

Accounting for spatial scale and temporal variation in fish-habitat analyses using baited remote underwater video stations (BRUVS)

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ABSTRACT: With the implementation of marine spatial planning in many coastal regions of the world, there is a need to understand how marine species and communities respond to environmental heterogeneity. Predictive modelling approaches are one efficient method for associating marine communities with variations across the seascape. These approaches, along with increasing access to spatially explicit environmental data, provide improved opportunities for modelling fish assemblages. Baited remote underwater video stations (BRUVS) are a popular means of gathering fish assemblage data in the coastal zone, but have biases in bait attraction, trophic groups sampled, and behavioral conditions. To account for these biases, spatial and temporal scales of analyses must be considered. In this study, we combined time-series BRUVS observations with seafloor and oceanographic variables in generalized additive models to model patterns of relative species richness and abundance in temperate coastal fish assemblages across multiple habitat types, functional trophic groups, and spatial scales from 5–500 m. We show that the spatial and temporal scale of analyses and behavioral characteristics of target species (such as mobility) are important considerations when predicting the spatial distribution of a particular assemblage or functional subset. The resulting models performed well, with prediction accuracies up to 79% while explaining between 24 and 83% of variance. These models were then used to extrapolate assemblage characteristics over broader areas of the seafloor to expand our understanding of fish distributions, providing valuable insights for marine spatial planning, including marine protected area assessment.

KEY WORDS: Stereo-BRUVS · Multibeam · Sonar · Generalized additive model · GAM · Species distribution model · SDM · Fish assemblages

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1. INTRODUCTION

Coastal marine ecosystems are productive and valuable (Costanza et al. 1997), yet they are also some of the most vulnerable environments to human-induced impacts (Crain et al. 2009). Anthropogenic pressures including climate change, coastal development, invasive species, pollution, and fisheries exploitation are particularly pervasive within these ecosystems (Harley et al. 2006, Crain et al. 2009). As

a result, it is essential for stakeholders to have an accurate understanding of assets within the coastal zone so that they can be managed adequately in the future. A sound understanding of resource distributions enables a better chance of maintaining biological diversity and retaining healthy ecological function (Ward et al. 1999, Curley et al. 2002, Schultz et al. 2014). Additionally, such information must be at a scale that is representative of the focal region of interest (Lecours et al. 2015).

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Recent technological advances have provided significant increases in the capabilities of seascape remote sensing and underwater video observations for mapping both abiotic and biotic characteristics of near-shore ocean environments. Detailed seafloor mapping techniques, such as multibeam echosounders (MBES) and light detection and ranging (LiDAR), now provide bathymetric and textural data sets at high resolutions over broad areas (Kennedy et al. 2014, Montereale Gavazzi et al. 2016, Ierodiaconou et al. 2018a). Furthermore, global high resolution data sets for oceanographic variables such as sea surface temperature and wave exposure are becoming widely available (Young et al. 2015, Silva et al. 2017). Additionally, observations from remotely captured video methods, including baited remote underwater video stations (BRUVS), autonomous underwater vehicles (AUVs), towed video (ToV) and remotely operated vehicles (ROVs), provide new opportunities for assessments of fish assemblages (Seiler et al. 2012, Ajemian et al. 2015, Galaiduk et al. 2017b, Logan et al. 2017, Macreadie et al. 2018), including individual species (Galaiduk et al. 2018), functional groups (Ferrari et al. 2018), and fish diversity (Sequeira et al. 2016). Of these methods, BRUVS have been identified as an efficient and cost-effective method for surveying demersal fish assemblages (Langlois et al. 2010). Whilst biases associated with this method must be considered (trophic biases, Goetze et al. 2015; bait biases, Langlois et al. 2015; behavioral biases, Coghlan et al. 2017), BRUVS have become widely adopted for the assessment of fish assemblages within Australia, and are starting to be used overseas (Whitmarsh et al. 2017). For example, a global archive created in 2017 currently has over 26 000 metadata records for BRUVS sample sites with extensive coverage in Australian waters and further abroad (<https://globalarchive.org>). BRUVS provide a low-impact, remote, and non-extractive method for rapid assessment of multiple locations (Langlois et al. 2010, Moore et al. 2010, Harvey et al. 2012) and a means for observing relationships between demersal fish and their surrounding environment (Moore et al. 2011).

Many studies have shown that demersal fish assemblages commonly present strong species–habitat relationships (Moore et al. 2011, McLean et al. 2016, Rees et al. 2018). Topographic variables, such as depth and complexity, are repeatedly shown to be major surrogates of diversity and biomass of assemblages (Friedlander & Parrish 1998, Gratwicke & Speight 2005, Pittman et al. 2007b, Wedding et al. 2008). The ability to obtain high resolution environmental information, combined with spatially explicit

biological observations and resulting knowledge of species–habitat relationships, provides an opportunity to model relationships between seafloor habitats and fish assemblage characteristics. Such methods, known as species distribution models (SDMs), are commonly used in spatial ecology (Guisan & Thuiller 2005, Elith & Leathwick 2009). Recently, BRUVS sampling has been used in SDMs targeting coastal fish assemblages (Galaiduk et al. 2017b, Henderson et al. 2017, Oyafuso et al. 2017, Ferrari et al. 2018). Despite BRUVS proving effective for collecting fish observations in a range of marine environments, there have been limited attempts to evaluate the influence of seafloor characteristics at variable scales, as well as effects of temporal variation on the fish assemblages observed.

Three types of scale are typically recognized in the ecological literature: spatial, temporal, and thematic. Understanding the effects of scale is essential for understanding marine ecosystems (Lecours et al. 2015). For instance, movement patterns of a highly mobile shark species may be best described at scales of kilometres, compared to a small, cave-dwelling reef fish whose home range may be limited to a few metres. In the same context, capturing temporal variation in fish observations will be dependent on factors ranging from hours, days, and up to months or years for migratory species (Schneider 1994). No single scale is appropriate for the study of all ecological questions, even if 2 groups are found in the same geographic area (Clark 1985, Wiens 1989, Levin 1992), requiring testing of environmental associations across multiple scales (Rees et al. 2018). To ensure that fish–habitat modelling studies are as representative as possible, it is recommended that species distributions be assessed at multiple scales (Lourie & Vincent 2004, Rees et al. 2014, Lecours et al. 2015). Organism responses to variations in seascape-scale patterns vary from species to species due to factors such as life-history and ecosystem dynamics (Charton & Ruzafa 1999, Moore et al. 2011, Mims & Olden 2012). Terrestrial studies have found that habitat selection of particular species can only be measured at certain spatial scales (Owen 1972, Boyce 2006, Wilbanks 2006). No single scale is thereby appropriate for studying all ecological groups; however, scale is rarely addressed (Johnson et al. 2013, Lecours et al. 2015). Consideration of spatial scale becomes even more important when sampling with BRUVS due to the inherent spatial uncertainty of bait attraction. BRUVS are sometimes used as a method of making inferences about fish–habitat relationships (Logan et al. 2017, Moore et al. 2017) and developing spatially explicit distri-

bution models (Moore et al. 2009, Monk et al. 2012, Galaiduk et al. 2017b), but often do not incorporate different scales of those associations. When relating environmental variables to observations at BRUVS locations, many studies only consider habitat values at the BRUVS site at a nominal radius, and not the surrounding habitat (Malcolm et al. 2011, Langlois et al. 2012). Other studies select an arbitrary radius scale, for example 10 m (Schultz et al. 2014), 100 m (Landro-Figueroa et al. 2016), and 200 m (Moore et al. 2011), around each BRUVS location, subsequently calculating a mean habitat value of this surrounding zone for model input and testing of associations. Availability of high resolution seafloor mapping and access to other environmental data provide new opportunities to investigate the impacts of scale on fish observations.

