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Statewide assessment of Victorian marine protected areas using existing data

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#### **Authors**

Mary A. Young, Peter Porskamp, Kay Critchell, Eric Treml, Daniel Ierodiaconou – Deakin University Jacqui Pocklington – Deakin University and Parks Victoria (former)

Michael Sams – Parks Victoria

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Front cover: Perch (Caesioperca spp.) swim around sponges and soft coral in Port Phillip

Photo: Parks Victoria

#### **Executive summary**

Along the 2,000 km Victorian coast, Parks Victoria manages a system of 13 marine national parks and 11 sanctuaries, which make up approximately 5.3% of Victoria's state waters. These marine protected areas (MPAs) were declared to be a comprehensive, adequate and representative sample of the state's marine habitats based on the best available knowledge at the time. Good park management requires an understanding of the natural values that occur within these parks, sanctuaries and reserves and the threats to these values. Since their designation, a large amount of data has become available, including information on seafloor habitat, surveys of biological communities, and satellite and modelled oceanographic data. The purpose of this study is to use this newly available information to assess the representation of habitats across the MPAs, the representation of environmental conditions, the change in environmental conditions through time and the connectedness of MPAs.

Using available data collected by multiple methods and groups from 1998 to 2019 across the entire coastal zone of Victoria, Australia, this study assesses the representation of habitat and conditions across the Victorian marine parks and the distributions of multiple marine species and groups.

#### This report aims to:

- produce derivatives of the bathymetry data and determine how well different habitats are represented and replicated across the Victorian MPAs
- incorporate biotope habitat maps (which used a combination of ground truth data including towed video, baited remote underwater video stations (BRUVS), remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs), and diver observations) produced for the Victorian Environmental Assessment Council (VEAC) to see how well biotopes are represented across Victoria
- use sea-surface temperature (SST) and hydrodynamic information to assess the representation of oceanographic characteristics across the Victorian MPAs and trajectories of change across the time series to determine which MPAs are experiencing changing oceanographic conditions, potentially putting them at risk
- use outputs from connectivity models to assess how well connected the MPAs
  are to each other and suitable habitats outside the MPAs. This information will
  allow us to determine whether MPAs are serving as sources and/or sinks for a
  variety of life history traits present in the Victorian state waters
- use a collated time series of biological data for subtidal reefs (data collected by Subtidal Reef Monitoring Program (SRMP) and Reef Life Survey (RLS) programs) and a machine learning approach to determine how fish, invertebrate and

macroalgae communities are changing through time while accounting for variations in habitat, oceanography and degrees of connectedness inside MPAs and their associated biological regions

- use the collated BRUVS data across the state to develop fish species and fish
  community distribution models for all mapped areas within state waters. The
  predictive maps from this objective will help to determine where hotspots for
  fish diversity and species abundance are across the state, allowing assessment of
  representativeness of the MPA network
- assess and rank Victorian MPAs for effectiveness based on whether they meet each of the 5 criteria adapted from Edgar et al. (2014) as well as whether biodiversity is increasing or decreasing in each of the MPAs. The 5 criteria are: level of human impacts (using the proximity of an MPA to population and ports as a proxy), how well enforced the MPA is, size of the MPA, relative biodiversity in the MPA and how isolated the MPA is based on habitat and depth barriers derived from the seafloor mapping data.

The main findings of this report are briefly summarised below.

Victorian MPAs represented the major habitat types and biotopes found within their biounits. However, subtidal rocky reef habitats and their associated biotopes tended to be over-represented in MPAs across the state, while sediment habitats and their associated biotopes tended to be under-represented. This was not always the case, though, with some MPAs over-representing sediment habitats, especially those encompassing deeper depth ranges like Wilsons Promontory Marine National Park (MNP). Some rarer biotope classes like Rhodolith beds and Non-reef epibiota were not well captured in MPAs.

The oceanographic and environmental conditions of the broader biological regions were well represented in MPAs, but marine sanctuaries tended to capture areas of higher energy (higher wave orbital velocities and currents speeds) due to their shallower depths. Overall, the larger marine national parks more adequately captured the oceanographic and environmental conditions in each region.

Connectivity models showed strong geographic patterns across the state, and patterns of connectivity were similar within the MPAs and their associated biounits. A higher total amount of larvae settled in the west and east of the state, and self-recruitment was higher in the central part of the state and in MPAs in the far west. Central and eastern parts of the state had a higher number of connections between habitats.

Machine learning approaches were effective at identifying the relationships between species and groups of species with environmental and habitat variables. Stronger relationships were found with communities, followed by the abundance of species and functional groups. Overall, cooler temperatures, lower wave energy, higher current speeds

and more complex seafloor habitat supported the greatest abundance and diversity of species. The relationships identified through this approach can be used to inform MPA management by providing information about the types of conditions that will best support a given species or group of species. These conditions can then be targeted for management interventions (e.g., compliance, enforcement or restoration) in an MPA if conservation of that species or community is a goal.

The combination of BRUVS and habitat mapping data allowed for effective species distribution models to be produced for the whole state. Models for species richness and diversity performed well and had good predictive power, showing that richness and diversity hotspots occurred around reef habitat. This suggests that the over-representation of reef found in MPAs is beneficial for preserving biodiversity. Models for individual species had mixed performance and predictive power. Models for highly site-attached species tended to perform better than those for less site-attached species, but all could be used to gain an understanding of the distribution of species inside and outside MPAs.

The assessment of MPA effectiveness found that fish species richness was higher inside MPAs than outside. Larger MPAs with fewer habitat and depth barriers supported a higher richness of fish, while fish richness declined in MPAs closer to human populations and ports. Invertebrate richness was also higher inside MPAs than outside, but MPA size and reef area had complex effects. High richness is found in both small and large MPAs, while there is an initial increase in invertebrate richness as reef area increases followed by a decrease and/or flattening off.

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# Part 1 – Habitat and oceanographic patterns across Victorian marine protected areas

#### 1. Introduction

Marine protected areas (MPAs) are place-based tools used for conservation in the marine environment. Usually set up with the goal of conserving biodiversity, MPAs both conserve fishery-targeted species and protect unexploited species and the habitats they depend on (Roberts and Hawkins, 2000; McNeill, 1994). Along the 2,000 km Victorian coast, Parks Victoria manages a system of 13 marine national parks and 11 sanctuaries, which make up approximately 5.3% of Victoria's state waters. These marine protected areas were declared to be a comprehensive, adequate and representative sample of Victoria's marine habitats based on the best available knowledge at the time. Victoria's marine national parks and sanctuaries were designated with the specific ecological goal of preserving examples of Victoria's biodiversity and associated ecological processes, including their variation in space and time, in a relatively natural condition for their intrinsic value to future generations. To achieve this goal, Victoria's MPAs must contain a variety of habitats that are representative of regional biodiversity, ecological processes and ecosystem functions. Replicating habitats across MPAs is important for safeguarding against localised disturbances, both naturally occurring (e.g. storms) and human-induced (e.g. oil spills) perturbations. Successful MPAs also need to function as a connected ecological network that supports the replenishment of populations. This requires that they are appropriately spaced and contain suitable amounts of habitat to support populations large enough to provide sufficient larval production for successful dispersal among MPAs.

Since the designation of Victoria's MPAs, a large amount of data has become available, including extensive surveys of biological communities, information on seafloor structure and depth from seabed mapping and on spatio-temporal variability in sea-surface temperatures (SST), and hydrodynamic data to understand trends in waves and currents and to provide information for modelling connectivity across MPAs. This newly available information provides an opportunity to re-assess the representation of habitats, environmental conditions and changes in environmental conditions through time, and the connectedness of Victoria's MPAs. It enhances our ability to determine if any habitats or environmental conditions are not well represented, providing an indication of whether biodiversity is being adequately protected, since some species may be only found in certain habitats or under certain environmental conditions. Additionally, any habitats or environmental conditions not currently represented could be the target of future MPAs if additional protection is necessary to preserve the biodiversity along the Victorian coast.

Seabed mapping has become an important process in the design and/or evaluation of MPAs across multiple spatial scales (Jordan et al., 2005). With the further development of sonar and aerial mapping abilities, seabed mapping has become the most cost-effective and reliable way to quantify habitat types across multiple spatial scales (Foster-Smith and Sotheran, 2003; Jordan et al., 2003; Kenny et al., 2003). Through these maps, managers can determine the distribution of marine ecosystems and habitats important to species targeted for protection (Bax and Williams, 2001; Roff et al., 2003). Information on the distribution of species and communities is often limited, and products from seabed mapping can also be used as surrogates for species diversity and distribution where direct measures are not available (Ward et al., 1999). Marine species are not randomly distributed throughout the marine environment; they are found in certain habitat types that can be derived from seafloor data. For example, differences in substratum type are a major cause of change in community assemblages, with different species relying on either consolidated (rocky) or unconsolidated (sandy) habitats (Bax and Williams, 2001). Further separation occurs within each of these habitats depending on the heterogeneity of the substrate. Within consolidated habitats, communities strongly associated with high relief, more complex rocky reef often differ from those associated with lower relief rocky habitat. Similarly, species found in soft-sediment communities can vary across grain size or structure (e.g. sand waves, flat sediment, scoured depressions) of the sedimentary habitat (e.g. Hallenbeck et al., 2012). Assemblages vary with depth in consolidated and unconsolidated habitats (e.g. Young and Carr, 2015). Many studies have shown how seabed surrogates derived from geophysical features help in assessing efficacy of MPAs (Rees et al., 2014; Young and Carr, 2015; Zacharias et al., 1998). Where the relationships between biotic composition and seabed surrogates are well understood, or have been identified through surveys, they can be used to further classify habitat into habitat categories defined by both the biotic and abiotic components of the environment. Thus, seafloor mapping data and the secondary derivation of its characteristics can greatly aid our understanding of the representativeness of habitat types in MPAs (Brown et al., 2011).

Environmental conditions are also important to consider in assessing representativeness because variations in conditions such as temperature and waves can affect the biodiversity present. Therefore, as well as including areas representative of the range of seafloor habitats, MPAs should also include areas representative of the range of environmental conditions; this becomes even more even more important as MPAs throughout the world are being affected by climate change (Bruno et al., 2018). Sea-surface temperatures (SST) are increasing as the oceans absorb 90% of the heat trapped in the atmosphere from anthropogenic greenhouse gas emissions (Gleckler et al., 2016), which could cause SST to exceed the thermal tolerances of species within the boundaries of MPAs (Bruno et al., 2018). Although much of the research on climate change impacts focuses on changing temperatures (Harley et al., 2017), waves and currents are also important aspects of the habitat and are changing with climate change. Wave energy has been shown to be a primary

variable influencing the morphology, community structure and spatial organisation of taxa in the marine coastal zone (Rattray et al., 2015), and it determines benthic habitat availability through a number of direct and indirect processes (Young et al., 2015). Wave exposure is also an important agent of stress and disturbance through sediment flux processes, specifically abrasion, burial and limitation of light availability, or mechanical tearing or removal of sessile species from their places of attachment. Future projections indicate that Victorian waters will continue to be impacted by a changing wave climate with a predicted increase in Southern Ocean wave heights through the 21st century (Fan et al., 2014). The southern and western coasts of Australia are exposed to this projected continued increase, with offshore significant wave heights projected to increase by a further 30 to 50 cm over the 21st century (Hemer et al., 2013). In addition, patterns and characteristics of ocean currents are important in determining larval dispersal patterns in most marine taxa as their pelagic larvae often have poor swimming capacity relative to the velocity of currents. Thus, currents determine patterns of connectivity among MPAs (Cowen and Sponaugle, 2009). Understanding how the SST and hydrodynamics vary off the coast of Victoria inside and outside MPAs can help to better manage them into the future.

