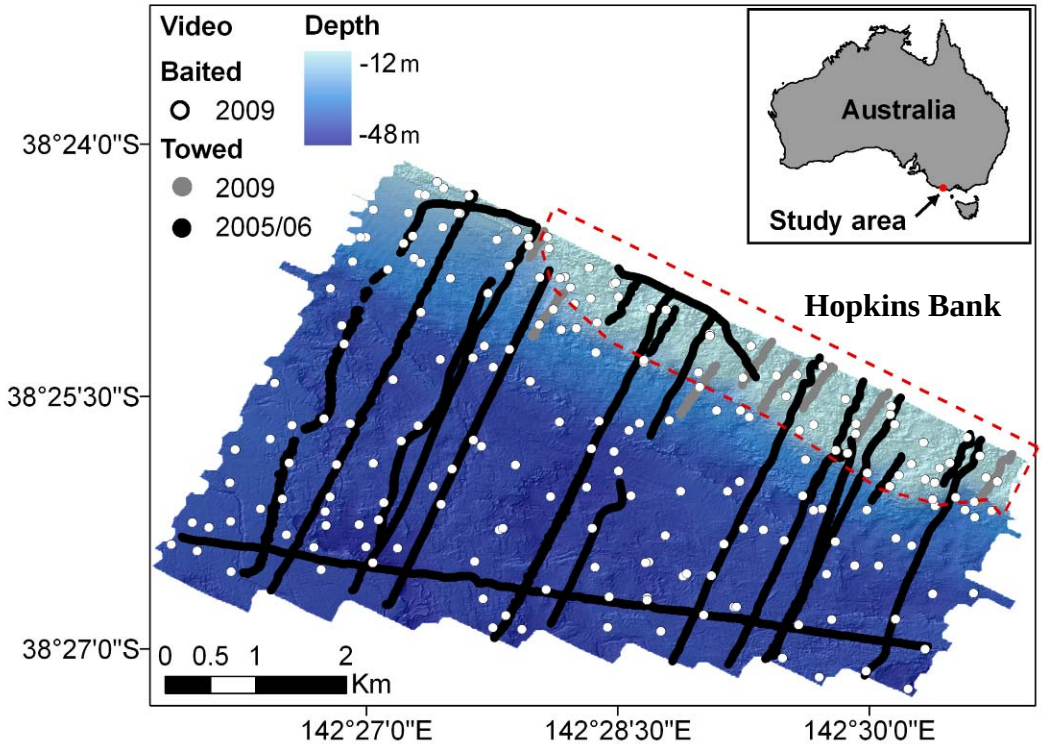

Figure 9. Location of the Warrnambool study area on the south-western coast of Victoria, south-eastern Australia. Shading indicates water depth. Black lines indicate towed-video transects captured in 2005/2006. Grey lines show towed-video transects captured in 2009. White dots indicate baited-video deployments. Red dotted line delineates the southerly extent of the Hopkins Bank.

Table 10. Description of factors used in multivariate statistical analysis.

Factor		Description
Habitat	MB	Mixed brown dominated algae community (predominantly canopy forming kelp)
	MBR	Mixed red and brown dominated algae community
	MR	Mixed red dominated algae community
	MRI	Mixed red algae and invertebrate dominated community
	NVB	No visible macro-biota
	SG	Seagrass (*Zosteraceae*) dominated community
Method	Baited-video	Baited remote underwater video system
	Towed-video	VideoRay towed-video system
Functional Group	Pelagic carnivore	Edgar (2000) and Fishbase were used to assign functional groups
	Benthic carnivore/omnivore	
	Herbivore	
Observability	Conspicuous	Edgar (2000) and Fishbase were used to assign observability
	Cryptic	

4.2.2 Fish surveying techniques

4.2.2.1 Baited-video deployments

The sampling strategy for the baited-video deployments was a randomly stratified design (Moore et al. 2010). This sampling strategy was used to ensure good spatial coverage and adequate representation across the major structuring seafloor gradients (e.g. depth) and predicted habitat types. Stratified deployments were allocated utilising the MBES bathymetry and predicted biotic habitat maps available for the study area (Ierodiaconou et al. 2007b). Ten replicate deployments were preformed across three multibeam sonar derived variables; (1) bathymetry was grouped into 10 m depth strata (i.e. 10-19, 20-29, 30-39 and 40-49 m), (2) rugosity was reclassified into high, medium and low strata and (3) Benthic Position Index (BPI) was classed into trough, flat and

peak. For predicted biotic habitat, 10 replicate deployments were performed in each of the six habitats. To ensure adequate spatial coverage 59 additional deployments were randomly allocated throughout the deeper (i.e. >20 m) regions of the study site. Fish were surveyed from February to March 2009, with a total of 219, 60-min baited-video deployments precisely positioned with a differential GPS to ensure accurate spatial location (Figure 9; Table 11). However, 17 deployments were excluded from the statistical analysis because they failed to record clearly (i.e. landed on their back or smothered in kelp).

The baited-video comprised two Sony HC 15E video cameras in underwater housings mounted 0.7 m apart on a base bar inwardly converged at 8 degrees to gain an optimised field of view with visibility of ~ 7 m distance (water clarity dependent; see Harvey & Shortis 1996). Up to six baited-video systems were deployed at survey localities at any one time to increase sampling efficiency. Each baited-video system was deployed by boat and left to film on the seafloor for a period of 1 h (excluding time lost in lowering the units over the side). At least 36 min of filming time is recommended to obtain measures for the majority of fish species, though 60 min is advisable to obtain measures of numerous targeted fish species (Watson 2006). Each camera system was equipped with a synchronising diode and ~ 800 grams of crushed *Sardinops sagax* (common pilchard) in a closed plastic-coated wire mesh basket, suspended 1.2 m in front of the two cameras. Adjacent replicate deployments were separated by at least 250 m to avoid overlap of bait plumes and reduce the likelihood of fish moving between sites within the sampling period (Cappo et al. 2001). Deployments were carried out between 08:00 and 18:00 to minimise the effects of diurnal changes in fish behaviour (Willis et al. 2006).

Table 11. Summary of survey time for each video method across benthic biological habitats (defined in Table 10).

Habitat	Baited-video survey time (h) 2009	Towed-video survey time (h) 2009	2005/06
MB	35	0.8	1.5
MBR	25	1.9	1.9
MR	17	0.4	1.5
MRI	102	0.5	18
SG	11	0.8	1.5
NVB	12	0.8	1.1
Overall	202	5.2	25.5

4.2.2.2 Towed-video transects

Twenty nine towed-video transects were used to provide fish occurrence data. The 29 transects were selected to encompass the main physical gradients across the study area (e.g. depth, topographic variation, exposure). Additional transects were undertaken throughout the shallow heterogeneous regions of the site (i.e. across the Hopkins Bank) to ensure adequate representation of habitats throughout the study site. The 29 transects covered 68 linear km (~ 30.7 h) of the study area (Figure 9; Table 11). Over eight days (December-March 2005/06 and February-March 2009) a micro remotely-operated vehicle (VideoRay Pro 3) was towed along the 29 transects at 0.5-1 ms^{-1} (1-2 knots). Details on the towed system are outlined in Chapter 2, section 2.4.3.

4.2.3 Video analysis

4.2.3.1 Baited-video analysis

All video footage was captured using Adobe Premiere Elements 4 in an AVI (Audio Video Interleaved) format. The right hand video of each stereo-pair was interrogated to obtain the maximum number of fish belonging to each species present in the field of view of the cameras at one time (MaxN; Cappo et al. 2001, Cappo et al. 2004). For deployments where fish occurred in high densities MaxN counts are considered conservative. Fish were identified to the

lowest possible taxonomic resolution and the same experienced observer was used to analyse both video datasets to minimise potential confound effects. A reference library containing video clips of the fish taxa was taken and quality checked by fish identification experts from Museum Victoria and Australian Marine Ecology. A qualitative assessment of the dominant biological habitat (i.e. seagrass, mixed brown algae, mixed red and brown algae, mixed red algae, mixed red algae and invertebrates, and no visible macro-biota; Table 10) was also completed at each deployment. For each deployment 60 min of tape was analysed. These observations were obtained using the program EventMeasure (SeaGIS Pty Ltd). EventMeasure is a program used for logging and reporting events occurring in digital video imagery. It is specifically designed to allow fast, efficient analysis of movie sequences when recording biological information and animal behaviour in underwater movie sequences. This software enabled the management of data collected from the field operations and video, to record the timing of events and capture reference images of the seafloor and fish in the field of view.

4.2.3.2 Towed-video analysis

Similar to the baited-video systems, all towed-video footage was captured using Adobe Premiere Elements 4 in an AVI format and interrogated to identify fish to the lowest possible taxonomic resolution. Video where the bottom type could not be distinguished was excluded from the analysis. As with the baited-video a qualitative assessment of the dominant biological habitat was also completed at each occurrence locality (Table 10). The exact spatial position (± 5 m accuracy) of each occurrence locality was then determined by matching the time stamp of the video with the corresponding

survey positional data. Details on the capture of the survey positional data (i.e. dGPS track) is outline in Chapter 2, section 2.4.3

4.2.4 Multivariate statistical analysis

To test the differences observed in terms of fish assemblages, functional groupings and observability obtained from baited and towed-video across six benthic habitats, data were each subjected to a two-factorial permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). The PERMANOVA approach was selected as there is no requirement for data to conform to parametric assumptions of normality, homogeneity of variance, independence and balanced designs. The latter being most important in this study as the number of data points from each method varied considerably across habitat types. Species within the fish assemblage were allocated against one of three broad functional groups based on Edgar (2000) and Fishbase (www.fishbase.org). These groups included pelagic carnivores, epibenthic carnivore/omnivores or herbivores. Similarly, each species was grouped into one of two observability classes (conspicuous or cryptic) also based on Edgar (2000) and Fishbase (www.fishbase.org). The data were considered to represent a two-way design of samples within benthic biological habitat (6 fixed factors; habitat) and within video survey method (2 fixed factors; method). Datasets were transformed into presence/absence to enable comparison between the MaxN obtained from the baited systems and the occurrence derived from the towed video. Using these presence/absence transformed datasets, PERMANOVAs and pairwise comparisons were all run with 9999 permutations of the residuals under a reduced model and all analyses were tested at $\alpha = 0.05$ based on a Bray-Curtis similarity measure. To visualise

the relationship between habitat and species, functional group or observability measure, a distance-based Principle Coordinates Analysis (PCO) was used for each video method. For these PCOs, averages of observations for each of the six habitat classes were used to reduce the inherent non-metricity within the datasets (i.e. a high degree of 0s or 100s within the distance matrices). The strongest correlated vectors (i.e. > 0.7), based on Spearman correlations, were overlaid on the PCO ordination to highlight which species and groupings provided the greatest contribution to the differences observed between the six habitats. As the overlaid vectors represent raw Spearman correlations calculated for each biological entity (i.e. species, functional group or observability measure) with the original PCO axes, excluding all other biological entities, it must only be used as a visual guide (Anderson et al. 2008). All analyses were conducted using the PERMANOVA+ add-on in the statistical package PRIMER-E (Plymouth Marine Laboratory, UK; Clarke & Gorley 2006, Anderson et al. 2008).

To justify pooling of the towed video datasets from the two sampling periods (i.e. 2005/06 and 2009) and to determine if the time discrepancy would confound the comparison between the towed and baited-video, the 2005/06 towed video dataset was sub-sampled to cover the same area as the 2009 footage. A single factor PERMANOVA (factor = time) was applied to measures of assemblages, functional groupings and observability. Since no significant difference was observed for any of the three analyses (all P(perm) > 0.05), it was concluded that the two datasets could be pooled and the time discrepancy between the towed and baited surveys would not confound the comparisons made between techniques.

4.3 Results

4.3.1 Assemblage description

A total of 71 species belonging to 43 families were observed at the study site (Appendix 2). Baited-video systems recorded a greater number of species and families (65 and 43, respectively) compared to the towed-video system (43 and 31, respectively; Table 3). Five species were only recorded by the towed-video system (7% of all species observed) with most of these being cryptic in nature (e.g. *Aracana aurita*; Shaw's cowfish, *Phyllopteryx taeniolatus*; weedy seadragon). Twenty-eight species were only recorded by baited-video (39% of all species observed). Many of these species are predatory or highly territorial (e.g. *Notorynchus cepedianus*; broadnose sevengill shark, *Arripis* spp; Australian salmon, *Seriola lalandi*; yellow-tail kingfish). Families that comprised the greatest number of species were similar for both survey techniques, but differed in the number of species within each family (Table 12). The most common families for both techniques were Monacanthidae followed by Labridae and Cheilodactylidae.

Table 12. Description of fish assemblages recorded by baited and towed-video for the study site.

	Baited video	Towed video	Total
Total # individuals	9,781	3,113	12,839
Total # species	65	43	71
Total # families	43	31	43
# spp unique to technique	28	5	
Top four families (# spp)	Monacanthidae (9) Labridae (5) Cheilodactylidae (5) Carangidae (5)	Monacanthidae (6) Labridae (5) Cheilodactylidae (4) Urolophidae (2)	Monacanthidae (12) Labridae (5) Cheilodactylidae (5) Carangidae (5)

4.3.2 Differences in observed assemblage composition

The PERMANOVA revealed that there were highly significant differences in observed fish assemblages between methods and across benthic biological habitats (Table 13a). However, the differences in the fish assemblages between methods were not consistent amongst benthic biological habitats (PERMANOVA interaction; Table 13a). Pairwise comparisons on the interaction term between methods and benthic biological habitats indicated that the differences in fish assemblages recorded by each method were highly significant for most habitats (P(perm) < 0.001). However, seagrass habitat showed a weaker difference between methods; albeit still significant (P(perm) < 0.05).

The PCO on each video method was used to visualise the habitat-averaged multivariate fish assemblage data (Figure 10). A total of 88.2% of the variation in the fish assemblage recorded by baited-video was explained by the first two PCO axes (Figure 10). In comparison, the first two axes of the PCO based on the fish assemblages recorded by towed-video explained a total of 92.2% of the

variation (Figure 10). Structuring between benthic biological habitats was observed for both video methods along PCO axes (Figure 10).