A further limitation of many SDM studies targeting fishes is that they include single sample events that rarely account for temporal variability. Temporal variability within assemblages is common in marine ecosystems (Charton & Ruzafa 1999, Quaas et al. 2019) and has been identified as important for modelling coastal fishes (Ault & Johnson 1998, Birt et al. 2012, Brodie et al. 2020). Accounting for temporal variation in BRUVS surveys may allow for greater SDM performance, as predictions will not be just a snapshot in time but will capture which features of the assemblage are constant and which fluctuate through time.

In this study, we combined high resolution environmental variables with time-series BRUVS observations in order to model relative species richness and abundance of a temperate coastal fish assemblage. Models were run across multiple spatial scales and for multiple habitats, functional trophic groups, and target species within the assemblage. Specific aims of this study were to (1) compare model performance across multiple spatial scales for the entire assemblage, functional subsets, and target species present and (2) evaluate predictor variables describing characteristics of the assemblage, each functional group, and each target species across spatial scales. We hypothesized that the assemblage, associated functional groups, and target species would show variations in model performance across scales, and overall variable importance. We expected trends to reveal insights into the importance of considering spatial scale of analyses and functional characteristics of target species when predicting the spatial ecology of a particular assemblage or functional group. We further hypothesized that accounting for temporal variation would improve the performance of models.

2. MATERIALS AND METHODS

2.1. Study site

This study assessed fish assemblages within and adjacent to the no-take Point Addis Marine National Park (IUCN Category II, established in 2002) (see Fig. 1) 3 times, over a period of 5 yr (2013, 2017, and 2018). The investigated site extends along 23 km of the western coast of Victoria, Australia, and covers an area of approximately 100 km² (of which 46 km² is within the marine national park), from the shoreline to Victorian state water limit (~5 km offshore) (Barton et al. 2012). The Point Addis Marine National Park was designed to represent the diversity of Victoria's marine environment, its habitats, and associated flora and fauna (Victorian Environmental Assessment Council 2014) and does not allow extraction of any kind to occur within its boundaries. Infralittoral reefs in this area consist of large canopy-forming brown algae (predominantly *Ecklonia radiata*, *Acrocarpia paniculata*, *Seirococcus axillaris*, and *Phyllospora comosa*) and a mixed red and green algal understorey. These reefs also provide refuge for commercially targeted invertebrate species such as abalone *Haliotis* spp. and southern rock lobster *Jasus edwardsii* (Woods et al. 2014). In the mesophotic zone, circalittoral reefs are dominated by sessile benthic invertebrates including ascidians, soft corals, sponges, and gorgonian fans (Barton et al. 2012). The Point Addis Marine National Park and adjacent waters also contain large rhodolith beds (free-living coralline algae) in deep, soft sediment areas (Holmes et al. 2008, Ierodiaconou et al. 2011). In addition to this wide variety of habitat types, the site also presents wide variation in physical variables including wave exposure, depths, and currents. As a result, the type and abundance of fish species varies considerably across the site.

2.2. Environmental variables

Two different remote sensing techniques were used to provide full bathymetric measurements of seafloor depth and structure (bathymetric LiDAR and MBES). Bathymetric LiDAR uses light to penetrate the water column and measure the seafloor; however, the technique is limited by the inability of light to penetrate deeper waters (Lecours et al. 2016). Ship-based MBES provides the ability to build coverage into deeper waters using sound. When combined, these methods are able to generate seamless bathy-

metric maps across extensive depth ranges. A 5 m horizontal resolution bathymetric grid of approximately 100 km² was generated for the extent of this site from a combination of MBES and LiDAR data. Multibeam bathymetry was acquired as part of the Victorian Marine Habitat Mapping Project (Ierodiaconou et al. 2007). Data were obtained from 2 surveys in November–December 2006 and November–December 2007, using a Reson Seabat 8101 multibeam echosounder operating at a frequency of 240 kHz and 150° angular sector coverage. Data logging, *in situ* quality control, display, navigation, and post-processing were all carried out using Starfix Suite v.7.1 (Fugro). LiDAR data were commissioned by the Victorian State Government's Department of Environment and Primary Industries to assess the impacts of climate change on the coastal zone. Bathymetric LiDAR data were collected in 2008–2009 using a LADS Mk II system coupled with a GEC-Marconi FIN3110 inertial motion sensing system and a dual frequency kinematic geographic positioning system (kGPS), mounted aboard a DeHavilland Dash-8 aircraft. Flight lines for the mapping survey were spaced at approximately 220 m with a swath width of 240 m, leading to a line overlap of 10 m (Quadros & Rigby 2010, Zavala et al. 2014, Young et al. 2015).

Derivatives of the seabed terrain were extracted using the Spatial Analyst module in ArcGIS v.10.5.1 (ESRI) and the 'benthic terrain modeller' tool for ArcGIS (Walbridge et al. 2018). Derivatives used included bathymetry (depth), vector ruggedness measure (VRM), slope, rugosity, aspect (northness and

eastness), bathymetric position index (BPI), curvature, and distance to reef (Table 1). Additionally, sea surface temperature data were sourced from Australia's Integrated Marine Observing System (IMOS) (IMOS 2018). These data were downloaded in NetCDF format at monthly intervals and converted into individual ArcGIS rasters for analysis. Average wave orbital velocity data were also obtained from a 25 yr hindcasted wave model developed by Water Tech (Ierodiaconou et al. 2018b). We calculated the mean of all variables at circular radius scales of 5, 10, 25, 50, 75, 100, 150, 200, 250, 300, 400, and 500 m using the 'focal statistics' geoprocessing function in ArcGIS's Spatial Analyst toolbox. This tool calculates the mean of each cell in an input raster using a roving window that varies in size depending on the scale being tested. The 'extract multi values to points' tool in ArcGIS was then used to extract the underlying seafloor variables of all spatial scales at each BRUVS deployment location. Pearson correlations were used to remove highly correlated variables (>0.6), a conservative cutoff compared to the 0.7 used in much of the literature (Dormann et al. 2013). One major grouping that was consistently correlated were measures of complexity including VRM, rugosity, curvature, slope, and standard deviation of bathymetry. Multiple scales of BPI were also correlated (inner and outer radius of 10–30, 25–50 and 100–200 m). Finally, mean bathymetry was highly correlated with average wave orbital velocity and sea surface temperature with year of sampling. As all variables from these groupings were correlated, a single

Table 1. Description of bathymetric variables tested in this study. All derivatives of bathymetry were made using the 'benthic terrain modeler' tool for ArcGIS (Walbridge et al. 2018)