This part of the report uses the more recently available datasets described above to assess the representation and replication of habitats across Victoria's MPAs. More specifically, this chapter aims to better understand how well habitats and environmental conditions are represented across the Victorian MPAs by:

- producing derivatives of the bathymetry data to determine how well different habitats are represented and replicated across the Victorian MPAs
- incorporating biotope habitat maps (which used a combination of ground truth data including towed video, baited remote underwater video systems (BRUVS), remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs), and diver observations) produced for the Victorian Environmental Assessment Council (VEAC) with bathymetry data to see how well biotopes are represented across Victoria
- using SST and hydrodynamic information to assess the representation of oceanographic characteristics across the Victorian MPAs and examine trajectories of change across the time series to determine which MPAs are experiencing changing conditions, potentially putting them at risk
- using outputs from connectivity models to assess how well connected Victoria's MPAs are to each other and suitable habitats outside the MPAs and to assess whether or not MPAs are serving as sources and/or sinks for organisms displaying a variety of life history traits present in the Victorian state waters.

Meeting these objectives will give a more complete picture of the habitats and environments protected within Victoria's MPAs and how well those habitats represent what is found in the entirety of the Victorian marine environment. This information can then be used to identify any gaps in protection of habitats under the current designation that may have implications for biodiversity conservation. It will also inform the placing of future MPAs to fill these gaps.

#### 2. Methods

#### 2.1 Study region

The study region for this project is within the coastal waters of Victoria, Australia, extending along ~2,000 km of coastline (Figure 2.1). This coastline encompasses a mix of seafloor topographic features, and there is a strong temperature gradient with warmer waters in the east (Hobday and Lough, 2011) and cooler waters in the west (Frusher et al., 2013). The orientation of the coast to dominant swell directions affects the distribution of persistent high-energy swells (Porter-Smith et al., 2004), which also vary along the coast. Currents also vary spatially and temporally. Prevailing westerlies drive the west-to-east water currents observed in Bass Strait (James and Bone, 2011) while geostrophic currents (which, instead of moving from an area of high pressure to low pressure, are forced by the counterbalancing Coriolis effect to move along a line of equal pressure) are primarily driven by tides, wind, coastally trapped waves and density-driven flows (Sandery and Kaempf, 2007). Further descriptions of each of the datasets used to assess the representation of habitats and environmental conditions along the Victorian coast are provided below.

## 2.2 Victorian biogeographical units (biounits)

To assess how well MPAs represent the habitats and environmental conditions along the Victorian coast, the MPAs were compared to the habitats and conditions within their corresponding biogeographical units (biounits). Biounits are local biogeographical units defined by their physiographical setting including oceanography, geomorphology and ecosystem types present (Edmunds and Flynn, 2018b). Biounits represent a further classification of the Integrated Marine and Coastal Regionalisation of Australia (IMCRA) provinces and bioregions (Commonwealth of Australia, 2006). There are 26 individual biounits located within the Victorian coastal waters (Figure 2.1). Each Victorian MPA is associated with one of these biounits.

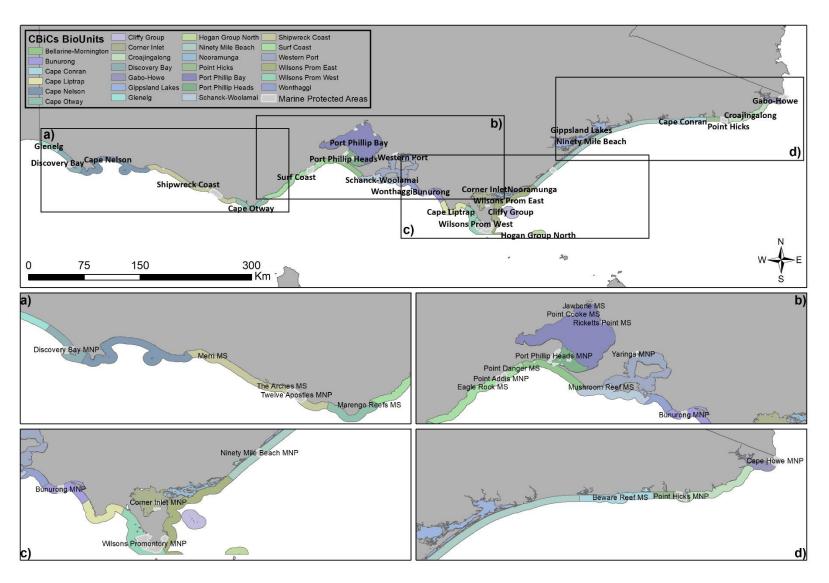


Figure 2.1: Victorian biogeographical units (biounits) across Victoria and the marine protected areas distributed within them

#### 2.3 Seafloor structure and depth datasets

LiDAR bathymetry data were commissioned by the Department of Environment, Land, Water and Planning (DELWP) of the Victorian State Government. This dataset includes seamless terrestrial—marine mosaics from elevations of +10 m to depths of –25 m, for a surface coverage exceeding 10,000 square kilometres (km²). These data were collected in 2008 and 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 swathe width of 240 m, leading to line overlap of 10 m and resulting in a topo-bathy raster grid at 5 m resolution registered to the Australian Height Datum (AHD).

Multibeam bathymetry data to fill the gap from the edge of the LiDAR survey to the state waters limit is ongoing, but many sections of the state have been mapped through multiple efforts. The Victorian Marine Habitat Mapping project has collected multibeam data over large parts of the state waters including the region around Cape Otway and the majority of the marine parks in collaboration with the Cooperative Research Centre (CRC) for Coastal Zone, Estuary and Waterway Management (the Coastal CRC). Parks Victoria programs have more recently supported seafloor mapping at Wilsons Promontory and Bunurong marine national parks and The Arches and Merri marine sanctuaries. The Victorian Coastal Monitoring Program is collecting data to fill a gap from the Cape Otway region west to Port Fairy, Victoria. The combination of all these efforts has resulted in a significant proportion of the state waters mapped to high resolution (1 to 5 m resolution). All these data are referenced to the Australian Height Datum to match up with the LiDAR dataset, providing full-coverage seafloor data from the coast to the 3 nautical mile limit for large sections of state waters.

Prior to assessing the representation of seafloor habitat within the MPAs and their associated biounits, we wanted to determine the total coverage of seafloor data available within each of the areas. The effort put in to map the areas within the MPAs means that a high percentage of the area within MPAs (up to 100%) is mapped. In contrast, the biounits are only consistently mapped to the depths of the LiDAR bathymetry (around 20 to 30 m), resulting in lower percentages being mapped. Therefore, we calculated the percentage of each area mapped within the biounits and MPAs to get an idea of how robust the habitat comparisons would be and incorporated these differences into our analyses.

#### 2.4 Substrate classification

The combination of multibeam and LiDAR bathymetry now allow for analysis of seafloor habitat representation and replication across Victorian MPAs. To assess the representativeness of MPAs based on seafloor habitat, we classified the seafloor into 2 distinct substrate classes: sediment and rocky reef. These substrates were classified using a

decision tree classification from the methods detailed in lerodiaconou et al. (2011) and Zavalas et al. (2014). Results from the decision tree classification were further edited using manual raster editing tools within the 'Raster Cleanup' toolbar (ESRI, 2011). The substrate classification for the state waters can be seen in Figure 2.2. The manual editing was conducted by removing any areas of misclassification due to data artefacts or clear classification errors to produce an accurate substrate classification for the state of Victoria. The substrate classification was then divided into 10 m depth bins. The final substrate by depth raster was used to calculate the area of each substrate class within each MPA and the corresponding biounit areas using the 'Tabulate Area' tool in ArcGIS Spatial Analyst 10.x (ESRI, 2011). We then calculated the percentage cover of each depth-substrate class within the biounits and MPAs and compared the proportions of each class. Using a difference in proportion of 20%, a common threshold when comparing percentages (Mapstone, 1995), we determined whether the habitat classes were proportionately captured in the MPAs. Habitat classes that exceeded the 20% difference in proportion threshold within MPAs were considered to be over-represented (where the proportion in the MPA was at least 20% higher) or under-represented (where the proportion in the MPA was at least 20% lower).

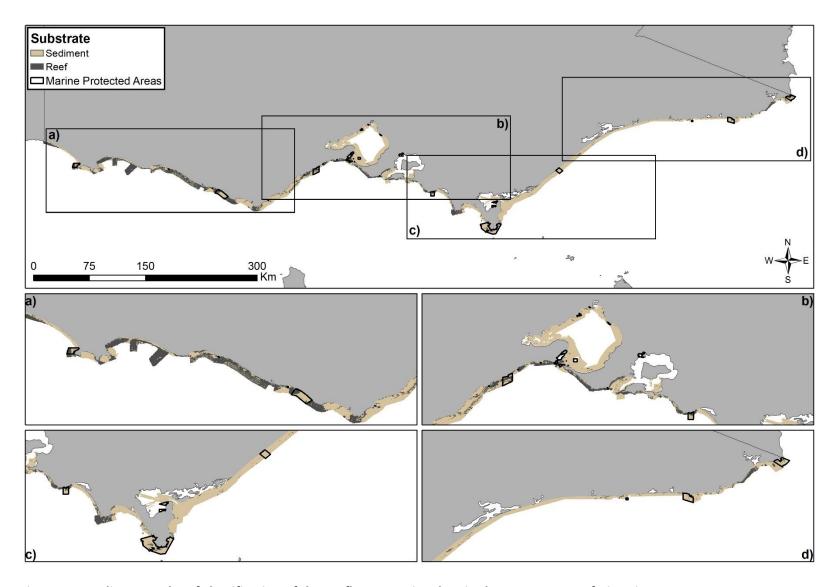


Figure 2.2: Sediment and reef classification of the seafloor mapping data in the state waters of Victoria

#### 2.5 Biotope complex classification

Prior to developing biotope classification maps, ground truth data were compiled from several sources along the Victorian coast including towed video, remotely operated vehicles, autonomous underwater vehicles and scuba in the shallower regions. Ground truth data were classified using the Combined Biotope Classification Scheme (CBiCS) (Edmunds and Flynn, 2018a) which has been adopted by the Department of Environment, Land, Water and Planning. The ground truth data were compiled for all available existing georeferenced classified benthic video and scuba transects throughout the Victorian coastline. This was compiled, processed and classified by Matt Edmunds and Adrian Flynn, funded by DELWP, and provided to the Deakin Marine Mapping Group.

The ground truth data were segmented into multiple categories of habitat type for each of the CBiCS hierarchy levels based on observations of biota, substrata, geoform, exposure, and biogeographic region (Edmunds and Flynn, 2015). CBiCS uses components of 2 systems: the Joint Nature Conservation Committee – European Nature Information System (JNCC– EUNIS) and United States Coastal and Marine Ecological Classification System (CMECS). There are a total of 6 hierarchical biotope levels within CBICs (BC1 to BC6). For a full breakdown and explanation of CBiCS, please see the CBiCS catalogue online: https://devcoastkit.cbics.org/cbics\_view. With the current ground truth dataset provided, only records to BC4 and coarser (i.e. B1 to B3) were deemed suitable for predictive classification modelling because the number of observations for most of the categories at the BC4 level and lower were sufficient to develop statistical models for extrapolation across the state. BC4 is the biotope complex level; it provides information on the environmental conditions (e.g. wave environment) and the dominant biological component (e.g. canopy-forming macroalgae, rhodolith beds). This level lacks information such as understorey species but still provides a good indication of the type of biological habitat present. Ground truth data at BC5 (biotope level) and BC6 (sub-biotope level) were not classified either because certain classes could not be separated using the current classification models or because too few ground truth records were available in the dataset. (Statistical analyses need a large number of observations for each class when predicting across broad geographic regions such as the state waters of Victoria.) Information for BC5 and BC6 was retained in the final habitat map with inclusion of direct 'video ground truthing observation' polygons. Biotope classes at levels BC2 (broad habitat level) and BC3 (habitat complex level) were classified using the direct hierarchical records corresponding to their BC4 habitat classification.