Examination of the species vectors for the baited-video dataset revealed that a total of 11 species were correlated with PCO1, eight were correlated with PCO2, and four were correlated with both axes (Figure 10; Table 14a). *Neosebastes scorpaenoides* (common gurnard perch), *Meuschenia scaber* (velvet leatherjacket), *Pseudolabrus psittaculus* (rosy wrasse) and *Upeneichthys vlamingii* (southern goatfish) were all strongly negatively correlated with both axes and coincided with PCO ordination of mixed red algae and invertebrate dominated habitats (i.e. MR and MRI; Table 10). Similarly, while *Trachurus declivis* (common jack mackerel), *Pseudophycis barbata* (bearded rock-cod), *Nemadactylus valenciennesi* (queen snapper), *Pagrus auratus* (snapper), *Nelusetta ayraudi* (chinaman leatherjacket) and an unidentified monacanthid species were only negatively correlated with PCO1, these species were still associated with the PCO ordination of mixed red algae and invertebrate dominated habitats. Further, *Caesioperca* spp. (perch), *Parequula melbournensis* (silverbelly), *M. flavolineata* (yellow stripe leatherjacket), *Mustelus antarcticus* (gummy shark), *Cheilodactylus nigripes* (magpie morwong), *Pempheris multiradiata* (common bullseye) and *N. douglasii* (blue morwong) were only negatively correlated with PCO2, and again associated with the PCO ordination of mixed red algae and invertebrate dominated habitats. By contrast, *Heterodontus portusjacksoni* (port jackson shark) was only positively correlated with PCO1, which reflected the PCO ordination of seagrass (SG; Table 10). Similarly, *Enoplosus armatus* (old wife), *M. hippocrepis* (horse-shoe leatherjacket), *Parma victoriae* (scalyfin),

Odax cyanomelas (herring cale) and *Notolabrus fucicola* (purple wrasse) were all only positively correlated with PCO1, which coincided with the PCO ordination of mixed brown algae dominated habitat.

Examination of the species vectors for the towed-video dataset indicated that only nine species were correlated with either PCO axes (Figure 10; Table 14a). Of these, three were correlated only with PCO1 and six only with PCO2. *Caesioperca* spp., *P. psittaculus*, *M. scaber*, *P. melbournensis* were all negatively correlated with PCO1 only, which coincided with the PCO ordination of deeper less structurally complex habitats (i.e. MR, MRI and NB; Table 10). Further, *Aplodactylius acrtidens* (dusky morwong), *O. cyanomelas* and *Dinolestes lewini* (pike) were only correlated with PCO2, which reflected the PCO ordination of mixed brown and red algae dominated habitats (i.e. MB and MBR; Table 10). By contrast, *Urolophus paucimaculatus* (sparsely-spotted stingaree) and *N. tetricus* (blue-throat wrasse) were only positively correlated with PCO1, which related to the PCO ordination of seagrass (SG; Table 10).

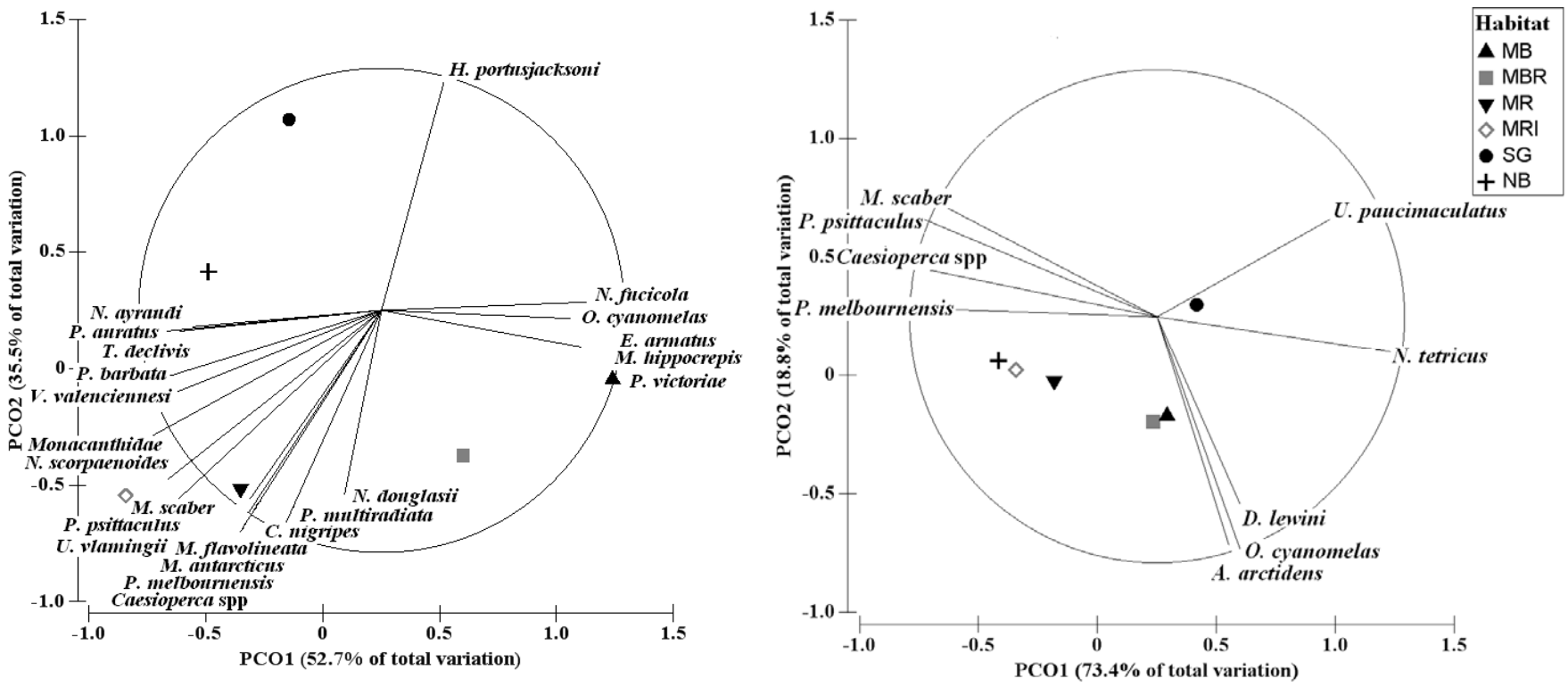

Figure 10. Principal Coordinates Analysis (PCO) of the fish assemblages recorded by baited (left column) and towed-video (right column). Data points are averaged and arranged by benthic biological habitats (MB= mixed brown algae; MBR= mixed red and brown algae; MR= mixed red algae; MRI= mixed red algae and invertebrates; SG= Seagrass; NVB= no visible macro-biota; habitat descriptions in Table 10). Equilibrium circle and vectors (Spearman correlations) are overlaid for the first two PCO axes. The length and direction of the vectors represent the strength and association of the relationship and depict the species that contributed most (i.e. >0.7) to the ordination graph.

4.3.3 Differences in observed functional groupings

PERMANOVA identified highly significant differences in functional groupings of fishes between techniques and across benthic biological habitats (Table 13b). However, the differences in fish assemblages based on functional groupings between methods were not consistent amongst benthic biological habitats (PERMANOVA interaction; Table 13b). Pairwise comparisons on the interaction term found highly significant differences between methods for most habitats (P(perm) < 0.001). In contrast to the species assemblage analysis, seagrass habitat showed no significant difference in functional group assemblages between methods (P(perm) > 0.05) and no visible macro-biota exhibited a weak difference between methods, albeit significant (P(perm) < 0.05).

Similar to the assemblage dataset, the functional group observations were subjected to habitat-averaging to reduce the non-metricity within the dataset. A total of 100% of the variation in the functional groupings of the fish was explained by the first two PCO axes for the baited-video dataset (Figure 11). In contrast, the first two axes of the PCO based on the functional groupings recorded by towed-video explained a total of 99.2% of the variation (Figure 11).

The functional group vectors for the baited-video dataset revealed that herbivores and pelagic carnivores were both only positively correlated with PCO1 (Table 14b). By contrast, epibenthic carnivores/omnivores were only positively correlated with PCO2 (Table 14b). Visual interpretation of these vectors suggested that herbivorous fish were associated with mixed brown

algae dominated habitat (MB; Table 10; Figure 11). However, epibenthic carnivores/omnivores and pelagic carnivores showed no clear association with any of the six habitats (Figure 11).

Interrogation of the functional group vectors for the towed-video dataset revealed that pelagic carnivores were only negatively correlated with PCO1, which reflected the PCO ordination of less structurally complex habitats (i.e. MRI, NB; Figure 11; Table 14b). Similarly, herbivores were only negatively correlated with PCO2, which coincided with the PCO ordination of mixed brown algae dominated habitat (i.e. MB, MBR; Figure 11; Table 10; Table 14b). In contrast to both of these functional groups, epibenthic carnivores/omnivores were only positively correlated with PCO1 and reflected seagrass habitat in the PCO ordination (SG; Figure 11; Table 10; Table 14b).

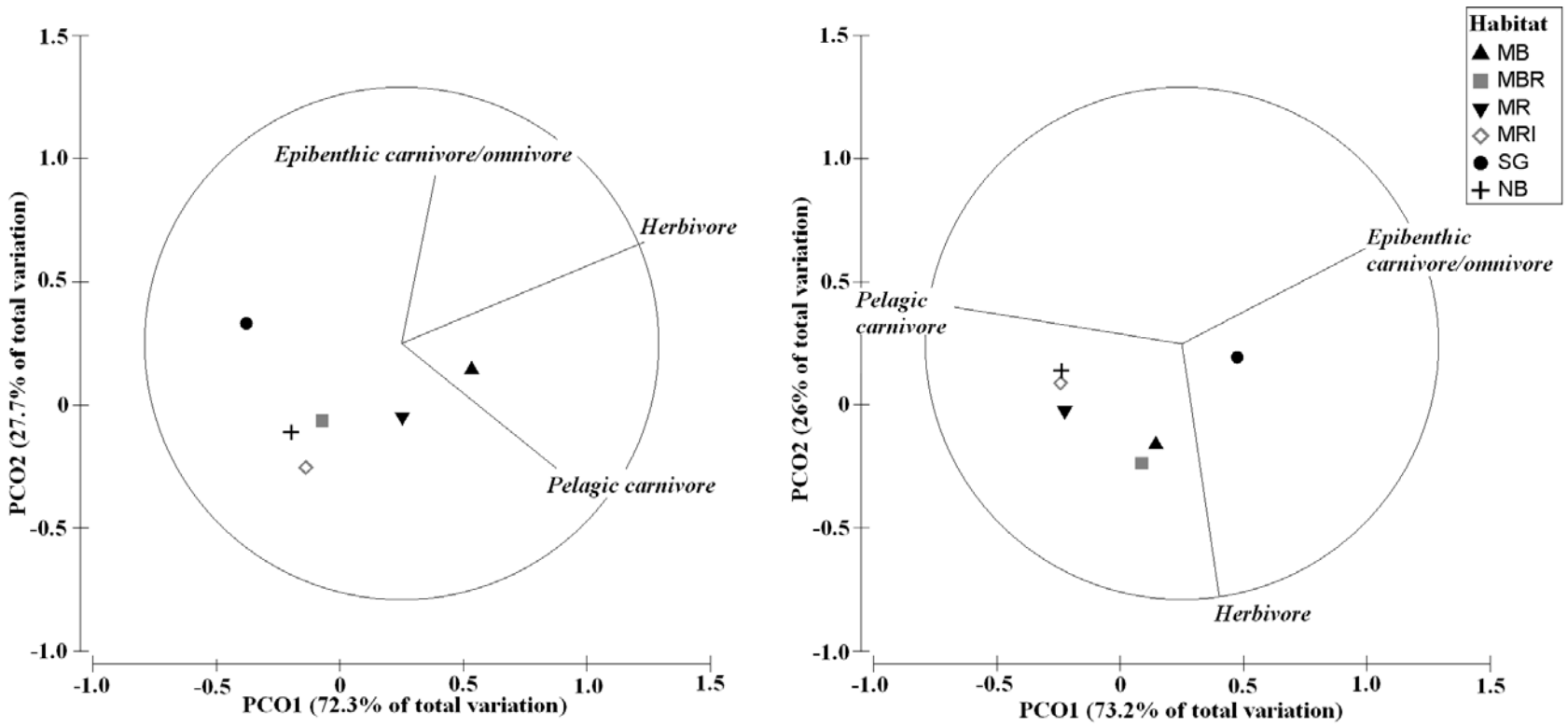

Figure 11. Principal Coordinates Analysis (PCO) of the functional groups recorded by baited (left column) and towed-video (right column). Data points are averaged and arranged by benthic biological habitats. (MB= mixed brown algae; MBR= mixed red and brown algae; MR= mixed red algae; MRI= mixed red algae and invertebrates; SG= Seagrass; NVB= no visible macro-biota; habitat descriptions in Table 10). Equilibrium circle and vectors (Spearman correlations) are overlaid for the first two PCO axes. The length and direction of the vectors represent the strength and association of the relationship and depict the species that contributed most (i.e. >0.7) to the ordination

4.3.4 Differences in observed observability

PERMANOVA suggested that there were highly significant differences between video techniques in their ability to detect species that reflect the two measures of observability and across benthic biological habitats (Table 13c). However, the differences in the assemblages of fish based on observability amongst methods were also not consistent amongst benthic biological habitats (PERMANOVA interaction; Table 13c). Pairwise comparisons on the interaction term between methods and benthic biological habitats indicated that baited and towed-video recorded highly significantly differences in observability measures across most habitats (P(perm) < 0.001). However, no visible macro-biota showed a weaker difference (albeit significant; P(perm) < 0.05), while seagrass showed no significant difference (P(perm) > 0.05) between methods in terms of observability.

Like the previous PCOs, habitat-averaged observations were used to develop the observability PCO. This PCO was used to visualise the differences between methods for habitat-averaged multivariate observability data (Figure 12). For both methods, 100% of the variation in the fish observability was explained by the first two PCO axes (Figure 12).

Examination of the observability vectors for the baited-video dataset revealed that cryptic species were positively correlated with only PCO1. By contrast, conspicuous species showed only negative correlations with PCO2 (Figure 12). Neither baited-video derived observability measures reflected the PCO ordination clustered by habitats.

In contrast to the baited-video, the PCO based on the towed-video-derived dataset showed that conspicuous species were only negatively correlated with PCO1 and reflected the PCO ordination of less structurally complex habitats (i.e. NB, MRI, MR; Figure 12; Table 10; Table 14c). By contrast, the cryptic species vector showed only positive correlation with PCO1, which to some extent coincided with the PCO ordination of more structurally complex habitats (i.e. MB, MBR; Figure 12; Table 10; Table 14c).