Derivatives	Description
Bathymetry depth (m)	Elevation of a plane passed through its closest grid point
Rugosity	A measure of topographic roughness, which relates ratio of surface area to planar area
Slope	Maximum change in elevation between each cell and cells in a specified surrounding neighborhood
Curvature	Second derivative of the bathymetric surface, or the first derivative of slope, computed in ArcGIS using the method of Zevenbergen & Thorne (1987)
Bathymetric position index	Measure of a location's elevation relative to the overall landscape. Calculated by using an annulus to compare elevation of a cell with the mean elevation of surrounding cells at various neighborhood sizes
Aspect (northness and eastness)	Azimuthal direction of the steepest slope through points in an analysis window. Northness relates to the sine component of the azimuthal direction, and eastness relates to the cosine
Distance to reef (m)	Reef position was obtained from a substrate layer classified into rock and sediment derived from the bathymetry/backscatter data. Euclidean distance tool (ArcGIS v.10.1) was used to create raster of distance to reef. Sites on reef had a distance value of 0 m

representative from each was chosen, and 7 uncorrelated variables were retained for final analysis (Table 1). These variables were extracted at all 12 spatial scales. Variance inflation factors were calculated following analysis, but values were all below 2.5, indicating no multicollinearity was present (James et al. 2013).

2.3. Fish sampling

Fish assemblages were sampled using BRUVS on 3 occasions. An initial survey took place in April and May 2013. For this survey, sample sites were stratified using existing seafloor bathymetry data and habitat maps to ensure that habitat variability across the site was captured. A further 2 surveys took place in March 2017 and March–April 2018. Sample sites for these surveys were selected using observations from the 2013 survey to haphazardly stratify drops across complexity, depth, and habitat type and to maximize spatial coverage. For all surveys, 2 high definition video cameras (Sony Legria HF G10 or M300) were fitted on each of 6 BRUVS frames. The pairs of cameras were mounted 0.7 m apart and angled in at 8° to allow for stereo imaging. This stereo imaging allowed for the fish lengths and distance from the camera to be determined (Harvey et al. 2001). To standardize the field of view between samples, biological data were only included within a distance of 6.5 m of the video system (Harvey et al. 2004). A synchronizing diode was placed in the field of view so the camera frames could be synced for size measurements. Each BRUVS frame was calibrated in a pool prior to fieldwork being undertaken. A bait bag made up of 1 kg of crushed pilchards *Sardinops sagax* was suspended 1.2 m in front of the cameras. Locations of BRUVS were separated by at least 300 m to minimize potential movement of fish between sites. A total of 60 min of footage on the seafloor was analysed for each drop location.

Analysis of BRUVS footage was completed using the program EventMeasure v.5.27 (SeaGIS). For each video, the maximum number of individuals of a particular species in the frame at any given time (MaxN) was recorded, providing a conservative measure of relative abundance. MaxN is a widely recognized way of obtaining fish population data from BRUVS and ensures that no individual is double-counted (Cappo et al. 2004). Species richness (total number of species detected) was subsequently evaluated for each individual drop location. Due to the use of stereo cameras, lengths of fish could also be measured using

EventMeasure. Fish were measured for total length using a minimum precision of 5 mm. Length–weight relationships were obtained for each species from FishBase (www.fishbase.org; Froese & Pauly 2010) and were used to calculate biomass for each individual measured fish. This was summed to provide a relative biomass measure for each drop location. To account for fish that were unable to be measured, a mean length for the corresponding species was assigned to each unmeasured individual to derive relative biomass measures for each drop location (Barley et al. 2017).

2.4. Broad habitat classifications

Scoring of habitat information from field of view was carried out to allow observations from different habitats to be compared. Classification of benthic composition and relief were recorded from still image grabs for each BRUVS deployment and were made using a simplified adaptation of the CATAMI classification scheme (Althaus et al. 2015). As outlined in Langlois et al. (2018), to enable direct comparisons between studies, a systemized approach to scoring habitat composition and relief from forward facing imagery was adopted. This method used the TransectMeasure program from SeaGIS (<https://www.seagis.com.au>) for annotations, and output was processed for percentage cover of benthos types using scripts from an open-access GitHub repository (Langlois 2017). For the purpose of this study, broad habitat classifications were then used to characterize BRUVS samples into either reef or sediment. Reef was then further split into infralittoral or circalittoral reef depending on the presence of macroalgal or sessile invertebrate assemblages. If a targeted habitat type was present in site classifications, the corresponding site would be included in models of that habitat. This meant that, as some sites captured transition zones between different habitats, these sites were included in models for multiple habitat types.

2.5. Functional feeding groups and key species

Fish assemblages were split into functional feeding groups using a table adapted from Stuart-Smith et al. (2013), which used FishBase (Froese & Pauly 2010) and dietary studies to classify species into trophic groups. Species not present in this 2013 study were grouped based on dietary studies and feeding groups of close relatives. These classifications re-

sulted in all species being classified as one of the following functional feeding groups: carnivore, herbivore, invertivore, or planktivore. Although invertivores are technically carnivores, these were classed separately to account for the likely differences in habitat use between those species that feed on small benthic invertebrates compared to those carnivores that feed on more mobile species, such as fish. All species and their feeding groups are outlined in Table S1 in the Supplement at www.int-res.com/articles/suppl/m640p171_supp.pdf.

Three individual species (*Chrysophrys auratus*, *Notolabrus tetricus*, and *Meuschenia hippocrepis*) were also included in this study to investigate if variations in model trends were present within functional groups. These species are all common invertivores at the site and were chosen as they have either been previously monitored at this site or are commercially important (Woods et al. 2014).

2.6. Statistical analysis

Generalized additive models (GAMs) were used to investigate the effect of environmental variables on coastal fish assemblages and to test effects of scale in making spatially explicit predictions of metrics, such as species richness. Models were initially run for each response variable across multiple spatial scales (Table S2). The model for the highest performing spatial scale was then assessed for variable importance, and a predictive map was made. Whilst length and biomass of fish were calculated from BRUVS imagery, initial models of these metrics showed poor performance as well as being highly variable across spatial scales, indicating that more samples may be needed to get a better understanding of trends (Table S3). Therefore, only relative species richness and abundance were modelled in this study. GAMs were selected for use in this study because of their ability to allow for nonlinear relationships (Yee & Mitchell 1991, Austin 1998) as well as being a common and well-developed method for modelling fish–habitat relationships (Valavanis et al. 2008, Galaiduk et al. 2017b). Prior to running GAMs, spatial autocorrelation of the response variables was tested using a spline correlogram generated in the R package ‘ncf’ v.1.2 (Bjornstad 2018). The R package ‘mgcv’ v.1.8 (Wood 2011) was then used to run GAMs, using relative species richness as a response variable for assemblage analyses and MaxN for single-species analyses. In GAMs, the number of predictor variables able to be included is limited by the ability of the sample size to