The compiled and processed observation dataset used to classify habitat types into CBiCS classes consisted of 25,006 individual records statewide. This dataset was then assigned to subsets determined by the spatial coverage of each biounit. A predictive classification model was produced for each subset of ground truth data within each biounit. For each classification model, only level BC4 classes with greater than 30 records were included. An exception was made for some individual classes with between 20 and 30 records that were

included due to physical uniqueness or the ecological value of the class (e.g. high-energy *Durvillaea* communities, rhodoliths). To ensure only a single towed video observation represented each raster cell, the observation data were thinned with a buffer of 4 m between observations. Where only polyline transect data were provided, lines were resampled to point data at 10 m intervals with a 10 m buffer, and only the original point data were retained within this buffer. These ground truth records were then associated with a variety of environmental variables outlined in Table 2.1 using machine learning, which is a statistical approach that determines significant relationships between biotope classes and seafloor and environmental characteristics. These associations were used to extrapolate the observation data across the state where mapped data were available.

Table 2.1: Predictor variables showing variable equations and descriptions

Derivative variable <sup>1</sup>	Abbreviation	Pixel kernel size (2.5 m resolution)	Description
Average current speed	Curr15	15 × 15	Average current speed (annual, 1990–2015)
Vector ruggedness measure	Vrm15	15 × 15	Incorporates the heterogeneity of both slope and aspect using 3-dimensional dispersion of vectors. See Sappington et al. (2007) for more details
Bathymetry mean	BathAvg17	17 × 17	Local mean value of pixel to neighbourhood $x = (\Sigma Xi)/N$
Average wave orbital velocity	WavA15	15 × 15	Average wave orbital velocity (annual, 1990–2015)
Eastness	East15	15 × 15	The sine of the angle of slope in the analysis window. Equation: sin(aspect) (Wilson et al., 2007)
Northness	Nor15	15 × 15	The cosine of the angle of slope in the analysis window. Equation: cos(aspect) (Wilson et al., 2007)
Complexity	Comp13	13 × 13	Rate of change of slope over designated neighbourhood size Equation: tan <sup>-1</sup> (rise(slope)/run(slope)) (Wilson et al., 2007)
Slope	Slop15	15 × 15	Change in elevation over designated neighbourhood size Equation: tan <sup>-1</sup> (rise/run) (Wilson et al., 2007)
Maximum curvature	Mcur15	15 × 15	Steepest curve of convexity for a pixel over designated neighbourhood size Equation: $K(x) =  e^x /(1 + e^{2x})^{3/2}$
Reef/sediment	R1S2	1×1	Binary existing statewide habitat classification of reef and sediment seafloor substrata

Note: 1 Predictor variables selected using Random Forest variable importance analysis. Variables with a Pearson correlation value greater than 0.7 were not retained for final models.

To classify the Victorian state waters into biotope complex classes, a random forests (RF) classification approach was used to produce rule-based relationships between predictor variables (Table 2.1) and corresponding ground truth training data using the 'randomForest' package in R (Liaw and Wiener, 2002). RF is a modelling approach that uses machine learning decision tree-type classifiers and bootstrap aggregation based on input data (Breiman, 2001). The RF classification approach has the benefit of keeping bias low via random predictor variable selection and reducing the chance of model overfitting by including the results of multiple trees from bootstrap samples of the training data. Furthermore, measures of variable importance for model outputs can be derived (Cutler et al., 2007). Stephens and Diesing (2014) have shown RF performs well when compared with other rule-based classification techniques. They reported that tree-based methods, including RF, performed best when predicting benthic seafloor classes from acoustic and ground truth data sets. Parameters for predictors randomly selected at each split (mtry), and the optimal number of trees within models (ntree) were set at 10 and 300, respectively, for classification models. The RF models produced were used to produce a biotope complex map based on predicted habitat classifications as rasters across the selected tiles using the 'ModelMap' package in R (Freeman et al., 2018).

Resulting machine learning classifications of each mapping tile were subjected to automated cleaning to reduce pixalisation and artefacts in final classifications. This was done by running a majority filter (neighbourhood = 8 pixels and replacement threshold = half) and the 'Boundary Clean' tool (sorting technique = descending) in ArcMap 10.4.1. The final statewide map product was provided in a single polygon layer. The statewide map has a total of 106 attribute fields. Attributes define characteristics such as map source, authors, biotope classification, biogeographic area, MPA presence, depth contours, finest classification levels and areas (m²) of each class mapped (Figure 2.3). Polygons do not overlap, so areas can be calculated and displayed for all individual map attributes as a percentage of the entire state waters or of regions.

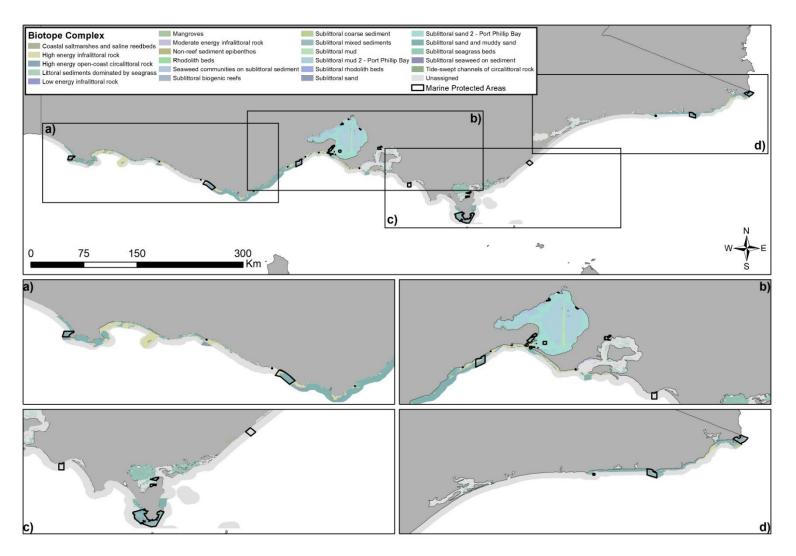


Figure 2.3: Biotope complex classification across the mapped areas of the Victorian state waters

As we did in assessing seafloor habitat, we used the final biotope complex classification map to calculate the area of each biotope complex within each MPA and the corresponding biounit areas using the 'Tabulate Area' tool in ArcGIS Spatial Analyst 10.7 (ESRI, 2011). In addition to calculating the total area of each habitat type present, we also calculated the percentage cover of each biotope class within the biounits and MPAs and compared the proportions of each class. Because the region is so much larger than the MPAs, especially the marine sanctuaries, analysing proportions lets us to determine whether habitats are represented at an adequate level while taking into account the area of the MPA. Using a difference in proportion of 20%, which is common threshold when comparing percentages (Mapstone, 1995), we determined whether the biotope complexes were proportionately captured in the MPAs. Biotope complexes that exceeded the 20% difference in proportion threshold within MPAs were considered to be over-represented (where the proportions in the MPA were at least 20% higher) or under-represented (the proportions in the MPA were at least 20% lower).

#### 2.6 Sea-surface temperature

Processed sea-surface temperature (SST) datasets, which are available from the Integrated Marine Observing System (IMOS; (IMOS, 2018)) as netCDF format at monthly intervals, were converted into individual ArcGIS rasters. These rasters provide monthly SST data from 1992 to the present day and can be used to derive seasonal and annual variations in SST across the state of Victoria (Figure 2.4a). With temperatures increasing with climate change, SST information can be used to help determine which MPAs are experiencing the biggest changes in conditions.

To look at spatial and temporal patterns in temperature across the Victorian MPAs and compare these patterns to those within their associated biounits, we used the 'Zonal Statistics as Table' tool within ArcGIS Spatial Analyst to compute the mean annual, summer and winter SST and the standard deviations of those means within each MPA and biounit. We then graphed the patterns through time to see how well the MPAs represented the overall pattern in the biounits.

## 2.7 Hydrodynamics

Hydrodynamic datasets for the coastal waters of Victoria were derived from downscaled and hind-casted hydrodynamic models that were developed as part of FRDC project 2015-025 (lerodiaconou et al., 2018a). These downscaled hydrodynamic models were developed by Water Technology using a coupled hydrodynamic and spectral wave model within MIKE from the Danish Hydraulics Institute (DHI, 2016). Resulting products included monthly statistics for current speed (max and average) (mean max is shown in Figure 2.4b), significant wave height (max, average), wave period for max significant wave height, orbital velocity (max, average) (Figure 2.4c), and wave power (max, average). These variables now allow for assessment of hydrodynamic characteristics across the MPAs in Victoria to

determine how conditions vary through time and how those varying conditions may be impacting biodiversity.

Using the same methods as for SST, we computed the mean and standard deviation of maximum wave orbital velocity, maximum wave power and maximum current speed for each MPA and biounit along the Victorian coast over the whole year and then seasonally in summer and winter. The trends in the MPAs were then compared to the trends in their associated biounits.

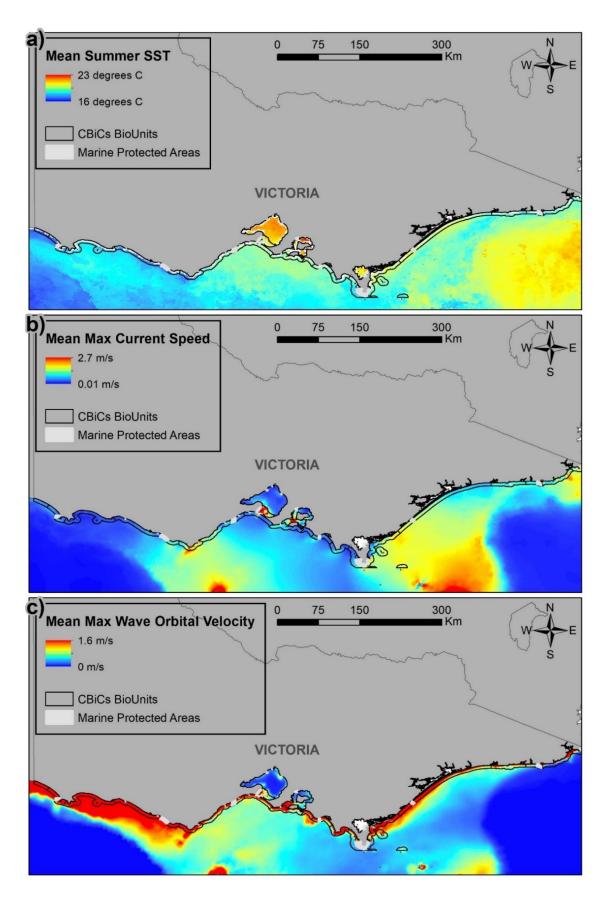


Figure 2.4: Patterns of mean summer sea-surface temperature (a), mean max current speed (b), and mean max wave orbital velocities (c) across Victoria