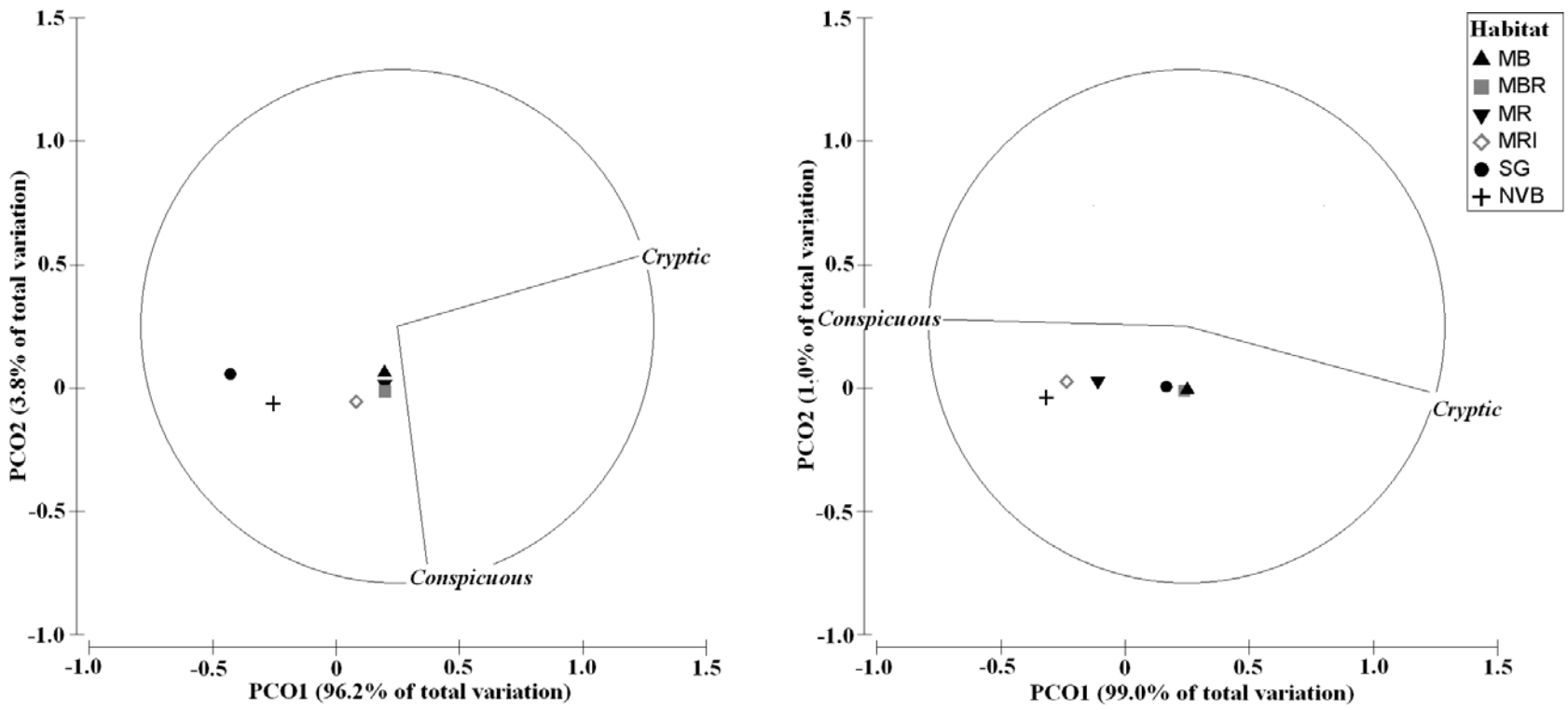

Figure 12. Principal Coordinates Analysis (PCO) of the measures of observability recorded by baited (left column) and towed-video (right column). Data points are averaged and arranged by benthic biological habitats. (MB= mixed brown algae; MBR= mixed red and brown algae; MR= mixed red algae; MRI= mixed red algae and invertebrates; SG= Seagrass; NVB= no visible macro-biota; habitat descriptions in Table 10). Equilibrium circle and vectors (Spearman correlations) are overlaid for the first two PCO axes. The length and direction of the vectors represent the strength and association of the relationship and depict the species that contributed most (i.e. >0.7) to the ordination graph.

Table 13. Summary of PERMANOVA results based on Euclidean distances for (a) fish assemblages, (b) functional groups and (c) observability in response to factors method (towed *v.* baited video), benthic biological habitat (habitat descriptions in Table 10) and their interactions.

a)					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
Method	1	49093	49093	15.485	**0.001**
Habitat	5	214240	42849	13.516	**0.001**
Method x Habitat	5	75191	15038	4.7435	**0.001**
Residual	1102	3493700	3170		
Total	1113	4204900			
b)					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
Method	1	54701	54701	26.005	**0.001**
Habitat	5	62921	12584	5.9825	**0.001**
Method x Habitat	5	20838	4168	1.9813	**0.026**
Residual	1102	2318100	2104		
Total	1113	2788700			
c)					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
Method	1	54843	54843	28.941	**0.001**
Habitat	5	57441	11488	6.0624	**0.001**
Method x Habitat	5	33644	6729	3.5508	**0.003**
Residual	1102	2088300	1895		
Total	1113	2549600			

Table 14. Summary of most influential (i.e. > 0.7) vectors based on Spearman correlations with the first two PCO axes based on each video method for: (a) species, (b) functional groups and (c) measures of observability.

a)	**Species**	**PCO1**	**PCO2**
Baited-video	Monacanthidae	-0.94	-0.52
	Trachurus declivis	-0.89	-0.09
	Neosebastes scorpaenoides	-0.88	-0.70
	Pseudophycis barbata	-0.88	-0.27
	Nemadactylus valenciennesi	-0.85	-0.34
	Meuschenia scaber	-0.84	-0.78
	Pseudoabrus psittaculus	-0.84	-0.78
	Upeneichthys vlamingii	-0.84	-0.78
	Pagrus auratus	-0.83	-0.09
	Nelusetta ayraudi	-0.78	-0.07
	Caesioperca spp.	-0.60	-0.94
	Parequula. melbournensis	-0.55	-0.84
	M. flavolineata	-0.54	-0.78
	Mustelus antarcticus	-0.54	-0.78
	Cheilodactylus nigripes	-0.39	-0.88
	Pempheris multiradiata	-0.39	-0.88
	N. douglasii	-0.15	-0.76
	Heterodontus portusjacksoni	0.26	0.94
	Enoplosus armatus	0.78	-0.03
	M. hippocrepis	0.78	-0.03
	Parma victoriae	0.78	-0.03
	Odax cyanomelas	0.82	-0.15
	N. fucicola	0.85	0.03
Towed-video	*Caesioperca* spp.	-0.99	0.20
	P. psittaculus	-0.94	0.39
	M. scaber	-0.85	0.44
	P. melbournensis	-0.81	0.03
	Aplodactylius arctidens	0.29	-0.93
	O. cyanomelas	0.33	-0.94
	Dinolestes lewini	0.33	-0.76
	Urolophus paucimaculatus	0.70	0.39
	Notolabrus tetricus	0.94	-0.14
b)	**Functional Group**	**PCO1**	**PCO2**
Baited-video	Pelagic carnivore	0.70	-0.49
	Epibenthic carnivore/omnivore	0.13	0.75
	Herbivore	0.94	0.39
Towed-video	Pelagic carnivore	-0.89	0.14
	Epibenthic carnivore/omnivore	0.71	0.37
	Herbivore	0.14	-0.99
c)	**Observability**	**PCO1**	**PCO2**
Baited-video	Conspicuous	0.12	-0.93
	Cryptic	0.94	0.27
Towed-video	Conspicuous	-0.99	0.03
	Cryptic	0.94	-0.26

4.4 Discussion

This chapter assessed the differences between towed and baited-video methods to record fish species assemblages, functional groups and measures of observability across six benthic biological habitats contained in a 25.7 km^2 area. Generally, it was found that across structurally complex benthic biological habitats (i.e. macroalgal-dominated, high-profile reef habitats; such as the mixed brown habitat) significant differences between baited and towed video were observed. However, as the habitat became less complex (e.g. seagrass and no visible macro-biota) both techniques appeared to provide similar assessments of fish in terms of assemblage, functional groups and measures of observability. This is an important difference when compared with previous studies. For example, Morrison and Carbines (2006) described a drift underwater video system (DUV) which was used to survey demersal fish assemblages at night over a sediment-dominated habitat. They found that while the DUV under estimated small (< 5 cm) *P. auratus* its ability to estimate fish biomass compared favourably with other fish surveying techniques (including baited-video). Results in the present study support this idea that, over sediment-dominated habitats, towed-video provides comparable estimates to baited-video for fishes in terms of species assemblage, functional groups and measures of observability. However, as the seafloor became more structurally complex baited-video systems recorded significantly more species, from a broader range of functional groups and including both conspicuous and cryptic species. Since shallow-water temperate marine ecosystems exhibit a high degree of heterogeneity in benthic habitats (Kenny et al. 2003, Brown et al. 2005, Jordan et al. 2005, Ierodiaconou et al. 2011), understanding how

differing habitat types influence fish survey methods is important. While numerous studies exist that quantify the differences between fish survey methods (Willis et al. 2000, Cappo et al. 2004, Harvey et al. 2004, Morrison & Carbines 2006, Colton & Swearer 2010, Watson et al. 2010), this study represents one of the first to explicitly assess how two video methods differ in the detection of temperate marine fishes in relation to variation in seafloor habitat.

The use of bait is well documented to increase the number of species; particularly pelagic or epibenthic carnivores (e.g. *Pseudocaranx dentex*; white trevally, *P. auratus*) in the vicinity of the camera deployment (Willis & Babcock 2000, Willis et al. 2000). In this study the baited cameras recorded more pelagic and epibenthic carnivorous/omnivorous species (e.g. *P. auratus, P. dentex, S. lalandi, Seriolella brama*; warehou) compared to the towed-video system. These species are typically piscivores, invertebrate carnivores and generalist omnivores. In contrast, these species were infrequently observed, or not recorded at all by the unbaited towed-video system. The presence of these carnivores around the bait may also reflect the reduced observations of cryptic or prey species recorded by the baited-video compared to the towed video (e.g. *A. ornata, T. novaezelandiae*; yellow-tail scad).

Guarding and territorial behaviour around the bait is another potential factor influencing observations (Godø et al. 1997). On numerous occasions, males of *N. tetricus* and *M. freycineti* (six-spine leatherjacket) were observed aggressively guarding the bait against other males of the same species and, in some cases, other species. This aggressive behaviour from these territorial

species could potentially lead to underestimates of species and densities on deployments where bait guarding is occurring.

Bait odour plume effects in shallow marine ecosystems with high wave and current energy are complex and difficult to quantify (Colton & Swearer 2010). This bait odour plume could potentially lead to the erroneous observation of fish species in sub-optimal habitat. For instance, if a baited system is set on reefs that contain a matrix of sand within the area of attraction of the bait it may attract species that prefer sand. Likewise, for a baited system set on sand where there is reef present within the plume area, it is likely to attract fish that prefer reef. On several occasions fish species that are predominantly associated with reef (e.g. *Scopis aequipinnis*; sea sweep) were observed over bare sand regions on the baited cameras. This suggests that attraction from nearby reef systems may have been present for some of the deployments. This is not necessarily an issue if the research is primarily concerned with quantifying assemblages at a study site or between locations. However, since these baited-video datasets are now being used in spatially-explicit, fine-scale predictions of habitat suitability of fishes (e.g. Moore et al. 2009, Moore et al. 2010), erroneously locating fish in a habitat that the species is not normally associated with due to attraction (or repulsion) could potentially, and significantly, bias any model output. One potential way to avoid this confounding is to use MBES or predicted habitat maps (e.g. Ierodiaconou et al. 2007b) to ensure baited systems are set within habitats that are homogenous within the bait plume area. However, it is difficult to quantify bait plumes (Colton & Swearer 2010), and by selecting only homogenous regions heterogeneous habitats are inherently not surveyed, which may support unique species assemblages. Additionally, if

the study site is extremely heterogeneous or has very strong currents (thus causing large bait plumes) it may not be possible to survey much of study site. This has the potential to have considerable effects on habitat suitability models. By contrast, the application a towed system poses considerable advantages as it does not rely on bait.

Fewer species (particularly pelagic carnivores) were recorded by the towed-video system. Many of these species were highly mobile (e.g. *S. lalandi*), thus may exhibit avoidance towards boat engine noise (generated whilst towing) or towards the tow camera system itself. After reviewing some of the baited-video footage where the deployment vessel is heard approaching to retrieve the unit after the 60-min deployment, it was noticed that on several occasions the large numbers of *P. auratus* that were observed feeding on the bait rapidly departed the field of view. This avoidance behaviour towards boat noise could potentially bias the towed-video dataset and has been reported by other researchers (e.g. Sarà et al. 2007, Popper & Hastings 2009). Sarà et al. (2007) found that agonistic behaviour of *Thunnus thynnus* (bluefin tuna) was more evident when exposed to sounds from outboard motors. Further, Stoner et al. (2008) found that the presence of underwater camera systems (e.g. towed-video system or remotely operated vehicles) could potentially bias the fish species observed; albeit difficult to quantify as most avoidance (or attraction) occurs outside the field of view. Although not negating the issue of camera avoidance, a possible way to circumvent issues surrounding boat engine noise is through the application of Autonomous Underwater Vehicles (AUV). With the improved access and affordability of AUVs, scientists are beginning to explore their use in seafloor habitat mapping (Williams et al. 2010c). With the addition

of forward mounted stereo cameras, AUVs may provide an efficient and relatively silent alternative to towed/drift video systems and warrant further investigation for fish assessments.

The tow-speed is another factor that potentially influences the species assemblage recorded by the towed-camera system. In this study, tows were conducted at 0.5-1.0 ms^{-1}. To the best of our knowledge, no quantitative research has been conducted into the influence of tow speed on the fish assemblage recorded using underwater video. However, research into the influence of trawl speed in net surveys has highlighted that different speeds affect the abundance, size classes and species assemblage caught (Dahm et al. 2002, Jones et al. 2008). Similarly, swimming speed of SCUBA divers conducting visual census alters the species assemblage recorded (Lincoln-Smith 1989). In fact, the surveying speed for assessing epibenthic species depends largely upon seafloor characteristics (i.e. the presence of canopy forming macroalgae species, refuge, overhangs and crevices), which require adequate time for a careful search (Lincoln-Smith 1989). Alternatively, for the assessment of pelagic species the survey speed depends less on the seafloor characteristics, and more on the ecological and behavioural features of the focal species (e.g. schooling, bright colouration; Lincoln-Smith 1989). One of the issues with both video techniques is their inability to search complex seafloor habitat to the same degree that SCUBA divers can (Watson et al. 2005, Stobart et al. 2007). For this reason, in the absence of comparative data for different tow speeds, towed surveys should be maintained at speeds similar to the swimming speed of SCUBA divers (i.e. < 0.3 ms^{-1}) to mitigate issues surrounding tow speed. Additionally, towed surveys should also be adjusted to

account for the mobility of the target species and seafloor characteristics of the study site (e.g. sediment or complex reef).

When undertaking the analysis of datasets obtained from inherently different video techniques there are numerous considerations that need to be confronted to achieve as realistic a comparison as possible. It is accepted that the collection of the two datasets 3 years apart is not ideal. However, the difference between data collection periods does not overtly affect the comparison between the two datasets for two reasons; (1) there was no significant difference between the subsampled 2005/06 and 2009 towed-video datasets and (2) many of the species recorded were highly territorial and maintain strict territories year round (e.g. labrids and monacanthids). Barrett (1995) studied the short- and long-term patterns to six temperate marine fishes (from the labrid and monacanthid families) and found that these species appeared to be permanent residents of the reef. While presence of migratory fishes (such as *P. auratus*) may vary throughout the seasons (due to spawning migrations), both datasets were collected in summer months (December-March). Previous summer fish assessments to the north-western end of the present study site have found that there is very little inter-annual variation in fish species richness from 2004-2006 (Crozier et al. 2007). Further, the additional towed-video data collected during the 2009 sampling season did not record as many migratory species as the baited-video deployments in the same area of the study site (i.e. the Hopkins Bank).