capture the variability across the study region. Bolker et al. (2009) recommended using a rule of thumb of >10–20 samples per experimental unit. Deployments from all 3 yr of sampling were included in a single model ($n = 181$ deployments). All combinations of the 9 predictor variables selected ($n = 511$ combinations) were modelled in order to obtain the highest possible model performance. These 9 variables included the 7 uncorrelated environmental variables as well as year of sampling and marine protected area (MPA) status as factor variables. Model selection was conducted using the ‘MuMIn’ v.1.43.15 package in R (Barton 2018), in which a confidence set of models was made. Because the ratio of Akaike weights for 2 candidate models can be used to assess the preference for one model over another (Anderson et al. 2000), the confidence set of models included only those candidate models with Akaike weights that were within 5% of the largest weight (Thompson & Lee 2000). These were selected after passing the general rule of thumb (i.e. 1/8 or 12%) suggested by Royall (1997) for evaluating if strength of evidence was met. To be included in the confidence set, models also had to have a difference in Akaike information criteria (AIC) value from the best model (ΔAIC) of less than 5. From the confidence set, the model with the lowest second-order AIC (AIC_C) was deemed the best model (Table S2). We randomly selected 75% ($n = 138$) of BRUVS for training of models, reserving the remaining 25% ($n = 45$) for testing the accuracy of predictions. Pearson’s correlations were used to assess the accuracy of the predicted data compared with observed data. To assess individual variable importance, models with best performance for each subset of the assemblage were run with and without each variable included in order to single out the contribution of the variable in question. Individual contributions were then summed and a percentage of relative importance in the model was derived. The R package ‘raster’ v.3.0 (Hijmans 2019) was used to create predictive maps extrapolating relative species richness and abundance predictions over the entire study area. Rasters were created for each year of sampling. The ‘raster calculator’ tool in ArcGIS was then used to combine rasters from all years into a single map by taking the mean of each point in the corresponding rasters.

3. RESULTS

A total of 8233 individuals across 83 taxa belonging to 51 families were observed in this study (Table 2). Observations came from 181 BRUVS deployments,

Table 2. Baited remote underwater video station (BRUVS) observations across all years and all habitats sampled. MPA: marine protected area

	2013	2017	2018	Total
Total no.				
Individuals	2268	2725	3240	8233
Taxa	64	63	65	83
Deployments	75	48	58	181
No. of deployments				
Inside MPA	42	30	37	109
Outside MPA	33	18	21	72
With reef present	64	34	39	137
With sediment present	36	21	24	81
With infralittoral reef present	36	34	39	109
With circalittoral reef present	34	11	18	63

with depths of sample sites ranging from 3–55 m (Fig. 1). Of these locations, 81 sampled sediment substratum and 137 sampled reef substratum (Table 2). The most abundant families observed were Carangidae (26.5%), Sparidae (17.8%), Serranidae (15.9%), Monacanthidae (14.6%), and Labridae (8.6%). The most abundant species were *Trachurus* sp. (25.4%), *Chrysophrys auratus* (17.8%), *Caesioperca* sp. (15.8%), *Meuschenia hippocrepis* (6.4%), and *Notolabrus tetra-ricus* (6.0%). The observed assemblage was dominated by invertivores (50%), followed by herbivores (28%) and carnivores (13%). Of these groups, carnivores had the largest mean size (324 ± 296 mm), followed by invertivores (272 ± 113 mm) and herbivores (243 ± 52 mm).

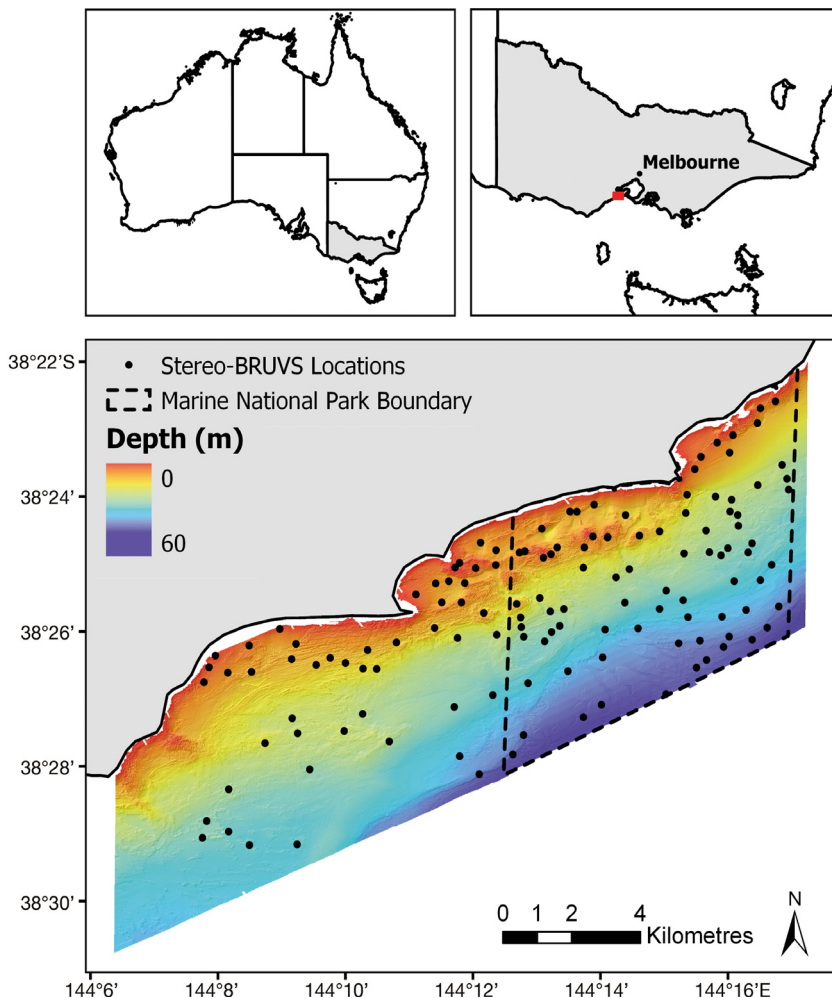


Fig. 1. Point Addis Marine National Park, Victoria, Australia, showing marine national park boundaries and baited remote underwater video station (BRUVS) locations from all sampling years, inside and outside of the park. Underwater video deployment locations are overlaid on high-resolution hillshaded bathymetry of the area

3.1. Model performance across spatial scales

Overall, when relative species richness was modelled for the entire assemblage, there was a distinct highest model performance at a spatial scale of 25 m (Fig. 2). At this scale, 54.3% of the deviance in relative species richness was explained (Table 3). When tested, positive spatial autocorrelation was present up to 1000 m. However, spatial autocorrelation was no longer significant in the residuals after GAMs were run. This suggests that spatial autocorrelation was accounted for within the model via the use of the environmental variables.

When samples were limited by broad habitat groups (reef and sediment), similar trends of decreasing model performance with increasing spatial scale were observed (Fig. 2). However, best model performance was observed at a much finer scale for reef (25 m) than for sediment (50 m). At optimal scales, models using observations from sediment habitats explained 35.6% more deviation than those using observations on reefs. When type of reef was modelled, infralittoral reef showed optimal model performance at a finer scale (50 m) than circalittoral reef (400 m).