#### 2.8 Connectivity modelling

To quantify connectivity across the Victorian MPAs, a larval transport model was developed for Victoria using a combination of hydrodynamic information and suitable habitat to predict larval transport and the locations of sources and sinks. This was done using a parametrisation of a biophysical dispersal model (Treml et al., 2012, 2015) to quantify the population connectivity patterns for Blacklip Abalone (Haliotis rubra), Golden Kelp (Ecklonia radiata), Snapper (Chrysophrys auratus) and Purple Sea Urchin (Heliocidaris erythrogramma). These species were chosen to represent differing life history and dispersal characteristics along Victoria: Purple Sea Urchin and Blacklip Abalone represent short-range dispersers, Golden Kelp intermediate and Snapper long-range dispersers. This modelling approach incorporates species-specific habitat, oceanographic and biological data to effectively estimate the probability that larvae will successfully disperse from potential source habitat sites to all destination habitat patches. Dispersal simulations were carried out by releasing a cloud of larvae into the model seascape at all individual habitat patches and allowing the larvae to be transported downstream with currents. Ocean current velocities, turbulent diffusion and larval behaviour move the larvae through the seascape at each modelled time-step. Larval competency, behaviour and mortality determine when and what proportion of larvae settle in habitat patches at each time-step. When larvae encounter habitat, the concentration of larvae settling within the habitat patch is recorded at that time-step. Dispersal simulation data were saved in the form of a 3-dimensional dispersal matrix representing the cumulative quantity of larvae released from each source patch i that have settled on any destination patch *j* throughout the entire dispersal period. This matrix was used to calculate the pairwise dispersal probability of moving from each source to destination, [P] matrix, and the migration matrix, [M], representing the likelihood that a settler to destination patch originated from each potential upstream source patch (Treml et al., 2012). Habitat and species-specific life history parameters were used for each species.

### 2.9 Biophysical models

A map defining suitable habitat was developed based on the best available reef habitat data derived from substrate classifications of the merged LiDAR and multibeam datasets (these datasets are described in Section 1.2.4). The substrate raster was aggregated into 500 m sections across the coast, providing a measure of the proportion of suitable habitat (reef) in each section. The habitat data were rescaled and projected onto our biophysical model of coastal Victoria. Hydrodynamic data quantifying the nearshore and far-field ocean currents around Victoria and the regional seascape were obtained from 2 sources: DHI-MIKE data from Water Technology for local-scale depth-averaged (~1,000 m and hourly averaged) and high spatial-temporal resolution products; and global HYCOM + NCODA Global 1/12 Reanalysis hydrodynamic data product providing regional scale 3-dimensional and moderate resolution data (~8 km and 3-hourly) for the Australia—New Zealand seascape. The MIKE data were provided by Water Technology at 5-minute time-steps for all years between 1990

and 2015 at a horizontal resolution ranging from 500 to 800 m within ~7 km of the shoreline, to ~10 km resolution through Bass Strait, and up to 25 to 35 km in the open ocean. The HYCOM data were obtained at 3-hourly time-steps for all years between 1992 and 2012 at 1/12° resolution (0 to 10 m depth) and interpolated to 1 km biophysical model grids. For more information on the modelling procedures, please see lerodiaconou et al. (2018a).

To identify those reefs or populations that may serve as strong and persistent larval sources, we used 4 complementary measures of replenishment: outflow, which quantifies each source's contribution to other sites; local retention, which is the proportion of larvae released from each source that settles back into that focal patch (derived from the probability matrix); inflow, which measures the total relative amount of larvae settling to each patch (including those larvae that are locally produced); and the 'sourceness' metric, which quantifies the relative source-strength of each patch as outflow/inflow (Cronin, 2007; Pulliam, 1988). For further information, the following parameters were also provided: selfrecruitment, which quantifies the proportion of settlers at each destination site that originated from that focal site (diagonal of the migration matrix); in-degree, which is the total number of 'significant' connections coming into a destination site (ignoring the strength of individual connections) derived from the migration matrix (see Section 2.8); and out-degree, which is the total number of 'significant' dispersal connections originating from a source site that leads to destination patches. For in- and out-degree, a demographically significant connection was counted if it contributed to more than 0.1% of settlers to a destination site in the migration matrix. Across all these measures, we also quantify the variability through years (i.e. standard deviation) to show the temporal stability or persistence. For our summaries, we used inflow, self-recruitment and in-degree to assess the connectivity of biounits and their associated MPAs.

#### 3. Results

## 3.1 Seafloor mapping coverage

Prior to assessing the representation of seafloor habitat within the MPAs and their associated biounits, we wanted to determine the total coverage of seafloor data available within each of the areas. We found that, overall, MPAs have much greater coverage of mapped data than the biounits (Table 3.1). This information is important for understanding how readily comparisons of representativeness can be made between MPAs and the biounit they aim to represent and can help guide the completeness of the representativeness results.

Parks that are almost completely mapped, such as Discovery Bay MNP (99% mapped), Bunurong MNP (99% mapped) and Point Hicks MNP (97% mapped) are in biounits that have not had as much coverage mapped outside MPAs. These include the Discovery Bay biounit

(45% mapped), Bunurong biounit (33% mapped) and the Point Hicks biounit (51% mapped) (Table 3.1). Therefore, comparing the representation of habitat in the MPA to the habitat in the biounit can only be done for the mostly shallower (<20 m) depth range available in the mapping data outside the MPA. The only biounit that is almost completely mapped, the Cape Otway biounit with 95% of its area mapped, only has one small marine sanctuary – Marengo Reefs Marine Sanctuary (MS). The Shipwreck Coast biounit also has a high proportion of its area mapped (91%), allowing for good comparisons with its corresponding MPAs (Twelve Apostles MNP, Merri MS and The Arches MS). The remaining comparisons between the areas mapped within the MPAs and the biounits show that significantly more area is mapped in the MPAs than in the biounits they are placed in, ruling out complete comparisons.

Table 3.1: Summary of area mapped within each of the marine protected areas and biounits along the Victorian coast

Area name	Area type	Associated biounit	Total area (km²)	Area mapped (km²)	Percentage mapped (%)
Bellarine- Mornington biounit	Biounit	Bellarine- Mornington	274.48	116.61	42
Barwon Bluff MS	MPA	Bellarine- Mornington	0.16	0.09	55
Bunurong biounit	Biounit	Bunurong	233.31	78.01	33
Bunurong MNP	MPA	Bunurong	20.49	20.25	99
Cape Conran biounit	Biounit	Cape Conran	346.35	97.79	28
Beware Reef MS	MPA	Cape Conran	2.20	1.36	62
Cape Liptrap biounit	Biounit	Cape Liptrap	256.21	155.59	61
Cape Nelson biounit	Biounit	Cape Nelson	697.63	376.13	54
Cape Otway biounit	Biounit	Cape Otway	251.88	239.87	95
Marengo Reefs MS	MPA	Cape Otway	0.13	0.08	62
Corner Inlet biounit	Biounit	Corner Inlet	349.06	80.13	23
Corner Inlet MNP	MPA	Corner Inlet	14.15	2.33	16
Croajingalong biounit	Biounit	Croajingalong	325.23	106.20	33
Discovery Bay biounit	Biounit	Discovery Bay	269.43	120.33	45
Discovery Bay MNP	MPA	Discovery Bay	28.33	28.17	99
Gabo-Howe biounit	Biounit	Gabo-Howe	192.28	106.11	55
Cape Howe MNP	MPA	Gabo-Howe	40.52	34.80	86
Gippsland Lakes biounit	Biounit	Gippsland Lakes	556.77	0.50	0
Glenelg biounit	Biounit	Glenelg	133.83	70.92	53
Ninety Mile Beach biounit	Biounit	Ninety Mile Beach	952.66	560.98	59
Ninety Mile Beach MNP	MPA	Ninety Mile Beach	26.53	22.87	86
Nooramunga biounit	Biounit	Nooramunga	176.83	11.37	6
Point Hicks biounit	Biounit	Point Hicks	158.72	80.46	51
Point Hicks MNP	MPA	Point Hicks	38.04	37.07	97

Area name	Area type	Associated biounit	Total area (km²)	Area mapped (km²)	Percentage mapped (%)
Port Phillip Bay biounit	Biounit	Port Phillip Bay	1,665.06	588.68	35
Jawbone MS	MPA	Port Phillip Bay	0.30	0.10	32
Point Cooke MS	MPA	Port Phillip Bay	2.92	1.82	62
Ricketts Point MS	MPA	Port Phillip Bay	1.21	0.77	64
Port Phillip Heads biounit	Biounit	Port Phillip Heads	274.38	211.83	77
Port Phillip Heads MNP	MPA	Port Phillip Heads	34.74	6.74	19
Schanck-Woolamai biounit	Biounit	Schanck-Woolamai	352.28	114.03	32
Mushroom Reef MS	MPA	Schanck-Woolamai	0.57	0.37	65
Shipwreck Coast biounit	Biounit	Shipwreck Coast	644.66	589.56	91
Twelve Apostles MNP	MPA	Shipwreck Coast	75.15	74.28	99
Merri MS	MPA	Shipwreck Coast	0.29	0.20	68
The Arches MS	MPA	Shipwreck Coast	0.48	0.48	100
Surf Coast biounit	Biounit	Surf Coast	490.09	415.14	85
Point Addis MNP	MPA	Surf Coast	44.16	42.90	97
Eagle Rock MS	MPA	Surf Coast	0.18	0.11	61
Point Danger MS	MPA	Surf Coast	0.22	0.07	32
Western Port biounit	Biounit	Western Port	650.05	124.14	19
Wilsons Prom East biounit	Biounit	Wilsons Prom East	599.71	415.23	69
Wilsons Prom West biounit	Biounit	Wilsons Prom West	467.24	187.01	40
Wilsons Promontory MNP	MPA	Wilsons Prom West	156.04	154.03	99
Wonthaggi biounit	Biounit	Wonthaggi	124.18	30.67	25

## 3.2 Seafloor habitat representation

The comparison of seafloor habitat inside MPAs with the available habitat in their associated biounits shows that the habitats are generally well represented within protected areas (Figures 3.1 to 3.3). In some cases, reef habitat, especially in the shallower depths, is more common in the MPAs than throughout the biounits (e.g. Bunurong, Mushroom Reef, Discovery Bay, Shipwreck Coast, Cape Otway, Surf Coast). The opposite pattern occurs with shallower sediment for which some biounits have a larger proportion of sediment than is

found in the MPAs (e.g. Discovery Bay, Port Phillip Heads, Bunurong, Wilsons Promontory). Some MPAs over-represent many habitats, such as the Point Hicks MNP, which has larger proportions of most habitats found within the Point Hicks biounit. The Cape Howe MNP also over-represents many habitats, especially in the deeper depth ranges.

Marine sanctuaries tend to be placed in areas with larger coverage of reef habitats and over-represent those habitats, while marine national parks are larger and capture more of the habitats in the biounit. In the 2 biounits with the most coverage of mapping data, Shipwreck Coast (91 mapped) and Cape Otway (95 mapped), the MPAs cover habitat in similar proportions to that found in the biounits (Figure 3.1b, c). Along the Shipwreck Coast, the same habitats are found in both biounits and MPAs across all depth ranges. In contrast, the Marengo Reefs MS is the only MPA within the Cape Otway biounit, and in its small area the sanctuary only contains the shallow habitats. Despite habitats from the biounits generally occurring within the MPAs, they tend to occur in different proportions. In almost all cases, the difference exceeds the 20 benchmark. This indicates that, based on currently mapped regions, seafloor habitat is not represented in protected areas in proportion to its occurrence in the respective biounits.