It is also acknowledged that differences between the two techniques may be a result of the imbalances in surveying effort at the study site. Approximately 10-

times less towed-video was collect compared to the baited systems. However, the discrepancies in survey effort were not considered a serious confounding influence. This is because the deployment times used were required for each method to adequately cover the known habitat types contained within the study area. For example, research using baited-video typically utilises multiple units, that are deployed concurrently, and left to record for 60 min so that the greatest number of individuals and species are recorded (Watson et al. 2005, Harvey et al. 2007, Stobart et al. 2007). Similarly, the design and deployment of the towed-video surveys used in the study have also been utilised in benthic habitat characterisation initiatives and fish assemblage assessments at other locations (e.g. Rattray et al. 2009, Ierodiaconou et al. 2011, Chapters 2 and 3). Consequently, the comparison shown here reflects the species compositions recorded by these two video techniques when used in popular fashion.

When making the choice between video techniques it is also important to consider the time associated in deploying the two systems and analysing the resultant video footage. While the two video techniques record slightly different species compositions, functional groups and measures of observability, the time associated in deploying the systems and analysing the footage differed substantially. The principal advantage of towed-video systems is that it can be deployed for extended periods due to the various options provided by remote power supply and data storage, and offer additional advantages in that the information can be interpreted in 'real-time' enabling operators to modify sampling strategies based on the information received. By contrast, the principal advantage of the baited systems is increased sampling efficiency through the ability to achieve simultaneous deployments over large

areas; thus reducing survey time. In the present study it took eight days to collect 30 h of towed-video, while the 219 baited-video deployments were achieved in 10 days. However, it took considerably longer to download and analyse the baited-video (i.e. towed-video took 30 h to interrogate, while 101 h was needed to view the baited-video). The results of the study are therefore particularly important for researchers needing to decide on a video-surveying technique, as these types of data are relatively expensive to collect and analyse.

4.5 Conclusions

There is a suite of challenges that need to be acknowledged when attempting to quantify the species assemblages, functional groups and measures of observability recorded by towed and baited video. This chapter has made inroads to enhancing our understanding of these two video systems. The results of this study are important as affordable video survey techniques are being increasingly used for fish census. Despite the inherent issues with each method, both video techniques have the advantages such as minimising inter/intra-observer variability and are not depth limited (i.e. no SCUBA decompression limits). Although not analysed here, the baited-video systems also have the added benefit of obtaining accurate measures of fish length (Harvey et al. 2002). Alternatively, while the towed-video used in this study was unable to provide length measurements, it is its ability to capture transitional habitat zones that may be of interest to researchers (particularly those interested in spatially-explicit predictions of habitat suitability). This is especially pertinent considering that towed-video is fast becoming a popular technique in many habitat mapping initiatives worldwide (Grizzle et al. 2007, Ierodiaconou et al. 2007b, Holmes et al. 2008, Lefebvre et al. 2009). As baited and towed video

techniques sampled very different assemblages, functional groups and degrees of observability (albeit variable across habitat types), coupled with the considerable difference in time associated with collecting and analysing video footage, careful consideration should be given to the goals of the research. If a single fish surveying technique is to be used, then the research here suggests the baited-video technique will provide measures for a far greater number of species (particularly pelagic and epibenthic carnivores) across a broader range of benthic biological habitats. However, the two video techniques provide complimentary information by recording different fish assemblages when compared to each technique used in isolation, especially over structurally complex habitats.

Are we predicting the actual or apparent distribution of temperate marine fishes?[5]

[5] The research in this chapter is in review as Monk J, Ierodiaconou D, Harvey ES, Rattray A, Versace VL (*In Review*) Are we predicting the actual or apparent distribution of temperate marine fishes? PLoS ONE

5.1 Introduction

Worldwide, human activity is having adverse impacts on the structure and function of marine ecosystems (Jackson et al. 2001). In response, many initiatives are underway to identify, prioritise and ultimately preserve areas of importance (Ward et al. 1999, Jones 2004, Jordan et al. 2005, Zacharias & Gregr 2005, Aswani & Lauer 2006, Harris & Whiteway 2009). An initial step in this process often involves delineating the distribution of species, assemblages or habitats (Guisan & Zimmermann 2000). This allows areas that support high diversity to be given the highest priority, which is particularly important when the maintenance and enhancement of biodiversity is the central goal of a management initiative (Myers et al. 2000). To support such strategies, management agencies are increasingly seeking the provision of accurate, quantitative and spatially-explicit information on patterns of species distributions at scales relevant to the assessment and management process (Vanderklift & Ward 2000, Harris & Whiteway 2009).

In this context, predictive modelling of species' distribution has become a fundamental tool (Guisan & Zimmermann 2000). These models have provided a popular analytical framework for relating geo-located observations of occurrence to environmental variables that contribute to a species distribution (Guisan & Zimmermann 2000). This relationship is based on statistically, or theoretically derived response functions that characterise the environmental conditions associated with the ecological niche of a given organism (Austin 2007). Presence/absence models are frequently used to predict species distributions, but there is a common problem related to the uncertainty in

determining absences (Hirzel et al. 2001), especially where the species is difficult to survey and does not appear to occupy all available suitable habitats (Gibson et al. 2007). In such cases, researchers have two options; (1) model presence/pseudo-absence (or background) data (e.g. Engler et al. 2004), or (2) model presence-only data (e.g. Elith et al. 2006). The use of a random sample from the background population to supply pseudo-absences may have unexpected consequences on results when true absences are expected (Wisz & Guisan 2009). In fact, it may be argued that on a theoretical basis at least, a presence-only approach may be preferable because there is no requirement for truly exhaustive and exclusive absences; a requirement that is not met by most biodiversity data.

Often such models are based on researchers' own survey occurrence datasets resulting in predictions that are reasonable depictions of species distributions. While there are many different methods available to provide occurrence datasets for fishes in the marine environment, baited and towed systems are increasingly being used as they overcome many issues associated with traditional survey methods (for a review see Murphy & Jenkins 2010). Moore et al. (2009), for example, modelled temperate marine fish distributions based on baited-video-derived occurrence and fine-scale MBES datasets using classification trees and generalised additive models. While the value of these data is not questioned, the representativeness of these occurrence localities is dependent on which survey technique is used. For example, Chapter 4 compared baited and towed-video systems, and found that a greater number of individuals and species were recorded by the baited system; especially carnivorous fishes. While research suggests that deploying a combination of

survey methods used concurrently provides a better assessment of fish assemblages (e.g. Colton & Swearer 2010), the logistical or financial constraints of most studies limit fish biodiversity assessments to only one method. Consequently, there has been limited research to demonstrate how models would differ by using a different data collection technique or modelling approaches in the marine environment. Understanding the influence of survey method used to collect occurrence datasets for modelling of fine-scale habitat suitability is especially crucial. If an observation of zero individuals has arisen because it was present, but not detected then any statistical inference based on such data are likely to be incomplete or wrong (Wintle et al. 2005). Consider a fish species that was observed in 10% of a study region. This fish may actually occur throughout the entire area, but was only detected 10% of the time (p = 0.1). Alternatively it may also be found in only 10% of the area and has been detected perfectly (p = 1).

Consequently, the aim of this chapter is to highlight the potential differences in model predictions brought about from the choice of survey method used to collect fish occurrence datasets. In this chapter towed and baited underwater video methods are used to provide occurrence datasets for nine temperate marine fishes. Further, given the potential for presence/absence and presence-only models to produce considerably different predictions of habitat suitability, three commonly applied SDMs (i.e. generalised linear models, generalised additive models and maximum entropy) are applied to the baited and towed-video occurrences datasets for the nine fish taxa. This will provide a comparison of survey method as well as determine how these datasets potentially influence both types of SDMs (i.e. presence/absence and presence-

only). With increasing application and emphasis of SDMs in the marine environment, this chapter will bring into focus the need for careful interpretation of predictions.

5.2 *Materials and methods*

5.2.1 Study site

The research presented in this chapter was undertaken at the Hopkins study location as detailed in Chapter 4 section 4.2.1.

5.2.2 Fish surveying techniques

The fish occurrences used in this chapter are derived from the same demersal fish surveying programs (i.e. baited and towed video) outlined in Chapter 4 section 4.2.2. From these two datasets the most common nine demersal fish between the two video survey techniques were selected (Table 15; Appendix 2). These nine fish taxa spanned a gradient of life history characteristics from cryptic site affiliated to cosmopolitan conspicuous taxa (Table 15)

Table 15. Summary of the number of occurrences used in model building for each taxon based on the two video methods. Life history characteristics assigned from Edgar (2000) and Fishbase.

Taxon	Common name	Video method	Presence	Pseudo-absence	Life history characteristics
Caesioperca spp.	Perch	Baited	115	87	Conspicuous, cosmopolitan preferring reef-crests, large schools, maximum length of 300mm
		Towed	431	431	
Cheilodactylus nigripes	Magpie morwong	Baited	38	164	Conspicuous, cosmopolitan preferring open habitats (e.g. invertebrate dominated), pairs to small loose schools, maximum length of 410mm
		Towed	32	32	
Meuschenia scaber	Velvet leatherjacket	Baited	106	96	Cryptic, cosmopolitan preferring open habitats (e.g. invertebrate dominated), single to small loose schools, maximum length of 310mm
		Towed	37	37	
Notolabrus tetricus	Blue-throat wrasse	Baited	114	88	Cryptic, limited on or near kelp dominated habitats, small loose schools, maximum length of 500mm
		Towed	50	50	
Odax cyanomelas	Herring cale	Baited	39	163	Cryptic, limited to kelp dominated habitats, single to pairs, maximum length of 510mm
		Towed	56	56	

Table 15. continued…

Parequula melbournensis	Silver belly	Baited	29	173	Cryptic, limited to open sandy habitats, small schools, maximum length of 500mm
		Towed	15	15	
Pempheris multiradiata	Common bullseye	Baited	15	187	Cryptic, limited to in or around caves, single to pairs, maximum length of 220mm
		Towed	154	154	
Pseudolabrus psittaculus	Rosy wrasse	Baited	61	141	Cryptic, cosmopolitan preferring open habitats (e.g. invertebrate dominated) pairs to small loose schools, maximum length of 250mm
		Towed	90	90	
Upeneichthys vlamingii	Southern goatfish	Baited	37	165	Cryptic, limited to on or near open sandy habitats, single to small loose schools, maximum length of 350mm
		Towed	31	31	

5.2.3 Species distribution models

For each of the nine fish taxa, generalised linear model (GLM), generalised additive model (GAM) and MAXENT models were built using the same training and evaluation data derived from either the baited or towed video datasets. By using the same training and evaluation dataset derived from baited and towed video model performance can be directly compared between modelling techniques. The GLMs and GAMs were fitted using presence/pseudo-absence, while MAXENT used only the presence datasets from each survey method. For the towed-video-derived models a 1:1 ratio of presence/pseudo-absence points were used (i.e. if there were 50 occurrences, then 50 pseudo-absence points were randomly generated; Table 15). For these towed-video datasets, pseudo-absence points were randomly generated along transects where no fish taxa were observed. For the baited-video-derived models pseudo-absences were generated from every deployment where the particular fish taxon was not observed (Table 15). All models used a set of relatively uncorrelated (i.e. spearman *rho* < 0.5) MBES-derived seafloor habitat variables as predictors (the same as those Table 1; Chapter 3 section 2.2.2, but generated for the Hopkins study site), and the fish occurrences as response variables. For more detail on the MBES and habitat variables see Chapter 3 section 2.2.2. In addition to those listed in Table 1, Euclidean distance to Hopkins bank was also used in the models as it is the predominant reef structure for the study site. This variable was extracted from the substrata classification for the study site (Ierodiaconou et al. 2007a) and was generated using the Spatial Analyst tool in ArcGIS 9.3. Habitat variables were log- or root-transformed as necessary to prevent extreme frequency distributions

within GLM and GAM. Semi-variograms and Moran's *I* statistics were built using SAM (Spatial Analysis in Macroecology) to check all model residuals for spatial autocorrelation. Only very weak spatial auto-correlation (i.e. all taxa < 0.1) was found and corrections were not needed (Dormann et al. 2007).

5.2.3.1 Generalised linear models

Generalised linear models are commonly used in ecological studies, and therefore serve as a benchmark for the other model types (Moisen & Frescino 2002). The GLMs were built in the Marine Geospatial Ecology Tool kit (MGET; Duke University), which interfaces between statistical software '*R*' (and its contributing packages; *R* Core Development Team 2008) and ArcGIS 9.3. Each fish taxon was individually modelled using a logit link and a binomial error term. All models were fitted with the predictor variables listed in Table 1 (at 3 x 3 kernel size) using a backward stepwise procedure. The Akaike Information Criterion (AIC) was used to determine variable contribution as predictor variables were sequentially added and then dropped from the model.

5.2.3.2 Generalised additive models

The generalised additive models (GAMs) are an extension of generalised linear models, allowing several transformations to be applied to individual independent variables before addition to the model. This improves the ability of the model to deal with nonlinear data. The GAMs were implemented using the *R* 'gam' package within MGET. Where necessary local spline smoothers equivalent to two degrees of freedom were used (Hastie 2008). Backward

stepwise procedure was again used to determine variable importance based on the AIC.

5.2.3.3 Maximum entropy

Maximum entropy (MAXENT) has emerged as a powerful and flexible alternative to GLM and GAM for assessing species habitat suitability in terrestrial studies (see Elith et al. 2006). The MAXENT models were built using the same settings outlined in Chapter 3 section 3.2.4.

5.2.4 Model evaluation

Using the occurrence datasets that were set aside for model testing, model performance was evaluated using the threshold-independent AUC (Fielding & Bell 1997) for each observation technique. The ROC curves and the AUC values were calculated in DIVA-GIS.

5.2.5 Similarity between distribution predictions

As proposed by Warren et al. (2008), a modified Hellinger distance was used in order to compare between models derived from the two observation techniques. This statistic (*I*) allows quantitative similarity assessments between distribution predictions (i.e. GIS grid layers) by computing the differences between them cell by cell. The *I*-values range from 0, indicating that the two predictions are completely different, to 1, suggesting that both are equal. The *I*-statistic is independent of sample size and predicted range sizes, making it superior to other metrics that have been proposed earlier (Warren et al. 2008). In this study, it is considered that *I* values > 0.8 (i.e. differences that are < 20 %) are indicative of high degree of model overlap, values between 0.7 and 0.8

as moderate and values < 0.7 (i.e. differences are < 70% agreement between predictions) indicate low similarity (Roubicek et al. 2010).

5.3 Results

5.3.1 Model evaluation

The majority of the 54 models of habitat suitability had AUC > 0.5 (Figure 13). Of these, MAXENT provided the top 12 highest performing models as measured by AUC. On 15 occasions GLMs and GAMs produced the same performing models as each other (as measured by AUC); with four of these being the equal highest performing model. In isolation, GLMs and GAMs only provided one model each that performed highest.