This consistent trend of small scales explaining the greatest deviance continued when the species modelled was limited to invertivores (Fig. 3). A total of

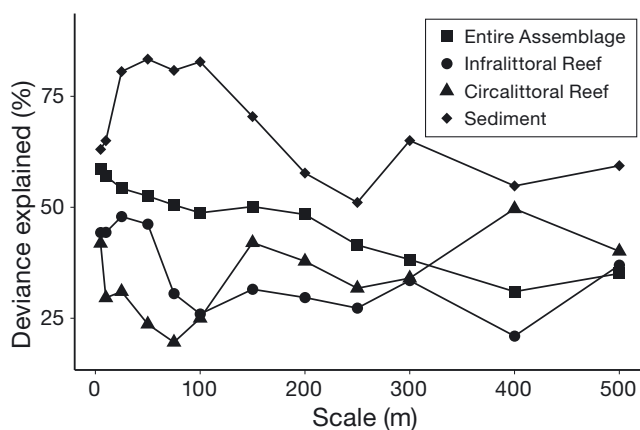


Fig. 2. Trends in model performance across spatial scales for generalized additive models of relative species richness for broad habitat groups

48.8% of the deviance in invertivores was best explained at a scale of 50 m (Table 3), and the general trend was a decrease in model performance with increasing scale (Fig. 3). Furthermore, 39% of the deviance in herbivores was explained at a scale of 25 m (where $\Delta AIC = 0$), with a general trend of a decrease in model performance with increasing spatial scale. Conversely, when the species modelled was limited to carnivores, only 24.4% of deviance could be explained. Carnivores showed a slight (2.6%) increase in model performance with increasing spatial scale between 0 and 500 m radius.

When relative abundances of individual species were modelled, considerable variation was present (Fig. 3). *N. tetricus* showed highest performance between 0 and 250 m scales, with a reduced model performance above the 250 m scale. *C. auratus* showed a pattern of scales between 0 and 300 m explaining the most deviance. However, *C. auratus* showed low predictive ability, with its optimal model explaining only 46.2%. *M. hippocrepis* showed highest model performance at scales between 25 and 200 m, where the optimal model explained 63.2% of the deviance in *M. hippocrepis* relative abundance (Table 3).

3.2. Predictor variable importance

Best performing models for each response variable found year of sampling to be the most common predictor variable across all subsets tested, being present in all optimal models except that of relative species richness on circalittoral reef (Fig. 4). Largest variability was observed for models of individual species, where *C. auratus* showed the largest importance of year, followed by *N. tetricus*. The second and third most common variables across all subsets of the sampled assemblage were depth and distance to reef, respectively. Protection status (MPA status) also proved important in explaining relative species richness on both reef and sediment, as well as for relative richness of herbivorous species.

Table 3. Summary statistics of best performing generalized additive models completed at spatial scales of 5, 10, 25, 50, 75, 100, 150, 200, 300, 400, and 500 m. Descriptor variables used are identified by (+). BPI: bathymetric position index. Summary statistics presented include degrees of freedom, second-order Akaike Information Criterion (AIC_c) (measure of model performance), deviance explained (indication of model goodness-of-fit), and test data correlation (Pearson correlation between test data and corresponding predictions)

Subset	Optimal Scale										Degrees of freedom	Second-order AIC_c	Deviance explained (%)	Test data correlation
		Year	MPA status	Depth	Distance to reef	Rugosity	Curvature	Fine BPI	Eastness	Northness				
Entire assemblage	25	+	+	+	+	+					12	691.83	54.26	0.494
Infralittoral reef	50	+			+		+	+		+	12	442.21	46.20	0.086
Circalittoral reef	400				+		+	+			5	216.66	49.66	0.009
Sediment	50	+	+	+	+	+			+		15	304.19	83.37	0.559
Carnivores	100	+		+			+	+			6	270.15	24.36	0.342
Herbivores	25	+	+	+	+	+	+			+	10	446.47	38.97	0.422
Invertivores	50	+		+	+			+	+	+	15	561.05	48.80	0.460
<i>Chrysophrys auratus</i>	25	+	+	+	+				+		12	869.27	46.23	0.307
<i>Notolabrus tetricus</i>	5	+		+	+			+	+		16	497.06	68.43	0.787
<i>Meuschenia hippocrepis</i>	150	+	+			+	+		+		16	581.22	63.15	0.352

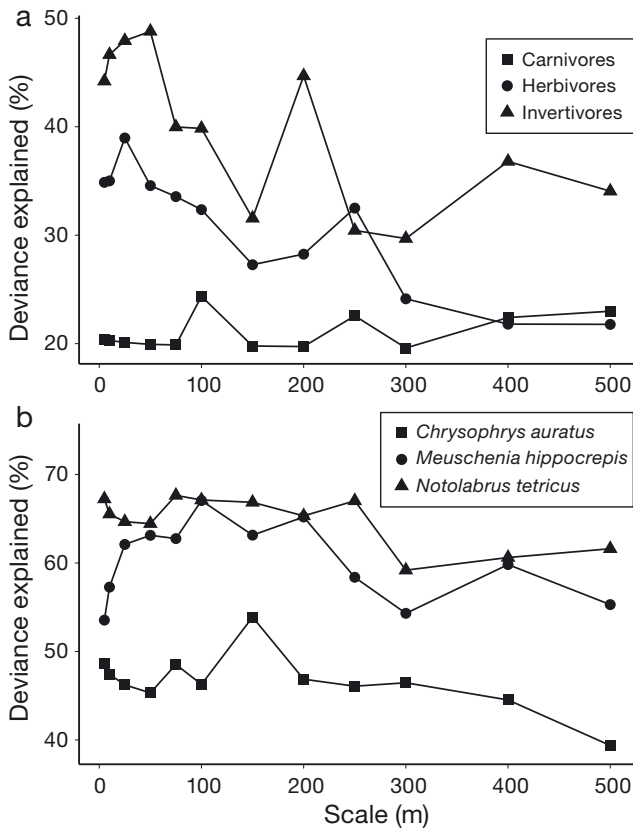


Fig. 3. Trends in model performance across spatial scales for generalized additive models of relative species richness for (a) major functional feeding groups and (b) key species

3.3. Trends of model predictions

When predictive maps were made at the best performing spatial scale for each response variable, considerable variation was present between groups. Models of relative species richness for the entire assemblage showed broad trends across the whole study site. Higher relative species richness was found in complex areas of reef, with lowest relative species richness on areas of soft sediment (Fig. 5). Relative species richness stayed reasonably consistent across the depth gradient, with no clear differences between infralittoral and circalittoral reefs.