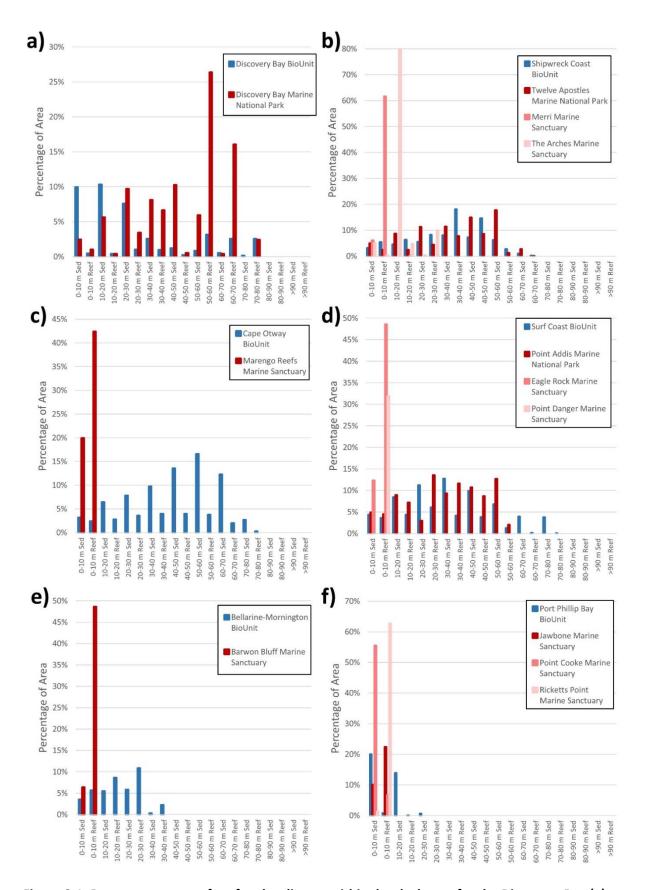


Figure 3.1: Percentage cover of reef and sediment within depth classes for the Discovery Bay (a), Shipwreck Coast (b), Cape Otway (c), Surf Coast (d), Bellarine-Mornington (e) and Port Phillip Bay (f) biounits and their associated marine protected areas

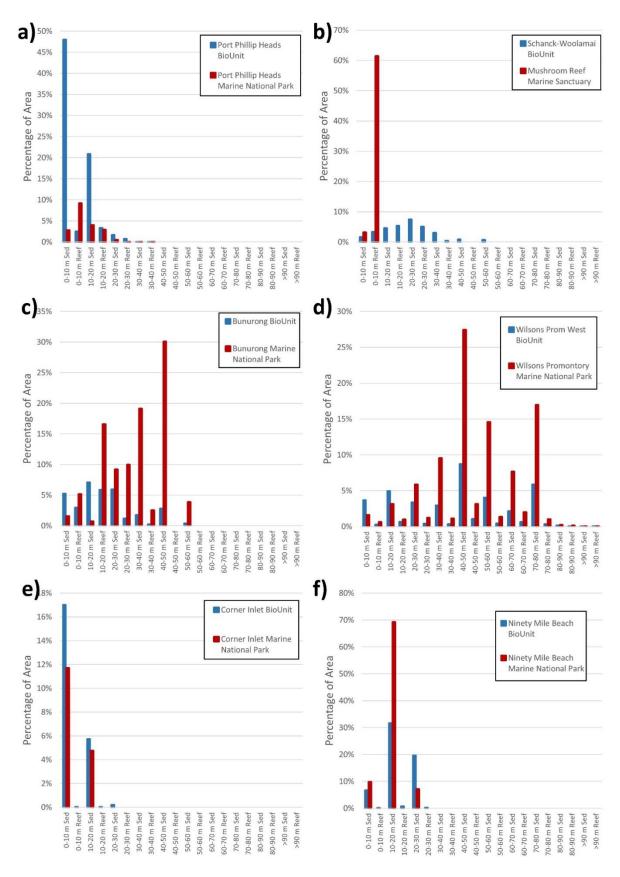


Figure 3.2: Percentage cover of reef and sediment within depth classes for the Port Phillip Heads (a), Schanck-Woolamai (b), Bunurong (c), Wilsons Prom West (d), Corner Inlet (e) and Ninety Mile Beach (f) biounits and their associated marine protected areas

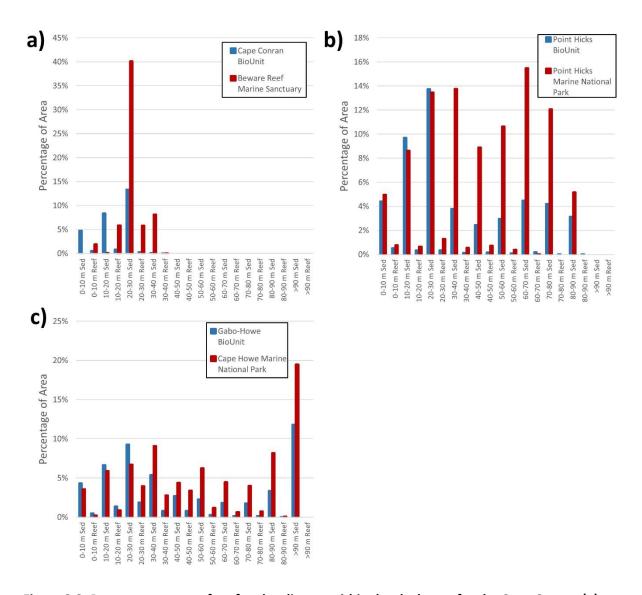


Figure 3.3: Percentage cover of reef and sediment within depth classes for the Cape Conran (a), Point Hicks (b) and Gabo-Howe (c) biounits and their associated marine protected areas

# 3.3 Biotope complex representation

The summaries of the biotope complex representation inside MPAs compared to the biounits show that most biotope complexes present in the biounits are also found in the MPAs (Figures 3.4 to 3.8). Again, the difference in mapped coverage inside the MPAs compared to outside prevents us from making complete comparisons. In the Cape Otway biounit, where there is high coverage of marine mapping data, the Marengo Reefs MS represents the shallow biotope complexes (High energy infralittoral rock; Sublittoral seagrass beds) well. However, the shallow depth range of the marine sanctuary means the deeper habitats are not represented. In the Shipwreck Coast biounit, the Twelve Apostle MNP, which extends across a greater depth range, does fairly well at including representatives of those biotope complexes found throughout the biounit. In addition, the Merri MS has very high representation of High energy infralittoral rock. As with seafloor

habitats, although many of the biotope complex classes found in the biounits are represented in their respective MPAs, they tend to occur in different proportions. In almost all cases, the difference exceeds the 20 benchmark. This indicates that, based on currently mapped regions, biotope complexes are not represented in protected areas in proportion to its occurrence in the respective biounits.

Under-represented classes are those that are rarer throughout the biounits. The Shipwreck Coast biounit has small areas of Sublittoral mixed sediments and Rhodolith beds, which are not captured within its MPAs. In the Point Hicks biounit, small areas of Sublittoral biogenic reefs, Sublittoral sand and Sublittoral seagrass beds are not captured within that biounit's MPA. Overall, sediment biotopes tend to be under-represented within MPAs, which is similar to the patterns observed from the substrate comparisons. For example, in the Port Phillip Bay biounit, Sublittoral mud is one of the most dominant classes yet it is not represented in 2 of the 3 marine sanctuaries. This is likely a result of the Port Phillip Bay MPAs occupying the shallow, near-coastal regions while most of Port Phillip Bay is made up of deeper sediment habitat.

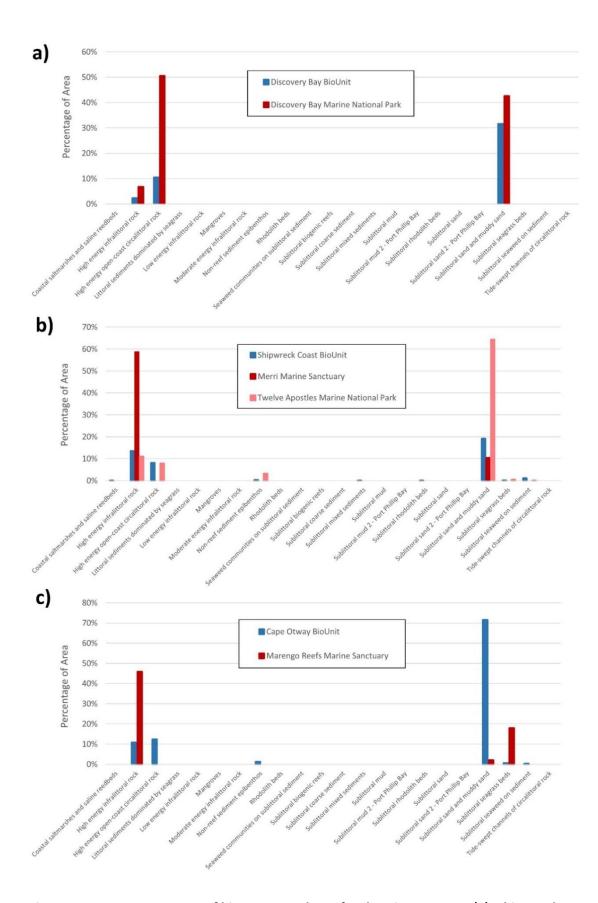


Figure 3.4: Percentage cover of biotope complexes for the Discovery Bay (a), Shipwreck Coast (b) and Cape Otway (c) biounits and their associated marine protected areas

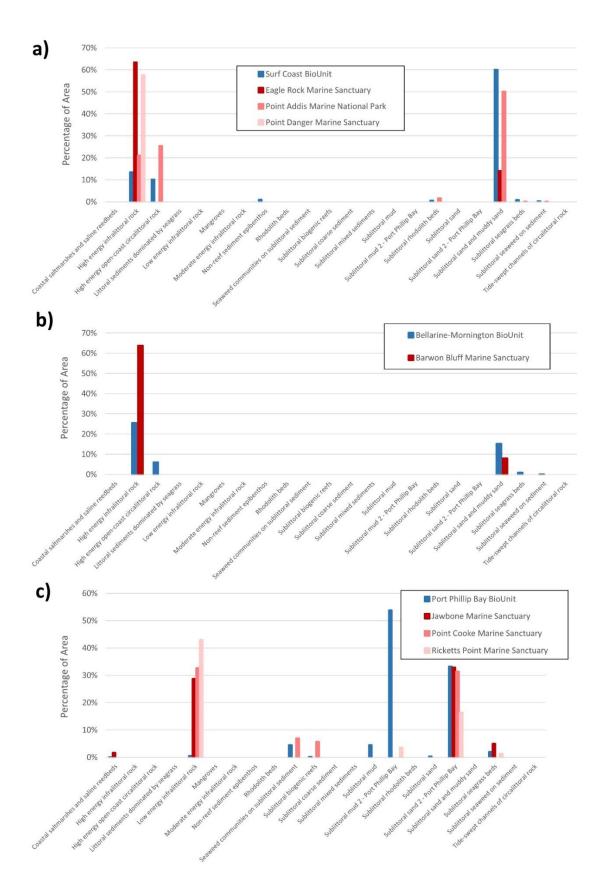


Figure 3.5: Percentage cover of biotope complexes for the Surf Coast (a), Bellarine-Mornington (b) and Port Phillip Bay (c) biounits and their associated marine protected areas