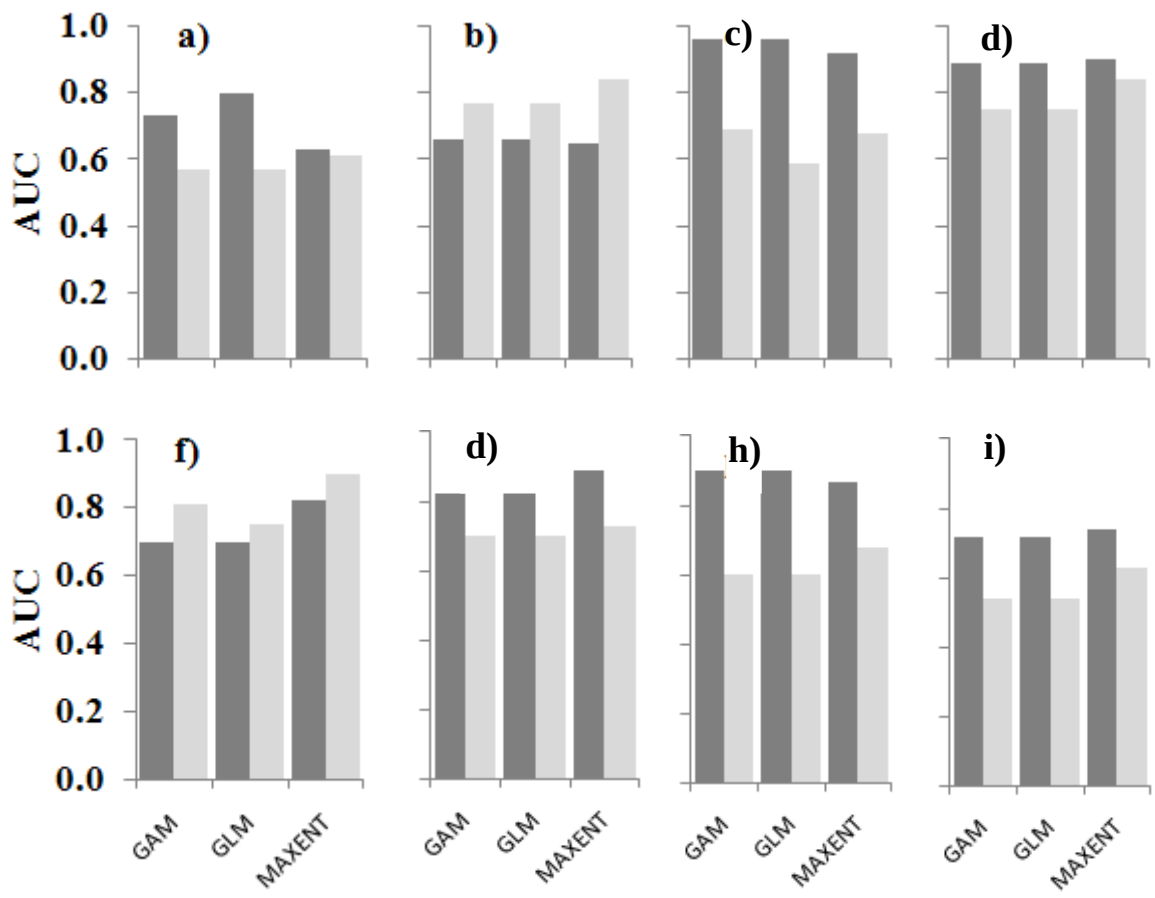

Figure 13. Summary of model performances as measured by AUC for baited (dark grey) and towed (light grey) video datasets. (a) *Caesioperca* spp., (b) *Cheilodactylus nigripes*, (c) *Meuschenia scaber*, (d) *Notolabrus tetricus*, (e) *Odax cyanomelas*, (f) *Parequula melbournensis*, (g) *Pempheris multiradiata*, (h) *Pseudolabrus psittaculus*, (i) *Upeneichthys vlamingii*.

5.3.2 Similarity in predictions of habitat suitability

5.3.2.1 Similarity in habitat suitability models derived from baited-video

Generally all three modelling approaches provided models with a high degree of similarity between habitat suitability predictions for the nine focal fish taxa based on the baited-video dataset (i.e. $I > 0.80$; Table 16; Figure 14; Figure 15). The GAMs and GLMs provided near identical models (i.e. $I \sim 1$) for all nine fish taxa. Only slight differences were observed between MAXENT and the other two modelling approaches; with the greatest difference being observed for predictions of habitat suitability for *Pempheris multiradiata* (Table 16).

5.3.2.2 Similarity in habitat suitability models derived from towed-video

When compared to the baited-video datasets, more variation in similarity between the three modelling approaches was observed across the nine fish taxa based on the towed-video datasets (Table 16; Figure 14; Figure 15). Similar to the baited-video-derived models, GAM and GLM provided identical or near identical predictions for eight of the nine taxa; with only moderate differences being observed for *Upeneichthys vlamingii* ($I = 0.78$). Similarly, comparison between MAXENT and the other two models showed a high degree of similarity for five of the nine fish taxa. For *U. vlamingii* GAM was moderately different to both GLM and MAXENT, but no difference was observed between GLM and MAXENT ($I = 1$). Similarly, both GAM and GLM were moderately different to MAXENT for *Parequula melbournensis*, but no difference was observed between GAM and GLM (Table 16). *Meuschenia scaber* showed the same trend as *P. melbournensis*, albeit to a greater degree (i.e. low similarity;

Table 16). The GLM and MAXENT showed only moderate similarity for *Odax cyanomelas*.

5.3.2.3 Similarity in habitat suitability models between video observation techniques

In contrast to models derived from the same dataset (i.e. baited or towed video), greater dissimilarity was observed when the predictions of habitat suitability based on the two video observation techniques were compared (Table 16). *Caesioperca* spp. was the only taxa to exhibit a high degree of similarity for all modelling approaches between the two observation datasets (Figure 14). With exception of the baited-video-derived MAXENT model for *Cheilodactylus nigripes* that showed a high degree of similarity with towed-video-derived MAXENT, models for *C. nigripes* had a moderate degree of similarity between observation datasets irrespective of modelling approach (Table 16). Identical predictions of habitat suitability were observed for GAM and GLM between observation datasets for *M. scaber* (Table 16). A high degree of similarity was observed for baited-video-derived GAM and GLM with towed-video-derived MAXENT (Table 16). Towed-video-derived GLM also showed a high degree of similarity with baited-video-derived MAXENT. A moderate degree of similarity was also observed between the towed-video-derived GLM and the baited-video-derived MAXENT. However, the towed-video-derived MAXENT showed a low degree of similarity with baited-video-derived MAXENT. For *N. tetricus* a high degree of similarity was observed between the two observation datasets for GAM, GLM and MAXENT. Towed-video-derived MAXENT, however, showed a moderate degree of similarity with baited-video-derived GAM, GLM and MAXENT (Table 16). Predictions

of habitat suitability using GAM, GLM and MAXENT based on either observation technique showed a high degree of similarity for *O. cyanomelas*. Towed-video-derived GLM, however, showed a moderate degree of similarity with all three models based on baited-video data. Towed-video-derived MAXENT for *P. melbournensis* showed a high degree of similarity with all three baited-video-derived models. Both towed-video-derived GAM and GLM showed the same trend; with a low degree of similarity between GAM and GLM between observation datasets (Table 16). Baited-video-derived MAXENT showed a moderate degree of similarity (i.e. $I = 0.70$). A moderate degree of similarity between the two observation datasets was observed for all models for *P. psittaculus* (Table 16). Towed-video-derived MAXENT for *U. vlamingii* showed a high degree of similarity with all three baited-video-derived models. In contrast, GAM and GLM showed a moderate degree of similarity with all three baited-video-derived models (Table 16). A low degree of similarity between the two observation datasets was observed for all models for *P. multiradiata* (Table 16; Figure 15).

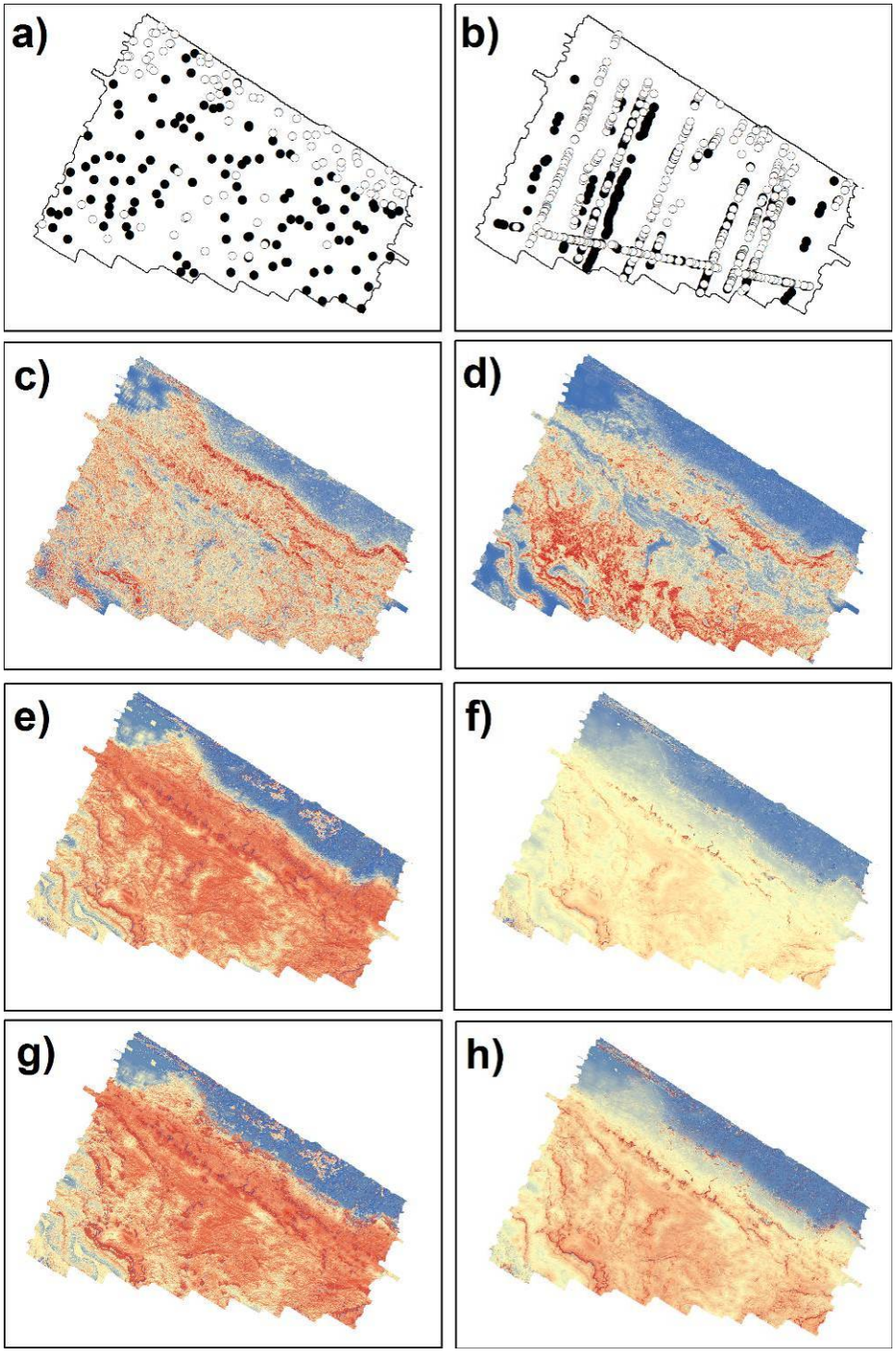

Figure 14. Example of predicted habitat suitability for *Caesioperca* spp. showing high similarity between predictions based on the baited and towed video datasets. Left column: baited-video. Right column: towed-video. (a-b) presence/pseudo-absence localities (presence: black; pseudo-absence: white). (c-d) MAXENT predictions. (e-f) GLM predictions (g-h) GAM predictions. Red shading indicates high suitability, while blue highlights low suitability.

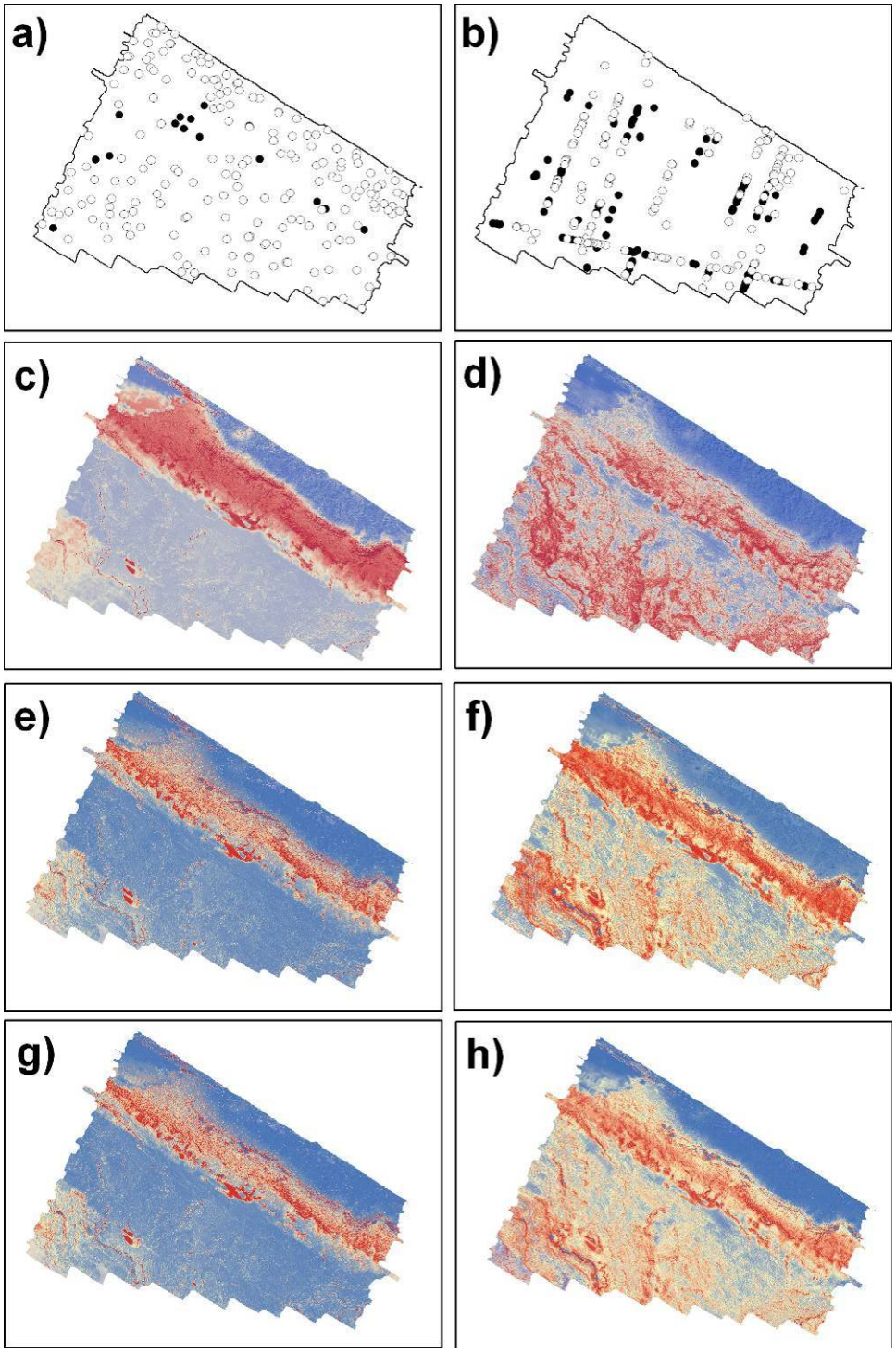

Figure 15. Example of predicted habitat suitability for *Pempheris multiradiata* showing low similarity between predictions based on the baited and towed-video datasets. Left column: baited-video. Right column: towed-video. (a-b) presence/pseudo-absence localities (presence: black; pseudo-absence: white). (c-d) MAXENT predictions. (e-f) GLM predictions (g-h) GAM predictions. Red shading indicates high suitability, while blue highlights low suitability.