Varying trends were found between predictions of functional groups across the entire site (Fig. 6). Highest relative richness of carnivores was observed in deep waters within the MPA. Relative species richness was generally much lower in shallow water. Habitat predictions for herbivores showed strong affinity to certain habitats. Shallow, near-shore reef, synonymous with the presence of macroalgae, presented the highest relative species richness of this group. There was also a discrete boundary of high

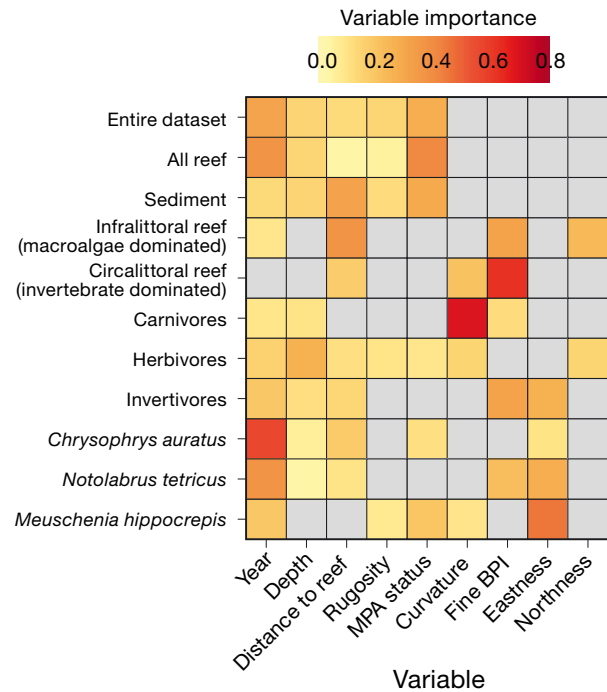


Fig. 4. Predictor variables (x-axis) used in each of the model subsets used in this study (y-axis). Color gradient: relative importance of each variable in its respective model. Values are on a scale from pale yellow (low importance) to dark red (high importance). Blue-gray squares are variables not used in each model subset

and low relative species richness that followed the transition between reef and sediment, with low relative species richness of herbivores present on soft sediment. Finally, relative species richness of invertivores followed reef coverage throughout the study area in the same fashion as herbivores, except invertivores were more predominant on deeper circalittoral reef dominated by sessile invertebrates.

Similar to functional feeding groups, trends at the individual species level were species-specific (Fig. 7). Apart from being slightly higher in deeper habitats, predictions of *C. auratus* relative abundance did not show strong associations with bathymetric features present. Conversely, models for *N. tetricus* showed strong trends of highest relative abundance on shallow macroalgal-dominated reef. Similar to herbivores, *N. tetricus* also observed a strong distinction between areas of reef and sediment, with little to no relative abundance in areas of sediment. Finally, *M. hippocrepis* was predicted to have highest relative abundances on shallow, near-shore infralittoral reef. This species, however, was also wide ranging, having its presence predicted on all broad habitats measured including both infralittoral and circalittoral reefs as well as areas of soft sediment.

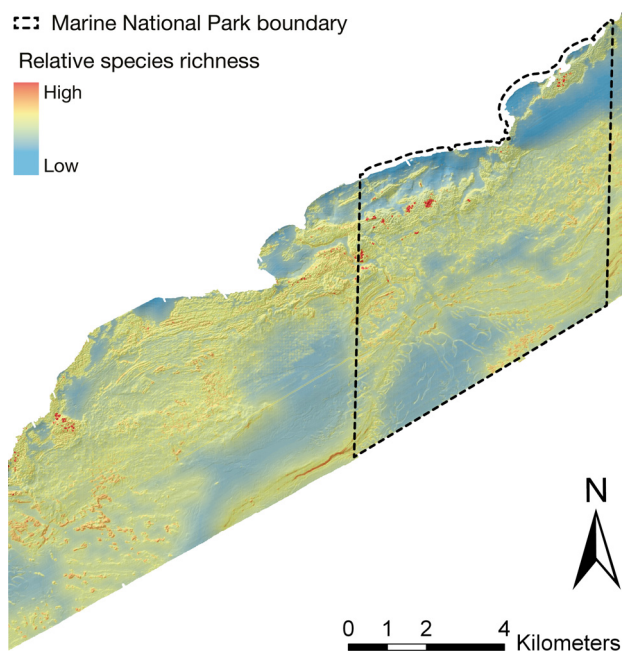


Fig. 5. Mean predicted relative species richness of all years sampled across the entire study site

4. DISCUSSION

These findings show the importance of considering spatial and temporal scales in studies that incorporate multiple functional groups and species of fish. Model performance varied across scales depending on the species and functional traits measured in this study. More specifically, through combining high resolution environmental variables at multiple spatial scales with time-series BRUVS observations, 3 major findings were made: (1) fine spatial scales (5–25 m radius) were found to be optimal for modelling relative species richness within this assemblage; (2) interactions with spatial scale are functional group- and species-specific; and (3) accounting for temporal variation produced increases in modelling performance and accuracy.

4.1. Assemblage-level findings

This assemblage as a whole, as well as habitat subsets, showed similar trends of the optimal spatial scale for modelling being predominantly 5–25 m (extending to 50 m for sediment), showing that the assemblage is predominantly responding to physical habitat characteristics of the seafloor at a spatial range of 5–25 m. These scales are logical when considering the prevalence of temperate fish species

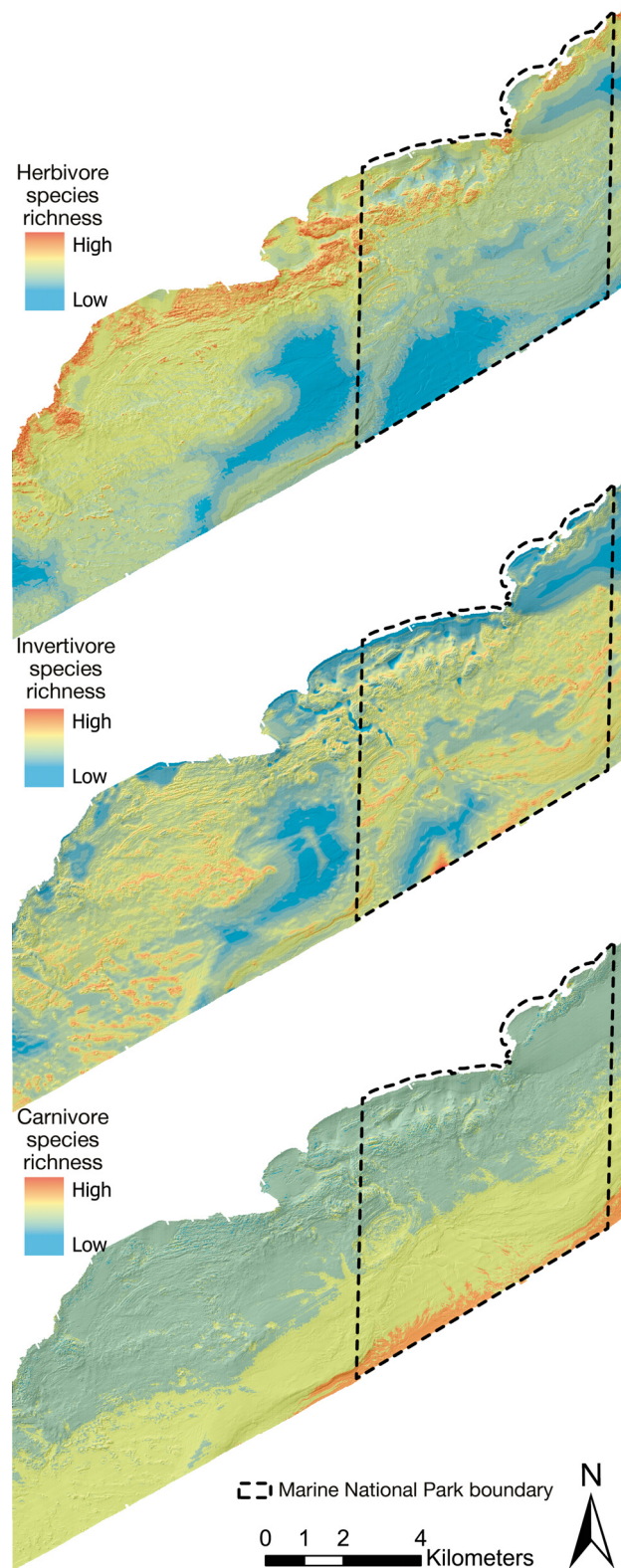


Fig. 6. Mean predicted relative species richness of all years sampled across the entire study site, broken down into functional feeding groups (carnivores, herbivores, and invertebrates)