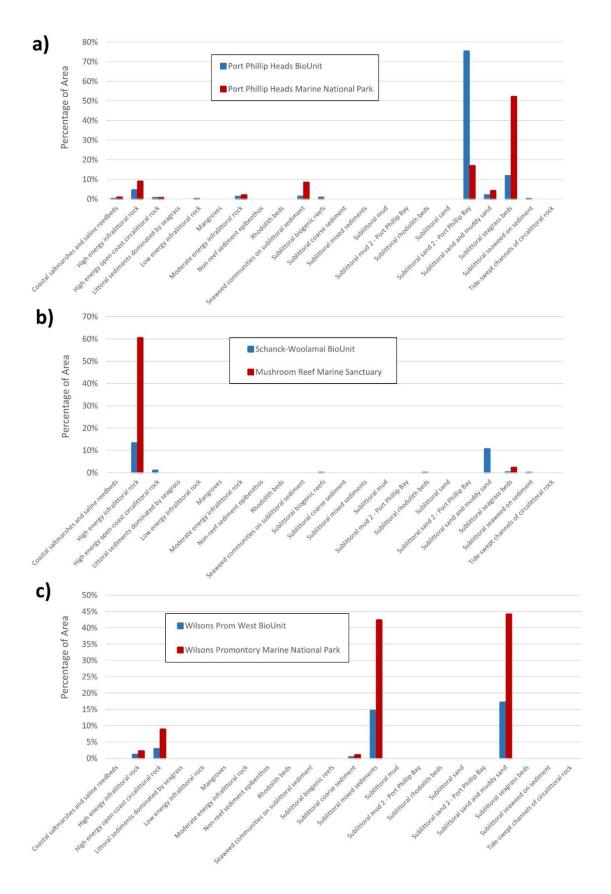


Figure 3.6: Percentage cover of biotope complexes for the Port Phillip Heads (a), Schanck-Woolamai (b) and Wilsons Prom West (c) biounits and their associated marine protected areas

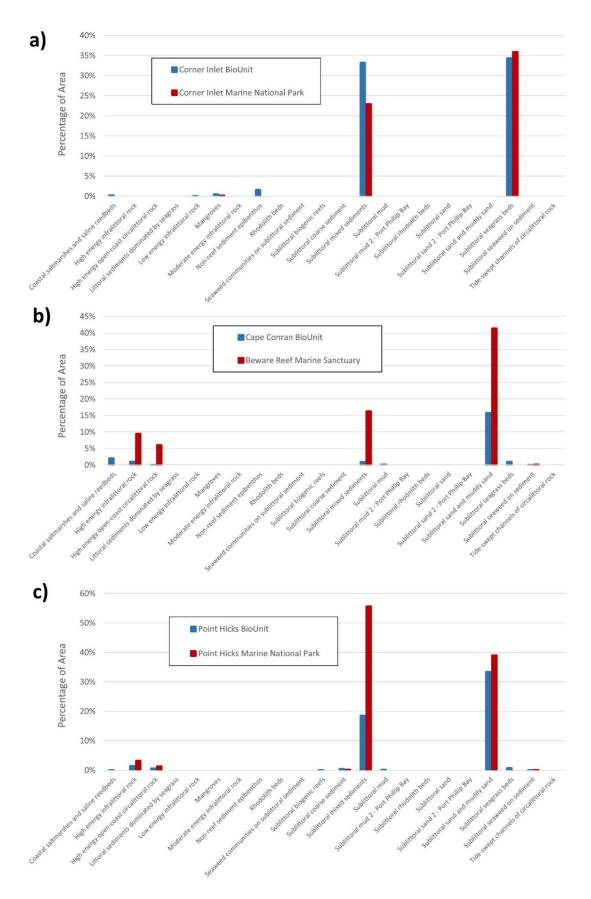


Figure 3.7: Percentage cover of biotope complexes for the Corner Inlet (a), Cape Conran (b), and Point Hicks (c) biounits and their associated marine protected areas

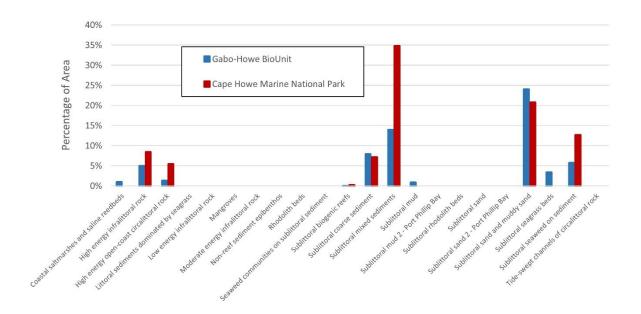


Figure 3.8: Percentage cover of biotope complexes for the Gabo-Howe biounit and its associated MPA

# 3.4 Hydrodynamic patterns

Evaluation of the patterns of current speed along the coast show the majority of MPAs experience the same patterns as their associated biounits (Figures 3.9 to 3.11). The few examples where the patterns within MPAs differ from the biounits are all associated with the smaller, nearshore marine sanctuaries. For example, Mushroom Reef MS has consistently higher current speeds than the Schanck-Woolamai biounit (Figure 3.10b). Marengo Reefs MS current speeds were consistently higher than the Cape Otway biounit until around 2003 when they began to converge on similar values (Figure 3.9c). Beware Reef MS current speeds were similar to the Cape Conran biounit until 2002 when the values became consistently lower within the marine sanctuary (Figure 3.11b).

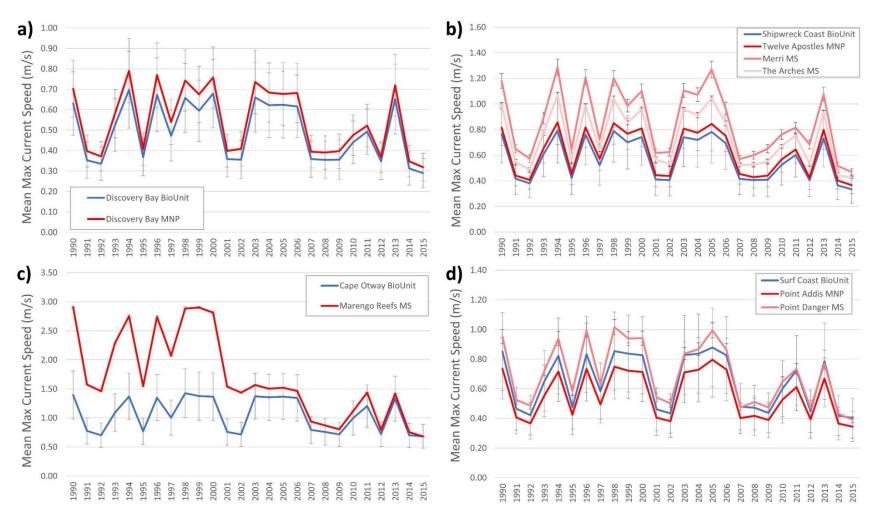


Figure 3.9: Temporal patterns in annual mean max current speeds for the Discovery Bay (a), Shipwreck Coast (b), Cape Otway (c) and Surf Coast (d) biounits and their associated marine protected areas

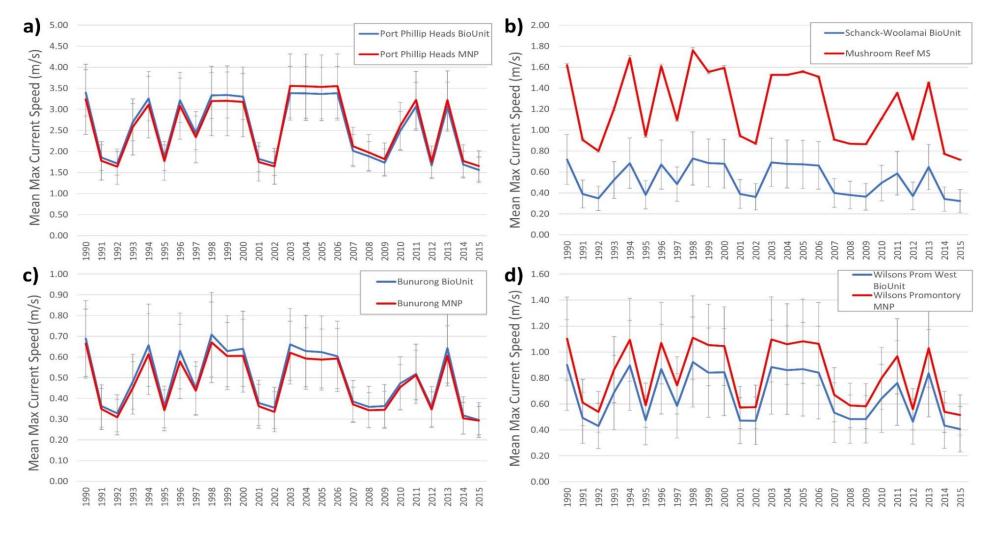


Figure 3.10: Temporal patterns in annual mean max current speeds the Port Phillip Heads (a), Schanck-Woolamai (b), Bunurong (c) and Wilsons Prom West (d) biounits and their associated marine protected areas

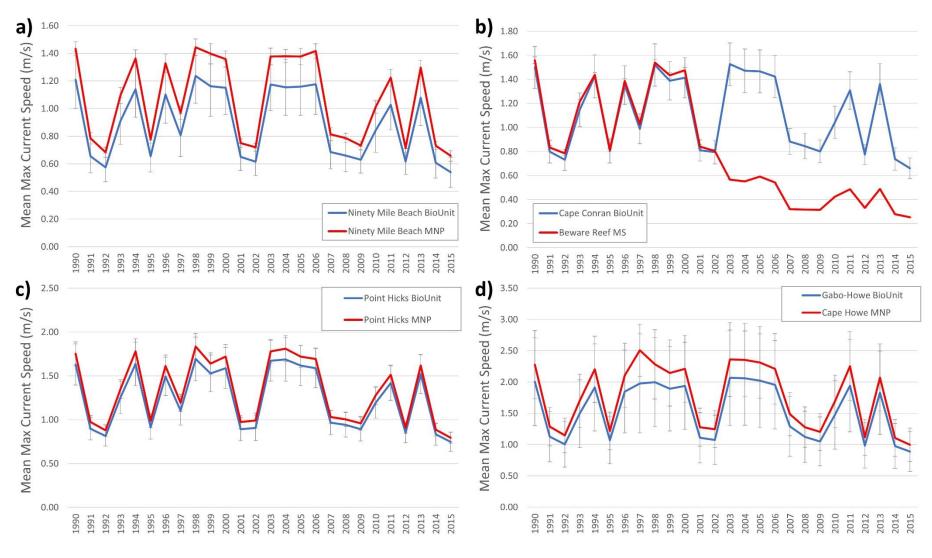


Figure 3.11: Temporal patterns in annual mean max current speeds for the Ninety Mile Beach (a), Cape Conran (b), Point Hicks (c) and Gabo-Howe (d) biounits and their associated marine protected areas

Wave orbital velocity patterns in the marine national parks were generally similar to those in their corresponding biounits (Figures 3.12 to 3.14). However, as with current speed, patterns in marine sanctuaries tended to differ from the biounits, often having higher wave orbital velocities. In the Shipwreck Coast biounit, the pattern in the Twelve Apostles MNP was very similar to the biounit pattern but the 2 marine sanctuaries, Merri and The Arches, had consistently higher wave orbital velocities (Figure 3.12b). The same pattern was seen in the Surf Coast biounit (Figure 3.12d). In the Cape Otway biounit, Marengo Reef MS had greater wave orbital velocities until 2003 when the patterns and magnitudes became more similar to the biounit (Figure 3.12c), while the Cape Conran biounit and its associated marine sanctuary, Beware Reef, experienced the opposite pattern (Figure 3.14b). Mushroom Reef MS had consistently higher wave orbital velocities than the Schanck-Woolamai biounit (Figure 3.13b).