Table 16. Summaries of the similarity between habitat suitability predictions using the *I*-statistic. *I*-values range from 0, indicating that the two predictions are completely different, to 1, suggesting that both are equal. Coloured cells indicate similarity groupings: green = high, orange = moderate, red = low similarity.

			Baited			Towed	
			GAM	**GLM**	**MAXENT**	**GAM**	**GLM**
***Caesioperca* spp.**	**Baited**	**GLM**	0.96				
		MAXENT	0.87	0.88			
	Towed	**GAM**	0.92	0.93	0.88		
		GLM	0.92	0.93	0.88	1.00	
		MAXENT	0.87	0.87	0.83	0.87	0.87
Cheilodactylus nigripes	**Baited**	**GLM**	0.99				
		MAXENT	0.82	0.82			
	Towed	**GAM**	0.76	0.76	0.83		
		GLM	0.76	0.76	0.83	1.00	
		MAXENT	0.76	0.76	0.82	0.90	0.90
Meuschenia scaber	**Baited**	**GLM**	0.98				
		MAXENT	0.90	0.90			
	Towed	**GAM**	1.00	1.00	0.75		
		GLM	0.75	0.75	0.82	0.80	
		MAXENT	0.82	0.82	0.64	0.66	0.60
Notolabrus tetricus	**Baited**	**GLM**	0.95				
		MAXENT	0.90	0.90			
	Towed	**GAM**	0.87	0.87	0.84		
		GLM	0.87	0.87	0.84	1.00	
		MAXENT	0.79	0.79	0.77	0.86	0.86
Odax cyanomelas	**Baited**	**GLM**	0.99				
		MAXENT	0.89	0.89			
	Towed	**GAM**	0.81	0.81	0.80		
		GLM	0.76	0.76	0.75	0.81	
		MAXENT	0.82	0.82	0.81	0.83	0.76
Parequula melbournensis	**Baited**	**GLM**	0.98				
		MAXENT	0.86	0.86			
	Towed	**GAM**	0.68	0.68	0.70		
		GLM	0.68	0.68	0.70	1.00	
		MAXENT	0.82	0.82	0.87	0.72	0.72

Table 16. continued…

Pempheris multiradiata	**Baited**	**GLM**	0.95				
		MAXENT	0.77	0.77			
	Towed	**GAM**	0.63	0.63	0.67		
		GLM	0.63	0.63	0.67	0.97	
		MAXENT	0.60	0.60	0.70	0.83	0.83
Pseudolabrus psittaculus	**Baited**	**GLM**	0.97				
		MAXENT	0.87	0.88			
	Towed	**GAM**	0.75	0.75	0.75		
		GLM	0.75	0.75	0.75	0.89	
		MAXENT	0.71	0.71	0.70	0.89	0.89
Upeneichthys vlamingii	**Baited**	**GLM**	0.99				
		MAXENT	0.87	0.87			
	Towed	**GAM**	0.78	0.78	0.79		
		GLM	0.78	0.78	0.79	0.78	
		MAXENT	0.80	0.80	0.82	0.78	1.00

5.4 Discussion

This study explored two commonly used underwater video techniques to provide occurrence data to develop and compare both presence/pseudo-absence and presence-only fine-scale habitat suitability models for nine species of temperate marine fishes. The habitat suitability models built in this study performed considerably better than random when assessed by AUC. The AUC values recorded in this study are similar to those observed in previous marine and terrestrial habitat suitability modelling studies, and supports the notion that presence-only models can provide predictions that can, at times be, better than presence/absence approaches (Segurado & Araújo 2004, Elith et al. 2006). Despite the fact that AUC has recently been criticised (because the size of the study site and number of occurrences influences the AUC values see; Lobo et al. 2008, Peterson et al. 2008), it does provide a preliminary indication of the usefulness of a model for the identification of suitable habitat for a particular

species (Elith et al. 2006). This study has also demonstrated this to be the case, and further, that baited and towed video survey techniques are capable of providing models of similar quality (AUC); a conclusion supported by other recent studies (Wilson et al. 2007, Moore et al. 2009, Pittman et al. 2009). For example, Moore et al. (2009) compared the ability of presence/absence methods (GAM and classification and regression trees) to predict fine-scale habitat suitability for demersal fishes based on baited-video and MBES datasets. They found that baited-video and MBES datasets were useful in providing a detailed understanding of demersal fish-habitat associations, as well as accurately predicting species distributions across unsurveyed locations where continuous spatial seafloor data were available (Moore et al. 2009). Similarly, Chapter 3 used towed-video and MBES-derived datasets to compare commonly used presence-only methods (i.e. BIOCLIM, DOMAIN, Ecological-Niche Factor Analysis, MAXENT). Chapter 3 concluded that towed-video-based occurrence data provided well-performing, fine-scale models and encouraged the ongoing use of presence-only approaches, particularly MAXENT, in modelling suitable habitat for demersal marine fishes. Despite these studies supporting the idea that underwater video-based occurrence and MBES-derived datasets are capable of providing well-performing models, this study is one of the first to contrast these two video observation techniques for generating occurrence datasets for predictions of fine-scale habitat suitability for temperate marine fishes (using both presence/pseudo-absence and presence-only modelling techniques).

and While numerous studies have compared modelling approaches in terms of model performance (i.e. via AUC or kappa; Segurado & Araújo 2004, Elith et

al. 2006, Leathwick et al. 2006, Tsoar et al. 2007, Ready et al. 2010; Chapter 3), the main purpose of this chapter was to highlight how sensible-looking, well-performing (based on AUC) models can provide very different predictions of habitat suitability depending on the choice of video observation dataset used. Overall, greater dissimilarity between the three modelling approaches was observed across the nine fish taxa when models based on the two occurrence datasets where compared (relative to models based on the same survey method). This finding suggests that the characteristics of the occurrence data are important. This concept is supported by Kadmon et al. (2003) who suggested that models are influenced by the reliability of occurrence data and distribution characteristics of the modelled species. The latter has been thoroughly discussed in previous marine and terrestrial studies (e.g. Kadmon et al. 2003, Segurado & Araújo 2004, Sérgio et al. 2007, Chapter 3), and suggest that narrowly distributed species that exhibit minimal niche variation provide more reliable models.

There are many factors that potentially influence the reliability of occurrence data of fishes, including traits such as; body size, crypticity, schooling behaviour, habitat and observer biases (MacNeill et al. 2008, Bozec et al. 2011). These are all inherently influenced by the choice of survey method. Although this study has used two underwater video techniques (with both datasets being processed by the same experienced observer to minimise inter-observer error) a potential explanation for the disparity between predictions of habitat suitability may be attributed to the deployment differences between the surveying methods (i.e. stationary *v.* moving). Consider habitat patches with comparable fish population density but varying in natural shelters such as

crevices or macroalgae. Sampling that relies on the use of a moving platform (e.g. an obliquely angled towed-video camera that is flown 2 m above the seafloor) to provide visual observations could result in incomplete detection in habitat patches with more natural cavities or canopy forming macroalgae (e.g. kelp). By contrast, sampling that relies on a stationary platform (e.g. baited-video) to provide a visual observation dataset may allow time for species that are hiding amongst the crevices or canopy forming macroalgae to be observed. However, the use of bait in these systems is well documented to increase the number of pelagic or epibenthic carnivores in the vicinity of the camera deployment (Willis & Babcock 2000, Willis et al. 2000, Watson et al. 2005), which may result in reduced observations of cryptic or prey species recorded by these systems. While the use of presence-only methods (such as MAXENT in this study) potentially negates the issue of non-detections, the fact still remains that different predictions were made because the two video survey methods detected presences in slightly different environmental niches. For example, the fish taxon that provided predictions that were most similar was *Caesioperca* spp. These are conspicuous aggregating fish that are commonly observed in cloud-like schools feeding above reef crests (Edgar 2000). Consequently, both video methods detected this species in similar ecological niches, and are thus reflected in the similar predictions of suitable habitat. Conversely, *P. multiradiata* showed the lowest similarity in model predictions between survey methods. This timid species inhabits caves ranging from shallow (~10 m) macroalgal-dominated reefs to deeper (~50 m) invertebrate colonised systems (Gomon et al. 2008). For this species, the two video methods detected individuals in different environmental niches. For example,

the stationary characteristic of the baited-video method enabled individuals hiding among the shallow, complex reef systems to be recorded. Further, the baited system recorded fewer occurrences in the deeper regions, which can possibly be attributed to the higher number of pelagic and epibenthic carnivores that were attracted to (and recorded by) the baited video throughout these areas. This may result in avoidance by *P. multiradiata* from baited video deployments on deployments were these predatory fishes were present in high numbers. By contrast, the towed video did not attract these predatory individuals, and recorded more *P. multiradiata* in the deeper invertebrate dominated regions of the study site.

Whilst all model predictions for the nine fish taxa reflect aspects of the known ecology, the results from this study suggest that differences between model predictions are actually reflecting the apparent species distribution (i.e. a combination of the habitat suitability of a fish species and the probability of detecting it; Kéry et al. 2010). This bias cannot be resolved without consideration of variations in detectability that may arise from differences between survey methods, habitats and species (Kéry & Schmidt 2008). Additionally, the strength of a habitat variable relationship in a SDM may be underestimated whenever imperfect detection is not accounted for, even with constant detectability (Tyre et al. 2003). Although some conventional SDMs allow for the problem of missing non-detection data to be partially addressed (i.e. missing zeros; Ward et al. 2009) or permit very general functional forms of covariates to be fitted, such as regression trees (Breiman 2001) and boosted regression trees (Elith et al. 2008), site-occupancy models may provide a useful alternative (Kéry et al. 2010). Site-occupancy models use the presence/absence

(or more correctly termed detection/non-detection) patterns at sites surveyed multiple times (i.e. at least twice) to separate the sampling method from the ecological process and thus obtain estimates of the true species distribution along with unbiased estimates of variable importance (MacKenzie et al. 2002, Tyre et al. 2003, Kéry et al. 2010). However, temperate marine fish studies have rarely addressed the issue of detectability in video-derived occurrence datasets as surveying a site (especially for the purpose of building localised, fine-scale SDMs) more than once is often impractical due to limited weather windows (for more multiple surveys in a single field season) and deployment costs (both in a single season and between seasons). While UVC methods have developed distance sampling techniques (e.g. Kulbicki & Sarramégna 1999) that enable detectability to be accounted for, further research is needed to determine the relative detectability of fishes using towed or baited video systems.

5.5 Conclusions

This study has demonstrated that the characteristics of the video-derived occurrence data are potentially more important than the chosen modelling technique in developing fine-scale models of habitat suitability for temperate marine fishes. However, based on the results in the present study it is difficult to draw any general trends in regards to which circumstances what survey video method provides more reliable occurrence datasets. Nonetheless, the main objective here was not to directly compare model performance, or even emphasise which of the two video methods compared are better for building models of habitat suitability for marine fishes. Instead, the purpose of this chapter was to raise awareness that interpretation of habitat suitability models

needs to account for the potential influence that the choice of survey method used to provide occurrence datasets may have. Whilst limitations within the datasets used in the present study precluded the use of site-occupancy models, which incorporate measures of detectability, it is suggested that these models may provide a practical alternative to conventional SDMs to predict the distribution of suitable habitat for demersal fishes. In the absence of repeat surveys, however, conventional SDMs could be built utilising occurrence datasets derived from different survey methods deployed at the same study site in a single field season. The similarity between these predictions could then be assessed (e.g. using *I*-statistic) to ensure that model outputs reflect as close to the actual distribution of suitable habitat for marine fishes as possible.

Summary of key findings and future research

6.1 Summary of key findings

As each chapter is a separate body of research, they each contain their respective discussions of the major findings in the context of current literature. Hence, this will not be revisited to the same level of detail in this concluding chapter. To illustrate the contribution this thesis has made to the field of marine quantitative spatial ecology, the purpose of this concluding chapter is to link the major findings of the research to the objectives defined in Section 1.2 of Chapter 1.

This thesis has examined the relationship between high-resolution, spatially-explicit MBES-derived seafloor characteristics and video-derived fish occurrences for two sites off the coast of south-eastern Australia. The thesis was motivated by the recognition of the potential role of species distribution models in managing marine demersal fish species and their habitats. Specifically, the results achieved in this thesis have contributed to a better understanding of temperate marine fish distributions in five ways:

(1) How the choice of spatial scale used to calculate MBES-derived seafloor datasets influenced the prediction of habitat suitability for demersal fishes;

(2) How habitat suitability predictions can be used to evaluate the representativeness of Marine National Parks;

(3) Which presence-only modelling approach better suits the modelling of habitat suitability of temperate marine fishes;

(4) The importance of spatially-explicit, continuous seafloor habitat variables in quantifying and predicting habitat suitability; and,

(5) How the relative detectability of fish species from video survey methods potentially influence the occurrence datasets and predictions of habitat suitability.

6.1.1. Importance of spatial scale on habitat suitability models

Since seafloor variables, and indeed species distributions, span a continuum of spatial scales, it is important to consider the scale at which variables are calculated before any attempt is made to quantify and predict the habitat suitability of marine species (Andrew & Mapstone 1987, Chesson 1998, Sale 1998, Wilson et al. 2007). Chapter 2 investigated how spatial scale used to calculate MBES-derived seafloor datasets influenced the performance of habitat suitability predictions by comparing the three different scale models (fine; 56.25 m^2, medium; 506.25 m^2, and coarse; 2756.25 m^2). The coarse model produced better suitability results compared to fine and medium, which supports the notion that habitat selection of space-demanding species may be dominated by variables operating above the home-range scale (Carroll et al. 1999). Similar scale-dependence of habitat variables has been found previously for marine fish species (Choat & Ayling 1987, Ault & Johnson 1998, Connell & Kingsford 1998, Connell 2002, Anderson & Millar 2004, Anderson & Yoklavich 2007). For example, Anderson and Millar (2004) examined the influence of tens of metres (transects), hundreds of metres to kilometres (sites) and hundreds of kilometres (locations) on the distribution and habitat associations of temperate reef fishes. They concluded that the greatest variation

in fish assemblages occurred at the finest spatial scale, between individual transects. Whilst establishing a general rule for identifying the appropriate scale to investigate individual fish species-habitat relationships is important, it is problematic; largely due to the fact that species response uniquely to their environment (O'Neill et al. 1996). For instance, fine spatial scales (i.e. metres) can provide improved predictive power compared to coarse spatial scales (i.e. hundreds of metres) for some demersal fish species (e.g. *Dascyllus aruanus*; Holbrook et al. 2000), but not for others (e.g. *Scarus iserti*; Tolimieri 1998). Consequently, it is recommended that variables in habitat suitability models should be included at different spatial scales (relevant to the focal taxon) so that subtle, but important, habitat preferences can be detected.