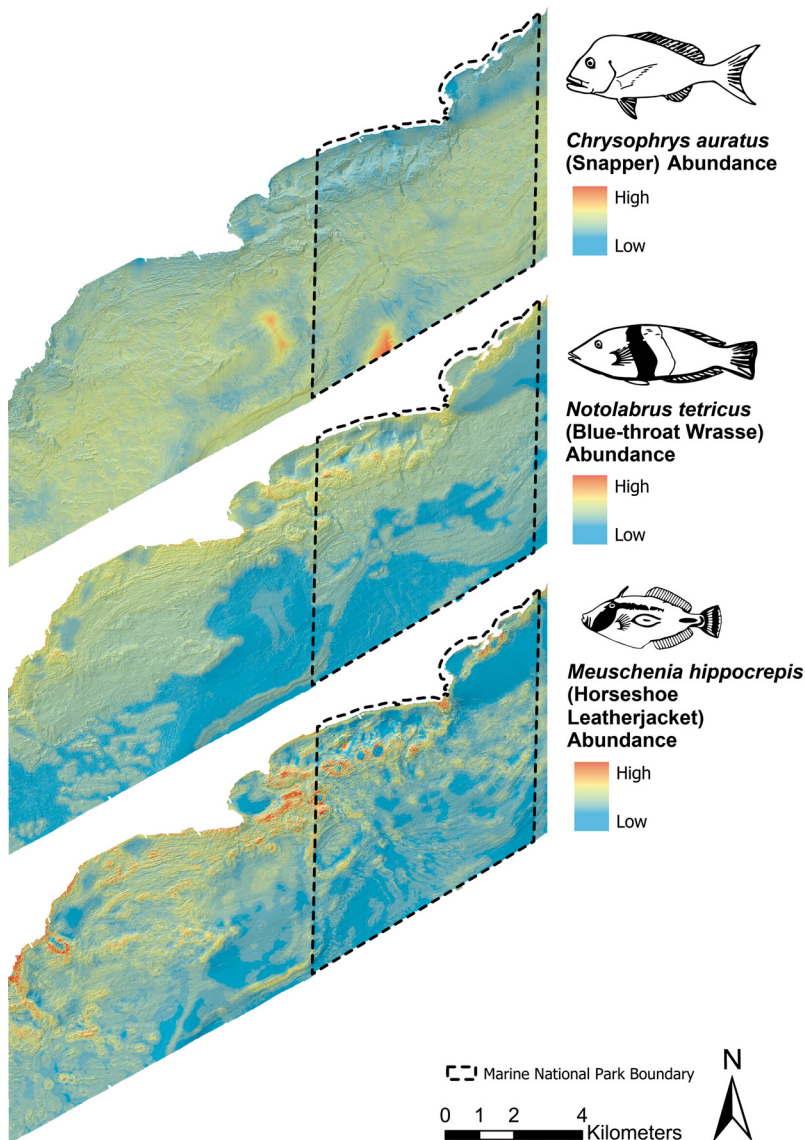


Fig. 7. Mean predicted relative abundance of all years sampled across the entire study site, broken down into key species (*Chrysophrys auratus*, *Notolabrus tetricus*, and *Meuschenia hippocrepis*)

previously shown to be site-attached, such as *Notolabrus tetricus* (Labridae), *Pictilabrus laticlavius* (Labridae), *Pseudolabrus rubicundus* (Labridae), *Cheilodactylus fuscus* (Cheilodactylidae), *Hypoplectrodes maccullochi* (Serranidae), *Ophthalmolepis lineolatus* (Labridae), and *Parma victoriae* (Pomacentridae) (estimated home range radius of 8–16, ~8, 10, 24, 4–23, 1–11.6, and 3–26 m, respectively), that were present (or had a close relative present) in this study (Norman & Jones 1984, Barrett 1995, Lowry & Suthers 1998, Kingsford & Carlson 2010). Models of sediment areas found a larger scale of 50 m to be optimal, potentially due to low relative species rich-

ness being present in sediment habitats (Fig. 5). This could mean that mobile species travelling to these samples will have a larger influence on trends, as they will make up a greater proportion of the overall relative species richness (Cappo et al. 2004). Furthermore, assemblages with a greater prevalence of higher-order mobile species will generally have a larger optimal spatial scale (Nash et al. 2015). Variability in optimal scale between habitats indicates that the optimal scale for sampling assemblages is dependent on the species composition present.

4.2. Functional/species-level findings

This study shows the importance of considering the relationship between spatial and temporal scales and the behavioral characteristics of the subject when trying to model distributions. Large variations in performance across scales were present for the species and functional groups measured in this study, as was found in Rees et al. (2018). Scale-dependent effects are likely to be driven by species affinity for terrain characteristics (Lecours et al. 2015), movement patterns such as home range (Kramer & Chapman 1999), and species behavioral traits and interactions (Pittman et al. 2007a). Pittman & Brown (2011) exhibited this when they predicted distributions of 5 fish species

at multiple spatial scales on coral reefs. Not only were species found to respond differently to environmental drivers, spatial scale was also found to be species-specific. Our study reiterates these previous findings with highly variant trends across models of functional groups and individual species. Our findings also extend the observations of Pittman & Brown (2011) from a coral reef setting into the temperate environment.

Observations of low model performance for carnivores indicate that occurrences of this group were unable to be strongly tied to environmental variables, even at the larger spatial scales tested in this study.

This pattern was further supported by trends in model performance which, although variation was small, showed high performance at larger scales (between 250 and 500 m). Higher-order predators such as carnivores are known to be highly mobile and utilize multiple habitat types (Chapman & Kramer 2000). This is further supported by our findings that the mean size of carnivores in this study was substantially larger than all other functional groups observed. Large body size is a common indicator of mobility in fish (Kramer & Chapman 1999). Therefore, it is expected that highly mobile species are difficult to model at fine habitat scales, as they travel across a broader range of habitats with high occurrence variability (Ward-Paige et al. 2010, Andradi-Brown et al. 2016). These results were further supported by *Chrysophrys auratus*, which showed similar patterns to the carnivore functional group when predicted across the entire site. This species similarly showed low overall model performance. *C. auratus* has previously been described as a 'non-territorial' species with a home range of approximately 300 m (Parsons et al. 2003), although movement patterns are known to vary between populations (Harasti et al. 2015). Logan et al. (2017) found significantly higher relative abundance of *C. auratus* when using BRUVS compared with a ToV method, indicating BRUVS may be aggregating these fish at a larger spatial scale. Our findings suggest that BRUVS sampling must consider the variability of occurrence and broader optimal spatial scales to develop strong delineations of spatial variation for higher order species such as *C. auratus*.