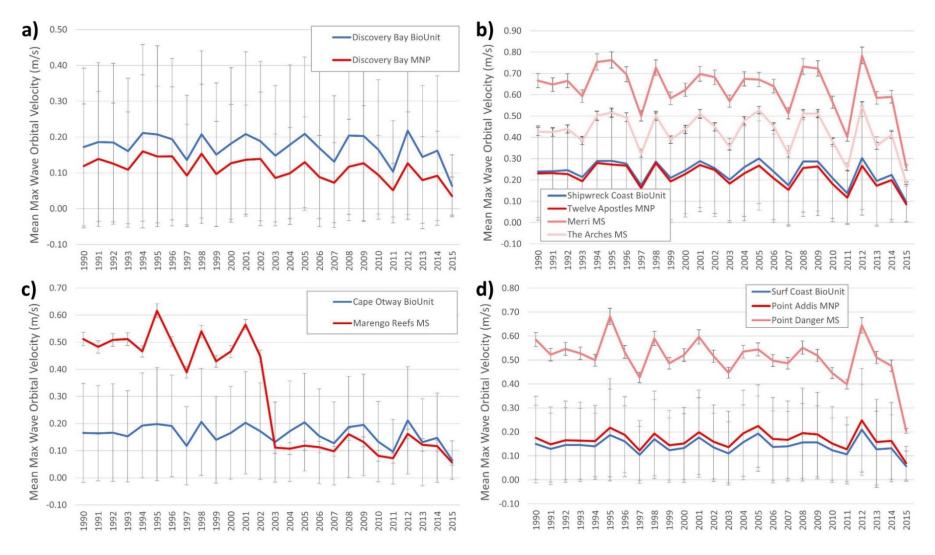


Figure 3.12: Temporal patterns in annual mean max wave orbital velocities for the Discovery Bay (a), Shipwreck Coast (b), Cape Otway (c) and Surf Coast (d) biounits and their associated marine protected areas

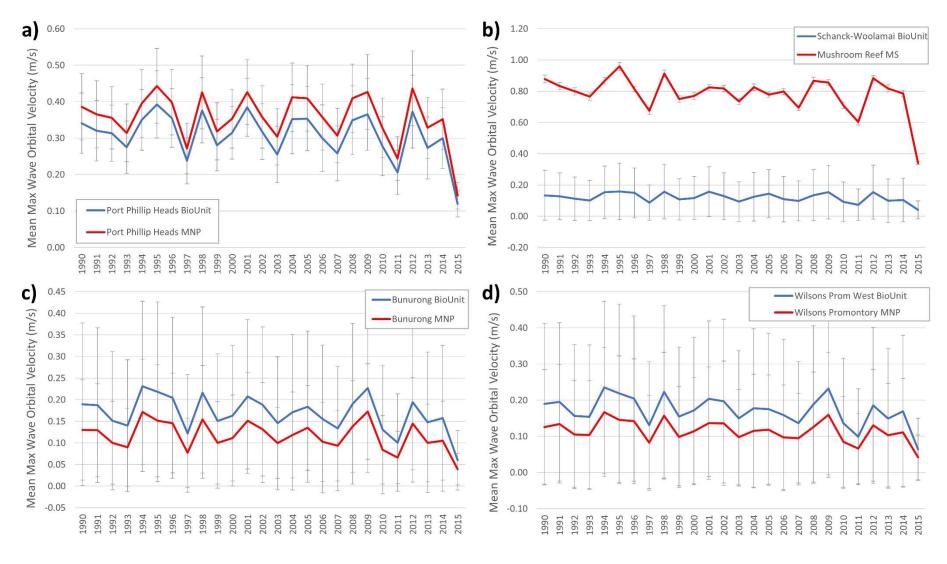


Figure 3.13: Temporal patterns in annual mean max wave orbital velocities for the Port Phillip Heads (a), Schanck-Woolamai (b), Bunurong (c) and Wilsons Prom West (d) biounits and their associated marine protected areas

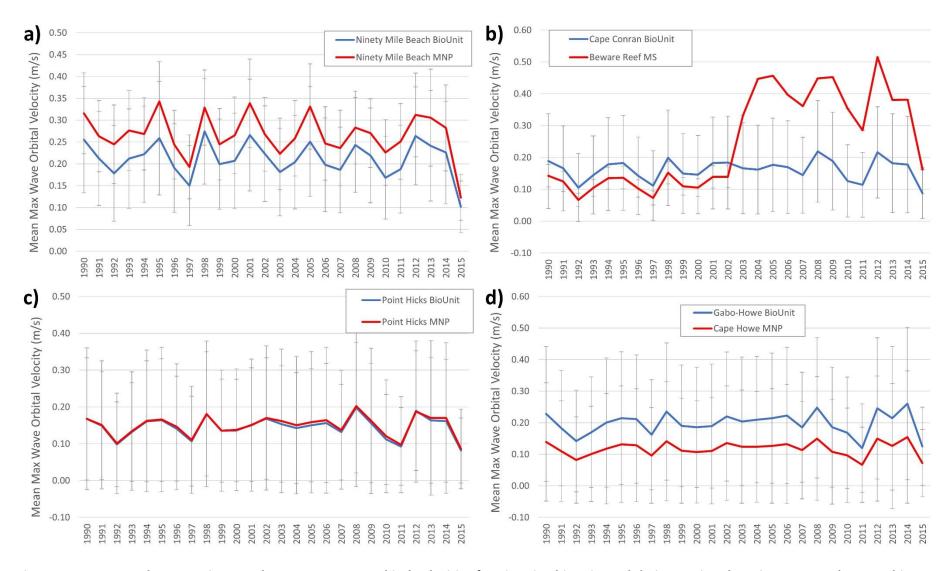


Figure 3.14: Temporal patterns in annual mean max wave orbital velocities for Victorian biounits and their associated marine protected areas. This Figure shows the Ninety Mile Beach, Cape Conran, Point Hicks, and Gabo-Howe biounits

# 3.5 Sea-surface temperature patterns

Patterns of SST across the biounits shows that summer temperatures are increasing slightly while annual and winter temperatures are remaining relatively steady with interannual fluctuations (Figure 3.15). There are some years of note in the data including 1997, which had generally high temperatures particularly during winter, and 2006, which had a high annual average. Both of these anomalies occurred during El Niño years. Additionally, there is more variability in summer and winter temperatures across the state than in annual averages, suggesting that the biounits experience a greater range of temperatures when analysed seasonally compared to averaging over the whole year.

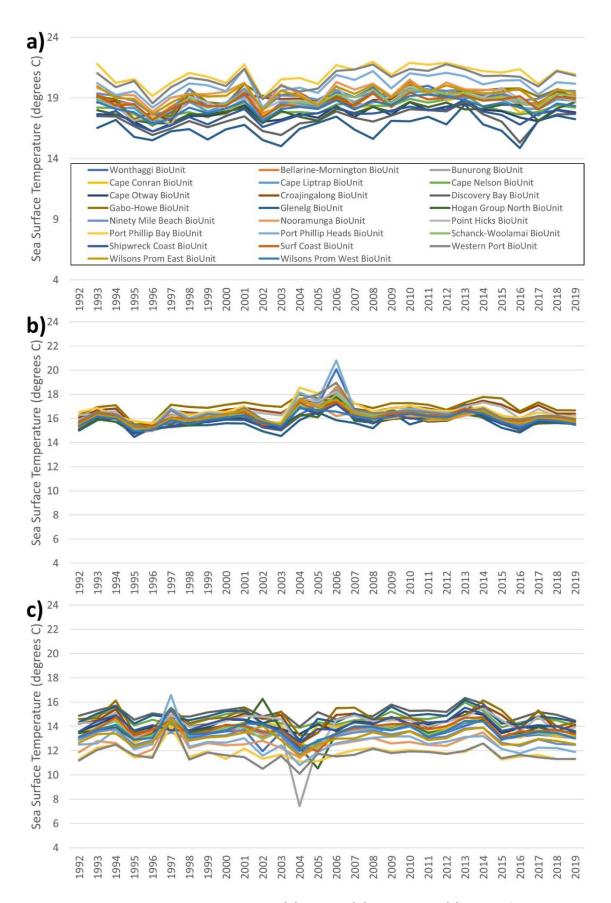


Figure 3.15: Temporal patterns in summer (a), annual (b), and winter (c) sea-surface temperature for each Victorian biounit

The MPAs represent the SST patterns of their corresponding biounits well for both summer and winter seasons (Figures 3.16 to 3.18). Generally, winter temperatures have stayed fairly constant from 1992 to 2019, with annual fluctuations, while summer temperatures have an increasing trend. Also, other than slight annual changes in SST, there were a couple of years that had notable increases in temperature, such as summer temperatures in 2001, which represented the peak temperatures reached in many of the biounits. A year of notable decrease in temperature during winter was 2004–05, when many biounits experienced their lowest temperatures, especially within the Bunurong MNP (Figure 3.17c).

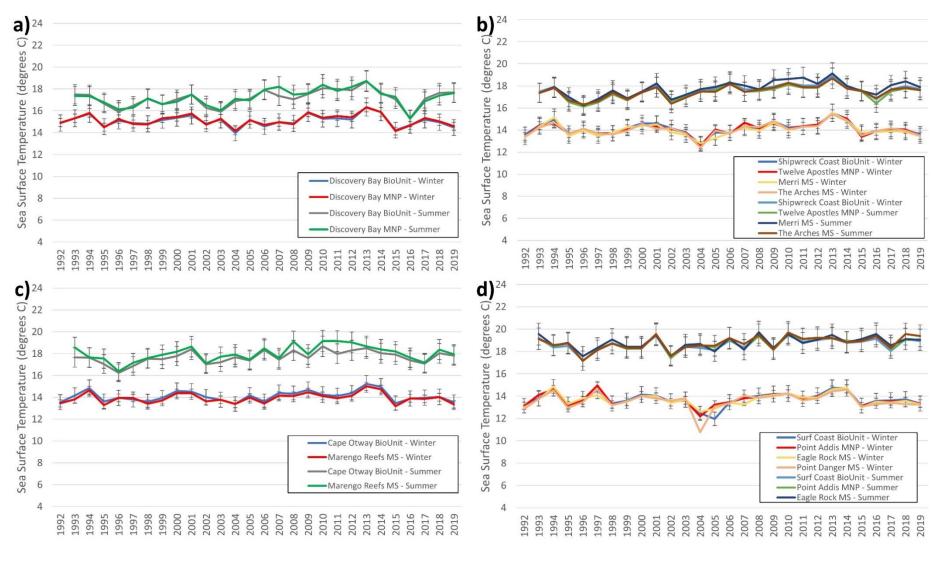


Figure 3.16: Temporal patterns in summer and winter sea-surface temperature within the Discovery Bay (a), Shipwreck Coast (b), Cape Otway (c) and Surf Coast (d) biounits and their associated marine protected areas