Calculating variables at multiple spatial scales is traditionally a time consuming process. However, advances in computing power coupled with new software algorithms now make the generations of these variables a less daunting task. For example, Landserf (http://www.soi.city.ac.uk/~jwo/landserf/) enables the batch calculation of elevation, slope, aspect, seven measures of seafloor curvature, and feature type (similar to BPI) at any user defined spatial scale. As computer power and software continues to advance the time it takes to batch calculate variables at multiple scales will be reduced considerably.

6.1.2. Evaluating Marine National Parks

Approximately 11% of Victoria's marine waters are contained within reserve type tenures, which include 5.3% in no-take protection zones and around 6% in multiple-use areas (Boxshall 2007). These no-take protection zones include 11

Marine Sanctuaries (MSs) and 13 MNPs (Boxshall 2007). While these MNPs and MSs are expected to have social and economic benefits (for a review of MPA benefits see; Kelleher & Kenchington 1992), their primarily purpose is to protect representative examples of biodiversity, ecological processes and natural features along the Victorian coastline (Boxshall 2007). When proclaimed, however, there was paucity in the understanding benthoscape features and ecosystems contained within these MPAs (Boxshall 2007). The data that existed were limited to shallow (i.e. < 10 m) regions and were derived from sparsely-located SCUBA diver transects (Boxshall 2007). However, MPAs whose objectives include conservation functions must have a solid foundation in biology to succeed (Kelleher 1996, Stevens 2002, Roberts et al. 2003). Roberts et al. (2003) suggested that an MPA with little biological value will provide few benefits, just as a bank account with little money will yield almost no interest. Thus, understanding the biological value of Victoria's MPAs has become the focus of MBES-derived mapping efforts (e.g. Holmes et al. 2008).

Given that Victoria's MPAs are supposed to protect representative examples of biodiversity, understanding how representative they are relative to their adjacent unprotected regions is also important. Currently, SCUBA diver transects are used to provide data to compare trends in- and outside each MPA (for details see; Edmunds & Hart 2003). Because of SCUBA-divers are used, these datasets have limited spatial and depth coverage. The second part of Chapter 2 showcased an alternative approach to assess representativeness of an MNP. This chapter examined observed spatial patterns in habitat suitability inside a MNP compared to adjacent unprotected waters. While the MNP was

representative with respect to the total area of the habitat suitability classes, some significant differences in spatial patterns were observed. For example, unsuitable and highly suitable habitat patches were distributed disproportionally within the MNP (i.e. significantly smaller Interspersion and Juxtaposition Index inside the MNP). In addition, unsuitable habitat was also more regularly arranged in the MNP (i.e. significantly larger Mean Shape Index). While this chapter focused on a single demersal fish, it is acknowledged that the purpose of Victoria's MNPs is to protect biodiversity in general. However, by applying similar approaches to more species (or to a keystone species), the predictions of habitat suitability can potentially provide a better understanding of the representativeness of suitable habitat within these MNPs with respect to those adjacent areas, and thus, are useful in not only selection of such sites but evaluation of their effectiveness.

6.1.3. Comparing modelling algorithms

Although modelling algorithms are the focus of a rapidly growing discipline, at present, we lack extensive comparisons of the relative performances of methods to model species distributions based on presence-only data in the marine environment. While there are many terrestrial studies (e.g. Segurado & Araújo 2004, Elith et al. 2006, Tsoar et al. 2007) that provide at least a preliminary understanding of methods' behaviour, it is important to use 'marine' data on species distributions to expand understanding of the relative performance of methods in the marine realm. Chapter 3 compared 10 commonly used SDM algorithms and provided a comprehensive evaluation of which presence-only techniques were most suited to modelling suitable habitat of demersal fishes. Generally, MAXENT produced the best performing models

for the taxa and study area examined, followed by ENFA GM, ENFA HM, DOMAIN, BIOCLIM, ENFA M, ENFA Min, ENFA Ma, ENFA Mae and ENFA Me algorithms. Given that these models span a continuum of model complexity (i.e. the differences in the models ability to fit the complex species-environment relationships), results from this chapter are consistent with the 'terrestrial' idea that increased model complexity increases model performance (Pearce & Ferrier 2000). It was also found that fish with clearly definable environmental niches can be modelled with higher performance than those of more generalist species. For example, the conspicuous cosmopolitan *Caesioperca* spp. generally yielded lower AUC values, while the strong site affiliated *N. tetricus* exhibited higher performing models. Based on the results from this chapter, the continued use of these presence-only models, particularly MAXENT, is recommended in the prediction of suitable habitat for demersal fishes.

6.1.4. Importance of spatially-explicit, continuous habitat variables

The second part of Chapter 3 used the best performing model (i.e. MAXENT) for each fish taxa to determine the importance of MBES-derived variables in predicting the distribution of habitat suitability for demersal fishes. Generally, Euclidean distance to nearest reef, HSI-b (derivative of backscatter), rugosity and maximum curvature were the most important variables in determining suitable habitat for the five demersal fish taxa investigated. The identification of many of these variables is consistent with previous studies that have identified the influence of seafloor characteristics on the distributions of suitable habitat for demersal fishes (Ault & Johnson 1998, Connell & Lincoln-

Smith 1999, Anderson & Millar 2004, Moore et al. 2009, Smith et al. 2010). For example, Lauria et al. (2011) found that substrata type was the main significant predictor of *Pleuronectes platessa* (European plaice) habitats. Similarly, Chatfield et al. (2010) found that substrata type, depth and macroalgal type significantly influenced fish assemblages. This is because they are either direct or indirect proxies that represent important physiological or ecological limitations; including the availability of territory, food, shelter or the existence of predation or competition (Choat & Ayling 1987, Friedlander & Parrish 1998, Priede & Merrett 1998, García-Charton et al. 2004, Chatfield et al. 2010). This chapter, however, highlighted the importance of having detailed spatially-explicit (i.e. full-coverage) seafloor data rather than the point-located descriptors relied on by earlier studies (Friedlander & Parrish 1998, Babcock et al. 1999, Westera et al. 2003, Willis & Anderson 2003). These spatially-continuous measures of seafloor data reflect subtle, but important, differences in habitat suitability which provide end users (e.g. management agencies or research scientists) with accurate and detailed spatially-explicit information about demersal fishes.

6.1.5. The influence of video method on occurrence data and predictions of habitat suitability

The quality of occurrence dataset is a key issue affecting reliability of model predictions (Stockwell & Peterson 2002, Zaniewski et al. 2002). Underwater video methods are increasingly being applied to survey demersal fishes in an attempt to overcome some of the challenges faced by traditional fish survey methods (e.g. SCUBA-derived underwater visual census). However, these video-based methods can be used without a thorough understanding of their

influence on resultant datasets. Chapter 4 investigated how the choice of video survey method influences the fish assemblages, functional group and measure of observability across six different seafloor habitats. It was found that baited and towed video techniques sampled very different assemblages, functional groups and degrees of observability. Based on this result, coupled with the considerable difference in time associated with collecting and analysing video footage, it is recommended that careful consideration should be given to the goals of future research programs. If a single fish surveying technique is to be used, then the research from this chapter suggested the baited-video technique will provide measures for a far greater number of species (particularly pelagic and epibenthic carnivores) across a broader range of benthic biological habitats (when deployed using multiple units concurrently). While the baited-video technique was more time efficient in the collection of footage, it took far longer to analyse compared to the data collected using the towed-video system. However, the two video techniques provide complimentary information by recording different fish species when compared to each technique used in isolation, especially over structurally complex habitats. Accordingly, if the ultimate aim of the study is to quantify species assemblages then the use of these two video techniques in parallel will provide better composition estimates.

As seen in Chapters 2 and 3, as well as elsewhere (e.g. Dolan et al. 2008, Moore et al. 2009), video-derived datasets are being increasingly used to provide occurrence data for spatially-explicit models of habitat suitability in the marine environment. The influence of these video-derived occurrence datasets on the predictions of habitat suitability was investigated in Chapter 5.

The main objective of this chapter was not to directly compare model performance or even emphasise which of the two video methods compared is better for building models of habitat suitability for marine fishes. Instead, it was to raise awareness that interpretation of habitat suitability models must account for the potential influence that the choice of survey method has on the resulting outputs. It was found that the choice of modelling approach did not considerably influence the prediction of distributions based on the same occurrence dataset. By contrasting presence/absence and presence-only models in this chapter, the results support the notion that presence-only methods can provide comparable performing models to presence/absence models (Elith et al. 2006). However, greater dissimilarity among model predictions was observed across the nine fish taxa when the baited and towed occurrence datasets were compared. Consequently, predictions may not actually reflect the species actual distribution but rather the apparent distribution (i.e. a combination of species distribution and the probability of detecting it). Because these predictions are increasingly being used to identify and prioritise potential regions for protection (e.g. the representation of essential fish habitat within marine reserves; Valavanis et al. 2004), it is encouraged that marine practitioners carefully interpret model predictions.

6.2 Recommendations for further work

The key findings of this thesis have contributed to an improved way species distribution models are used in marine environment. Furthermore, model predictions presented in this thesis also provide an accurate baseline that may facilitate researchers in addressing more targeted biological questions (e.g. effects of climate change), as well as helping conservation practitioners to

ensure that resources are managed in a sustainable manner (Araújo & Williams 2000, Rondinini et al. 2006). For example, Araújo and Williams (2000) used SDMs, which they later transformed into estimates of persistence using information on expected threats and species' vulnerability, to select complementary regions to ensure the proposed reserves contained high estimates of persistence for each species. Considering the results and findings of this thesis, a number of recommendations for future work can be made to further develop the methods of quantifying and predicting the habitat suitability of demersal fishes based on remotely-sensed video and MBES datasets. These recommendations are briefly discussed below.

6.2.1 Addition of other explanatory variables

Although it is notable that models had strong predictive performances, even when restricted to MBES-derived seafloor variables, it is suspected that model performance could be improved with the inclusion of unaccounted-for environmental (e.g. bottom shear-stress; Vaz et al. 2007, oceanographic currents; Malcolm et al. 2010b) and ecological (e.g. inter/intra specific competition, predation) variables (if and when they become available at the appropriate resolution). While it is possible to calculate some of these variables (e.g. bottom shear-stress), at present they are not available at the resolution of the MBES datasets. However, as technology continues to develop, downscaling of these variables may be possible and it is envisaged that they could be incorporated into fine-scale models of habitat suitability in the future.

6.2.2 Temporal changes in habitat suitability predictions

Annually, many fish species exhibit temporal migration patterns between habitats and regions (Malcolm et al. 2007). Models were based on once-off surveys. As a consequence, model predictions reflect a 'snap-shot' of where a species is likely to generally occur. Although the fish taxa used to create SDM predictions of suitable habitat within this thesis exhibit minimal inter-annual migration between regions (i.e. species maintain populations at the study site year-round), some fine-scale diurnal movement between habitats is likely to be evident. For example, observations of feeding behaviour for *C. nigripes* suggest that this species is diurnally active; sheltering in caves and crevices during the night and feeding in less structurally complex habitats (e.g. mixed red algae and invertebrate habitats) during the day (Cappo 1980). Additionally, larger specimens of this species are more active earlier in the morning and later in the afternoon than smaller individuals, which feed consistently throughout the day in shallower regions (i.e. 0-20 m depth; Cappo 1980, Cappo 1995). These two concepts (i.e. fine-scale movements between habitats and variations in diurnal feeding activity between size-classes) should be kept in mind when interpreting the SDM predictions generated in this thesis.

Acoustic tagging is one way to assess the potential for the confounding of fine-scale movement patterns in the SDM predictions of suitable habitat contained within this thesis. By tagging a number of individuals from different size-classes, estimates of the home range for the focal taxon could be achieved (Lucieer & Pederson 2008). Home range is an estimation of the area used by the organism in its 'normal' daily activities of foraging, resting and sleeping

(Burt 1943). Although animal telemetry data contains the movement for each tagged individual, the Home Range Extension (HRE) within ArcGIS (Rodgers & Carr 1998) could be used to calculate habitat use. For example, Topping et al. (2005) used acoustic telemetry and HRE to estimate the habitat use of the labrid *Semicossyphus pulcher* (California sheephead). They found that *S. pulcher* were strictly diurnal and that there was a significant relationship between fish length and proportion of time spent in different habitats (i.e. sand υ reef). They also found that *S. pulcher* occupied rocky-reef areas 54% of the time, and, within these areas, a greater percentage of daytime was spent in high-relief areas. By combining HRE estimates of habitat use with the SDM predictions of suitable habitat in a GIS may allow predictions to be more rigorous assessed. This concept is novel to the research of marine quantitative spatial ecology and warrants further investigation.

6.2.3 Predicting suitable habitat for different demersal fish life-stages

It is widely regarded that length is really important as an indicator for fisheries management (e.g. Berkeley et al. 2004) and MPAs (e.g. Roberts et al. 2001), but fish size has rarely been included in models; with the exception to grouping into 'juvenile' or 'adult' classes. For example, Stoner et al. (2001) used generalised additive models to predict the distribution of adult and juvenile life-stages of flounder separately. The models highlighted that juvenile flounder preferred deep depositional environments, whereas adults occurred more frequently in shallower waters (Stoner et al. 2001). Since many demersal fish exhibit age-dependent ontogeny between habitats (Gratwicke et al. 2006, Shepherd & Brook 2007, Laurel et al. 2009), including length information into

the models could improve our ecological understanding, as well as providing better predictive power. Stereo camera systems (such as those used in Chapters 4 and 5 of this thesis) are capable of accurately triangulating length measurements for fishes recorded during deployment (for a review see; Shortis et al. 2009). Accordingly, these length measurements could be used to as a predictor variable in SDMs. While these measurements were collected with the datasets used in Chapter 4 and 5, they are yet to be incorporated in habitat suitability models.