Models for herbivore and invertivore species performed better than those for carnivores. An indicator of good model performance was that predictions followed well-known spatial patterns in habitat use. For example, models of herbivores showed a discrete reef–sediment boundary (Harvey et al. 2007), and highest abundances of *N. tetricus* were predicted on infralittoral (macroalgae-dominated) reef (Shepherd & Clarkson 2001, Monk et al. 2011) whilst still being present on circalittoral reefs (Edgar 2008). There is very little existing information about the final species modeled in this study, *Meuschenia hippocrepis* (Matsuura et al. 2010). This species has previously been observed at depths to 120 m and in areas of shallow macroalgal reef, and its diet is known to consist of predominantly sponges, and red and brown algae (Rodgers et al. 2013). Our findings indicate that *M. hippocrepis* does have higher relative abundance on shallow macroalgal reef, but can also be found in sizeable relative abundances on circalittoral, sessile-

invertebrate dominated reef. Structural characteristics of the seafloor were the dominant predictor of *M. hippocrepis* relative abundance. Highest relative abundances were observed in areas of highest seafloor complexity. The corroboration of our results in the literature provides confidence in this modeling approach to capture suitable habitat for these species.

These findings indicate that future studies should carefully consider the subject of their study and, additionally, the optimal scale of their subject in order to obtain best model performance. We found that BRUVS sampling provides a suitable approach for fine-scale spatially explicit modelling of herbivore and invertivore species. Our findings also indicate that highly mobile species, many of which are carnivores and targeted by fishers, cannot be modelled with high performance at fine scales using BRUVS sampling due to the nature of their mobility and lack of habitat affinity. Nevertheless, BRUVS may still provide a useful method of monitoring mobile species and informing management, if sampling is conducted over broader regions and across more years. Further studies may also find merit in implementing a truly multiscale approach, as used in Porskamp et al. (2018), where multiple scales of variables can be included in a single model.

4.3. Variable importance

Year of sampling was the most important variable for explaining deviance within this assemblage. Temporal variation in fish assemblages is a well-documented phenomenon (Charton & Ruzafa 1999), but is often overlooked in BRUVS sampling designs, as it is more cost-effective to complete sampling in one campaign as opposed to multiple campaigns. Whilst it depends on the question of a particular study, here we showed the potential extra variation that can be captured using temporal sampling, especially in an SDM context. Across the entire assemblage, the inclusion of year of sampling as a variable contributed 31% to model performance. This could be influenced by a range of underlying factors, including fluctuations in water temperature due to events such as El Niño (which occurred in this region between 2015 and 2016), variations in sampling design, variation in environmental drivers between years, or protection effects over time. Without a longer time-series, however, understanding directionality or cause of changes between years is not possible due to low statistical power to detect change

(White 2019). Furthermore, high variability across years was observed for some species such as *C. auratus*, in which temporal variation explained 56% of the total deviance in its respective model. *C. auratus* is a higher trophic order species, and whilst it exhibits high variation in movement patterns between populations (Harasti et al. 2015), is known to have considerable seasonal variation (Willis et al. 2003, Egli & Babcock 2004). Sampling designs for such species should ideally incorporate longer sampling periods to understand inter-annual variability, reduce potential effects of outlier years of sampling, and detect trends of these species through time (Malcolm et al. 2015). Regardless of the underlying drivers, however, these results show the considerable benefits of including time-series data in SDMs.

Whilst not as important as year of sampling, our results demonstrated depth and various measures of topographic complexity to be among the most important covariates used in this study. These variables are widely recognized as important predictors of fish assemblage structure (Friedlander & Parrish 1998, Anderson & Millar 2004, Moore et al. 2010, Cameron et al. 2014). The importance of depth is commonly reported throughout the literature (Malcolm et al. 2010, Moore et al. 2011, Schultz et al. 2014). Our findings supported this, with depth being the second most important variable in our study. Depth is often correlated with (and can thereby act as a proxy for) variables such as light attenuation and wave energy in benthic environments (Logan et al. 2017), thereby explaining results for herbivorous species, which showed decreasing relative species richness at deeper depths where their food source is limited (Fig. 6). For the entire assemblage, as well as for carnivores and invertivores, relative species richness was found to increase with depth (Figs. 5 & 6), which supports the work of Moore et al. (2010), who found that species richness of a temperate fish assemblage increased with depth and was highest between 20 and 50 m. Our study showed these trends to be especially prevalent in models created for carnivores and invertivores, where highest relative species richness was predicted to be found in the deeper, mesophotic zone (>30 m depth) (Fig. 6). Areas of high complexity are also commonly related to higher fish abundance and species richness than less complex areas (Galai-duk et al. 2017a). Our results support these observations, with distance to reef and rugosity being the third and fourth most important variables in this study, respectively. Furthermore, highest relative species richness and abundance was commonly observed in highly rugose areas.

4.4. Management implications and future challenges

The inclusion of BRUVS sampling in monitoring programs provides a means of conducting high densities of spatially explicit sampling across entire seascapes. This sampling allows management agencies to understand spatial variability through marine environments and track these environments through time. When supplied with appropriate environmental surrogates (such as temperature or seafloor structure) that capture the environmental variability of a site, SDM approaches allow patterns of biodiversity to be predicted beyond sampled locations (Araújo & Guisan 2006, Sequeira et al. 2016, Ferrari et al. 2018). SDM is relevant for a range of applications, such as identifying diversity hotspots in MPA creation and management (Ferrari et al. 2018), tracking invasive species, and researching effects of climate change (Elith & Graham 2009). This study, for example, was able to predict areas of high relative species richness and abundance across an area of over 100 km², including across the entire extent of a marine national park. Alternatively, if statistical patterns in temperate species richness, biomass, and environmental variables extend beyond the region sampled, they can be used to infer potential patterns in biodiversity in new, under-represented regions (Sequeira et al. 2016). Globally, high resolution seabed bathymetry is recognized as important for informing ecosystem-based management (Cogan et al. 2009, Mayer et al. 2018). As global initiatives to improve our understanding of seabed structure expand, greater opportunities for testing the transferability of such models to new less explored areas will increase (Mayer et al. 2018).

Predictive modelling approaches, such as those used in this study, provide an important, cost-effective tool for understanding fish assemblages across large spatial areas, including across MPAs and networks of MPAs. However, knowledge of the spatial scale at which a survey method samples is important for providing the most representative models. We have shown that the scale of the analyses and the characteristics of target species are important considerations when predicting the spatial ecology of a particular assemblage or functional subset. We further illustrated the potential extra variation that can be captured via temporal sampling, especially in an SDM context. These results provide evidence that BRUVS sampling can be a powerful tool for spatially explicit distribution modelling for applications in marine spatial management if scale, functional characteristics, and temporal variation are sufficiently incorporated.

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