6.2.4 Determining the influence of tow speed on demersal fish detection rates

Survey speed is an influencing factor when surveying demersal fishes. For example, Lincoln-Smith (1989) found that the swimming speed of SCUBA divers had a critical, though differential, effect upon sample counts. He found that small or cryptic fishes were severely underestimated at relatively fast observer speeds because not enough time was available to search thoroughly for them. Some highly mobile species, however, were overestimated at slow speeds, due to their movement across survey transects during counting periods, or to inadvertent double counting (Lincoln-Smith 1989). However, there is a lack of quantitative assessment of the influence of tow speed on the assessment of demersal fishes using towed video. Consequently, trials need to be undertaken to quantitatively assess the influence of tow speed on the demersal fish assemblages recorded by towed video.

6.2.5 Modelling suitable habitat based on relative abundance

The models in this thesis were based on presence/pseudo-absence or presence-only datasets. In terrestrial systems, there has been increasing interest in the potential for modelling of relative abundance or density data instead of presence/absence data as a means of improving predictive mapping of habitat quality and delineation of high quality habitat (Pearce & Ferrier 2001). This interest is based on the assumption that relative abundance is likely to be a good indicator of habitat quality; reflecting key factors such as reproductive success and susceptibility to extinction (Hobbs & Hanley 1990). A positive correlation between habitat quality and species abundance has been assumed in several terrestrial fauna and flora studies in Australia (e.g. Stockwell et al. 1990, Lindenmayer et al. 1991), and elsewhere (e.g. Lavers & Haines-Young 1996, Leathwick 1998). Given that there is a major difference in habitat suitability between observations of a single fish compared to multiple individuals at a site, incorporation of relative abundance datasets (from the stereo baited-video) into models may also provide better quantification and prediction of habitat suitability of temperate marine fishes. While relative abundance models have been used in the marine environment to predict the abundance of fishes (e.g. Connolly et al. 2009), it has received considerably less attention relative to terrestrial ecosystems, and warrants further investigation.

6.2.6 Modelling the actual distribution of demersal fishes

Imperfect detection is a fundamental issue in species distribution modelling (Kéry et al. 2010). Underwater video methods are increasingly being used to

provide occurrence datasets for models. Imperfect detection in datasets used in conventional species distribution models potentially results in underestimates of the extent of distributions (Kéry et al. 2010). Furthermore, patterns in detectability will erroneously be ascribed to species distributions. In contrast, site-occupancy models applied to replicate detection/non-detection data offer a powerful framework for making inferences about species distributions while correcting for imperfect detection. For example, Rota et al. (2011) contrasted hierarchical occupancy models (that explicitly estimate and adjust for detectability) with logistic regression models (that do not correct for detectability) and MAXENT models (that attempt to circumvent the detectability problem by using data from known presence locations only). Overall, they found that occupancy models were similar to or better than the other approaches tested in terms of predictive performance (as measured by the AUC and kappa). They also established that predictive performance varied across a gradient in species detectability; with logistic regression providing lower relative performance for less detectable species and MAXENT providing lower performance for highly detectable species. Considering the issues mentioned previously in this thesis in relation to the reliable detection of demersal fishes from remotely-sensed underwater video, the application of occupancy models may ultimately allow actual distribution of habitat suitability to be disentangled from apparent habitat suitability (i.e. an unknown proportion of species distributions), and warrants further investigation.

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Appendix 1

The family, genus, species and common name of all fish recorded using the towed-video within the Discovery Bay study site. Species authorities were identified according to Gomon et al. (2008).

Family	Species	Common Name	Relative abundances	Number of Occurrences
Aplodactylidae	*Aplodactylus arctidens* (Richardson, 1839)	Southern seacarp	3	3
Aracanidae	*Aracana aurita* (Shaw, 1798)	Shaw's cowfish	2	2
Aulopidae	*Aulopus purpurissatus* (Richardson, 1843)	Sergeant baker	1	1
Callionymidae	*Foetorepus calauropomus* (Richardson, 1844)	Common stinkfish	3	3
Carangidae	*Trachurus declivis* (Jenyns, 1841)	Common jack mackerel	2607	25
Cheilodactylidae	*Cheilodactylus nigripes* (Richardson, 1850)	Magpie morwong	37	33
	Cheilodactylus spectabilis (Hutton, 1872)	Banded morwong	4	4
	Dactylophora nigricans (Richardson, 1850)	Dusky morwong	3	3
	Nemadactylus valenciennesi (Whitley, 1937)	Queen snapper	1	1
Dinolestidae	*Dinolestes lewini* (Griffith, 1834)	Pike	4	3
Gempylidae	*Thyrsites atun* (Euphrasen, 1791)	Couta	1	1
Girellidae	*Girella zebra* (Richardson, 1846)	Zebra fish	1	1
Heterodontidae	*Heterodontus portusjacksoni* (Meyer, 1793)	Port jackson shark	2	2
Labridae	*Achoerodus* sp.	Blue grouper	3	3
	Dotalabrus aurantiacus (Castelnau, 1872)	Pretty polly	6	5
	Notolabrus fuciola (Richardson, 1840)	Purple wrasse	8	8
	Notolabrus tetricus (Richardson, 1840)	Blue-throat wrasse	61	61
	Pictilabrus laticlavius (Richardson, 1839)	Senator wrasse	9	7
	Pseudolabrus psittaculus (Richardson, 1840)	Rosy wrasse	488	376
Latrididae	*Latridopsis forsteri* (Castelnau, 1872)	Bastard trumpeter	2	2
Monacanthidae	*Eubalichthys bucephalus* (Whitley, 1931)	Black reef leatherjacket	1	1
	Meuschenia flavolineata (Hutchins, 1977)	Yellow stripe leatherjacket	1	1

	Meuschenia scaber (Forster, 1801)	Velvet leatherjacket	7	7
	Monacanthidae sp.	Unidenitifiable leatherjacket	18	16
	Scobinichthys granulatus (Shaw, 1790)	Rough leatherjacket	7	6
Moridae	*Pseudophycis barbata* (Günther, 1862)	Bearded rock-cod	1	1
Mullidae	*Upeneichthys vlamingii* (Cuvier, 1829)	Southern goatfish	15	13
Pempherididae	*Pempheris multiradiata* (Klunzinger, 1879)	Common bullseye	86	50
Platycephalidae	*Platycephalus bassensis* (Cuvier, 1829)	Sand flathead	13	12
Rhinobatidae	*Trygonorrhina guaneria* (Whitley, 1932)	Southern fiddler ray	2	2
Sciaenidae	*Argyrosomus holoepidotus* (Lacepède, 1802)	Mulloway	2	1
Scorpaenidae	*Neosebastes scorpaenoides*(Guichenot, 1867)	Common gurnard perch	18	18
Scorpididae	*Scorpis aequapinnis* (Richardson, 1848)	Sea sweep	39	18
Serranidae	*Caesioperca* spp. (a combination of *C. rasor* (Richarson, 1839) and *C. lepidoptera* (Forster, 1801))	Perch	3842	948
Triglidae	*Lepidotrigla vanessa* (Richardson, 1839)	Butterfly gurnard	8	8
Urolophidae	*Urolophus cruciatus* (Lacepède, 1804)	Cross-back stingaree	2	2
	Urolophus paucimaculatus (Dixon, 1969)	Sparsely-spotted stingaree	3	3
		Total	**7311**	**1651**

Appendix 2

The family, genus, species and common name of all fish recorded using towed and baited video within the Hopkins study site. Species authorities were identified according to Goman et al. (2008).

			Baited-video		Towed-video	
Family	**Species**	**Common Name**	**Relative abundance**	**Number of Occurrences**	**Relative abundance**	**Number of Occurrences**
Alopiidae	*Alopias* sp.	Thresher shark	2	2	0	0
Aplodactylidae	*Aplodactylus arctidens* (Richardson, 1839)	Southern seacarp	2	2	10	10
Aracanidae	*Aracana aurita* (Shaw, 1798)	Shaw's cowfish	0	0	2	2
Arripidae	*Arripis* sp.	Australian salmon	3	1	0	0
Berycidae	*Centroberyx gerrardi* (Günther, 1854)	Red snapper	4	4	0	0
	Centroberyx lineatus (Cuvier, 1829)	Swallowtail	5	3	0	0
Callorhinchidae	*Callorhinchus milii* (Bory de St Vincent, 1823)	Elephant fish	2	2	0	0
Carangidae	*Pseudocaranx dentex* (Bloch and Schneider, 1801)	White trevally	632	21	0	0
	Seriola lalandi (Valenciennes, 1833)	Yellow-tail kingfish	5	1	0	0
	Trachurus declivis (Jenyns, 1841)	Common jack mackerel	3133	33	163	4
	Trachurus novaezelandiae (Richardson, 1843)	Yellow-tail scad	292	10	0	0
	Trachurus sp.		26	1	0	0
Centrolophidae	*Seriolella brama* (Günther, 1860)	Warehou	30	2	0	0
Cheilodactylidae	*Cheilodactylus nigripes* (Richardson, 1850)	Magpie morwong	52	38	32	31
	Cheilodactylus spectabilis (Hutton, 1872)	Banded morwong	4	3	2	2
	Dactylophora nigricans (Richardson, 1850)	Dusky morwong	1	1	2	2
	Nemadactylus douglasii (Hector, 1875)	Blue morwong	7	6	0	0

	Nemadactylus valenciennesi (Whitley, 1937)	Queen snapper	29	23	10	9
Congridae	*Conger wilsoni* (Bloch & Schneider, 1801)	Conger eel	3	2	0	0
Cyttidae	*Cyttus australis* (Richardson, 1843)	Silver dory	10	2	0	0
Dasyatidae	*Dasyatis brevicaudata* (Hutton, 1875)	Smooth stingray	6	6	1	1
Dinolestidae	*Dinolestes lewini* (Griffith, 1834)	Pike	389	23	12	4
Diodontidae	*Diodon nicthemerus* (Cuvier, 1818)	Globefish	2	2	4	4
Enoplosidae	*Enoplosus armatus* (White, 1790)	Old wife	6	4	4	4
Gempylidae	*Thyrsites atun* (Euphrasen, 1791)	Couta	32	14	1	1
Gerreidae	*Parequula melbournensis* (Castelnau, 1872)	Silverbelly	42	29	22	15
Heterodontidae	*Heterodontus portusjacksoni* (Meyer, 1793)	Port jackson shark	11	11	1	1
Hexanchidae	*Notorynchus cepedianus* (Péron, 1807)	Broadnose sevengill shark	1	1	0	0
Kyphosidae	*Girella zebra* (Richardson, 1846)	Zebra fish	6	1	0	0
Labridae	*Dotalabrus aurantiacus* (Castelnau, 1872)	Pretty polly	18	14	9	9
	Notolabrus fuciola (Richardson, 1840)	Purple wrasse	31	25	3	3
	Notolabrus tetricus (Richardson, 1840)	Blue-throat wrasse	335	115	50	50
	Pictilabrus laticlavius (Richardson, 1839)	Senator wrasse	88	61	4	4
	Pseudolabrus psittaculus (Richardson, 1840)	Rosy wrasse	275	98	99	90
Monacanthidae	*Acanthaluteres vittiger* (Castelnau, 1873)	Toothbrush leatherjacket	13	10	1	1
	Meuschenia flavolineata (Hutchins, 1977)	Yellow stripe leatherjacket	4	2	1	1
	Meuschenia freycineti (Quoy & Gaimard, 1824)	Six-spine leatherjacket	62	52	5	5
	Meuschenia galii (Waite, 1905)	Blue-lined leatherjacket	5	5	0	0
	Meuschenia hippocrepis (Quoy & Gaimard, 1824)	Horse-shoe leatherjacket	6	6	2	2

	Meuschenia scaber (Forster, 1801)	Velvet leatherjacket	358	106	38	37
	Monacanthidae sp.	Unidentifiable leatherjacket	79	36	0	0
	Nelusetta ayraudi (Quoy & Gaimard, 1824)	Chinaman leatherjacket	9	7	1	1
	Scobinichthys granulatus (Shaw, 1790)	Rough leatherjacket	1	1	0	0
Moridae	*Pseudophycis bachus* (Bloch & Schneider, 1801)	Red rock-cod	1	1	0	0
	Pseudophycis barbata (Günther, 1862)	Bearded rock-cod	14	10	2	2
Mullidae	*Upeneichthys vlamingii* (Cuvier, 1829)	Southern goatfish	68	37	34	31
Myliobatidae	*Myliobatis australis* (Macleay, 1881)	Eagle ray	1	1	0	0
Odacidae	*Odax cyanomelas* (Richardson, 1850)	Herring cale	63	39	32	28
Parascyllidae	*Parascyllium variolatum* (Duméril, 1853)	Varied catshark	2	2	0	0
Pempherididae	*Pempheris multiradiata* (Klunzinger, 1879)	Common bullseye	30	15	223	154
Pentacerotidae	*Pentaceropsis recurvirostris* (Richardson, 1845)	Long-snouted boarfish	0	0	1	1
Pomacentridae	*Parma victoriae* (Günther, 1863)	Scalyfin	3	3	2	2
Rajidae	*Raja whitleyi* (Iredale, 1938)	Whitley's skate	3	3	1	1
Rhinobatidae	*Aptychotrema vincentiana* (Haake, 1885)	Western shovelnose ray	3	3	0	0
Rhinobatidae	*Trygonorrhina guaneria* (Whitley, 1932)	Southern fiddler ray	8	8	0	0
Scorpaenidae	*Gymnapistes marmoratus* (Cuvier, 1829)	Soldierfish	4	4	0	0
Scorpaenidae	*Neosebastes scorpaenoides*(Guichenot, 1867)	Common gurnard perch	25	23	4	4
Scorpididae	*Scorpis aequapinnis* (Richardson, 1848)	Sea sweep	20	3	12	9

	Tilodon sexfasciatus (Richardson, 1842)	Moonlighter	7	5	1	1
Serranidae	*Caesioperca* spp. (a combination of *C. rasor* (Richarson, 1839) and *C. lepidoptera* (Forster, 1801))	Perch	2919	115	2302	431
Sillaginidae	*Sillaginodes punctata* (Cuvier, 1829)	King George whiting	1	1	0	0
Sparidae	*Pagrus auratus* (Block and Schneider, 1801)	Snapper	571	118	7	7
Sphyraenidae	*Sphyraena novaehollandiae* (Günther, 1860)	Snook	7	3	1	1
Syngnathidae	*Phyllopteryx taeniolatus* (Lacepède, 1804)	Weedy seadragon	0	0	1	1
	Syngnathidae sp.	Unidentifiable pipefish	1	1	0	0
Tetraodontidae	*Contusus* sp. (most probably *Tetractenos glaber* (Freminville, 1813))	Unidentifiable toadfish	1	1	0	0
Tetraodontidae	*Omegophora armilla* (Waite and McCulloch, 1915)	Ringed toadfish	1	1	4	4
Trachichthyidae	*Trachichthys australis* (Shaw and Nodder, 1799)	Roughy	0	0	1	1
Triakidae	*Mustelus antarcticus* (Günther, 1870)	Gummy shark	6	6	0	0
Urolophidae	*Urolophus cruciatus* (Lacepède, 1804)	Cross-back stingaree	1	1	4	4
	Urolophus paucimaculatus (Dixon, 1969)	Sparsely-spotted stingaree	0	0	1	1
		Total	**9781**	**1190**	**3112**	**976**