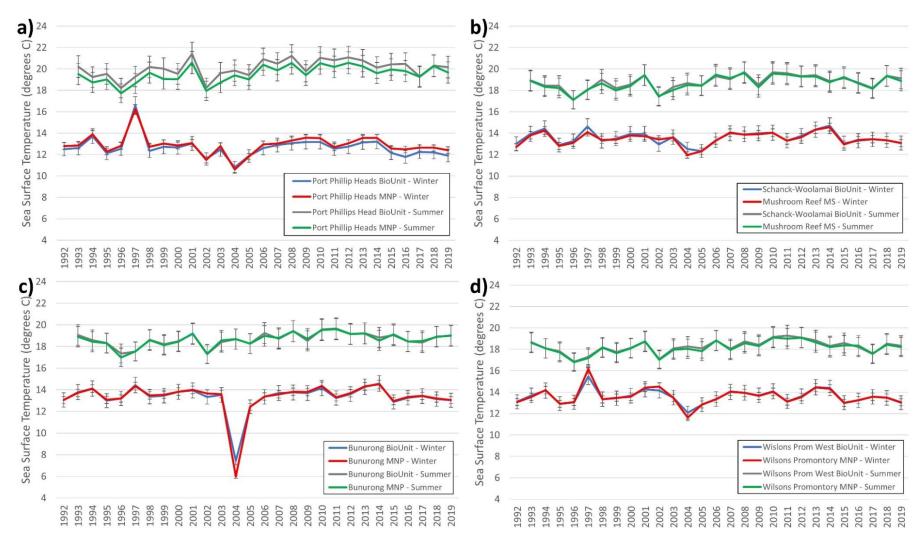


Figure 3.17: Temporal patterns in summer and winter sea-surface temperature within the Port Philip Heads (a), Schanck-Woolamai (b), Bunurong (c) and Wilsons Prom West (d) biounits and their associated marine protected areas

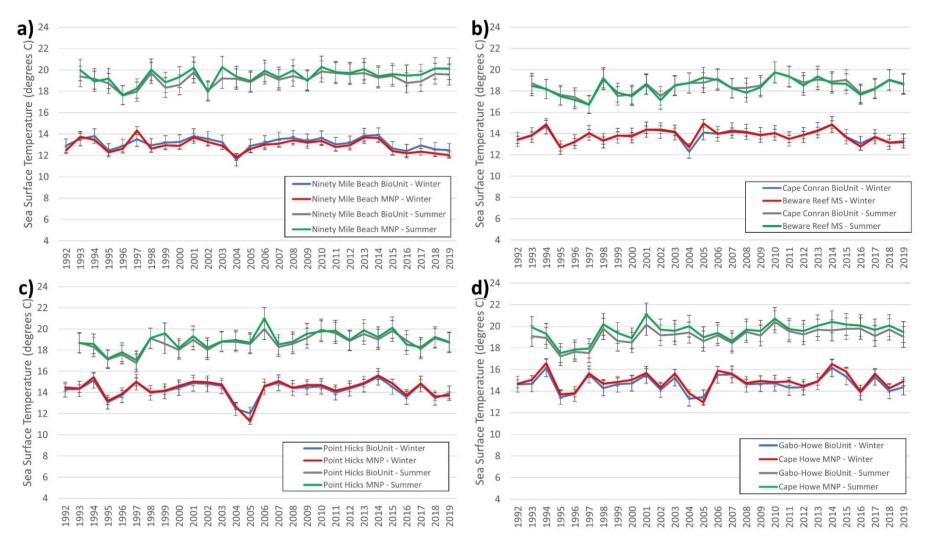


Figure 3.18: Temporal patterns in summer and winter sea-surface temperature within the Ninety Mile Beach (a), Cape Conran (b), Point Hicks (c) and Gabo-Howe biounits and their associated marine protected areas

## 3.6 Connectivity patterns

We looked at patterns of total inflow, self-recruitment and in-degree across the biounits and MPAs of Victoria. Inflow measures the total relative amount of larvae settling to each patch (including locally produced larvae). Analysing the patterns across the state, total inflow was higher in the western part of the state for all life history types but Purple Sea Urchins and Golden Kelp experienced much greater inflow in the west (Figure 3.19). Snapper and Blacklip Abalone tended to have lower inflow across the state, suggesting that the recruitment available for those species is much lower. In most cases, MPAs and their associated biounits had similar degrees of inflow. However, in some biounits, the MPAs had slightly higher inflow for some life history types (e.g. Blacklip Abalone in Discovery Bay MNP, Blacklip Abalone in Twelve Apostles MNP, Purple Sea Urchin in Point Addis MNP), but other MPAs had lower inflow than their associated biounits (e.g. Blacklip Abalone in Merri MS, Golden Kelp in Marengo Reefs MS, Golden Kelp in Barwon Bluff MS).

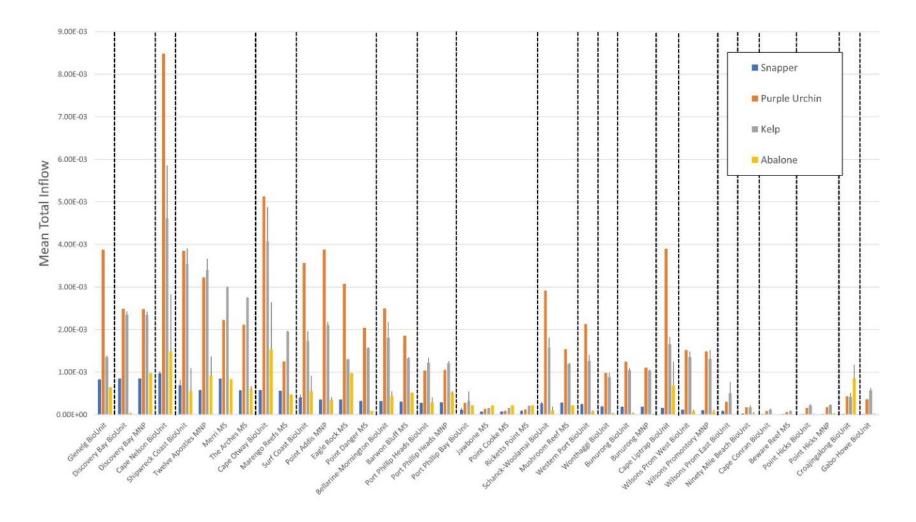


Figure 3.19: Mean total inflow across each of the biounits and marine protected areas in Victoria. Left to right represents west to east along the coast. The separate biounits are defined by the black dashed lines

We also assessed patterns of self-recruitment, which is the relative proportion of settlers at each destination site that originated from that focal site (therefore, this measure has a maximum of 1 or 100). Across the state, Blacklip Abalone tended to have the highest self-recruitment among all life history types with the highest levels occurring towards the centre of the state (Figure 3.20). Purple Sea Urchins and kelp had similar levels of self-recruitment with the highest occurring in the eastern half of the state around Wilsons Promontory. Snapper had similar levels of self-recruitment across the state with slightly higher levels in the Wilsons Promontory area and the lowest to the east. Overall, the patterns of self-recruitment in the biounits were well represented within the system of MPAs. Except for a couple of MNPs in the west of the state (Discovery Bay MNP and Twelve Apostles MNP) with higher abalone self-recruitment than the biounits as a whole, self-recruitment was very similar across biounits and their associated MPAs.

The final connectivity pattern we looked at was in-degree. In-degree is the total number of connections coming into a destination site (ignoring the strength of individual connections) derived from the migration matrix. All life history types had similar patterns across the state, although at varying levels, with all life history types displaying higher in-degree in the central areas of the state around Port Phillip Heads and in the east (Figure 3.21). This pattern means that all life history types examined in this analysis have the greatest incoming connections into the central portion of the state and the far east. Snapper had the highest levels of in-degree in almost all regions, followed by Blacklip Abalone. Patterns in MPAs closely followed the patterns in their associated biounits.

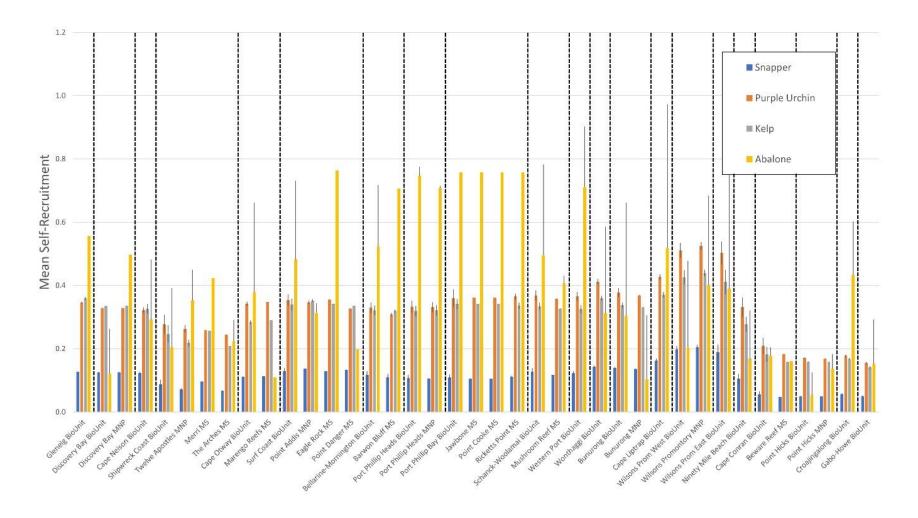


Figure 3.20: Mean self-recruitment across each of the biounits and marine protected areas in Victoria. Left to right represents west to east along the coast. The separate biounits are defined by the black dashed lines

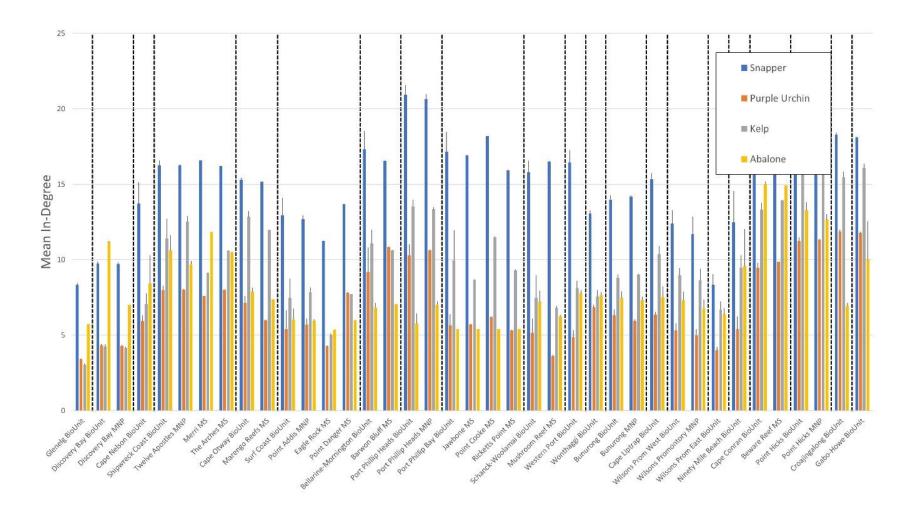


Figure 3.21: Mean in-degree across each of the biounits and marine protected areas in Victoria. Left to right represents west to east along the coast. The separate biounits are defined by the black dashed lines

#### 4. Discussion

Our analysis of the representation of seafloor habitat by depth within and outside the MPAs in many of the biounits showed that there was representation of the different habitat/depth categories but the proportions of those habitats inside the MPAs was not the same as in the biounits and generally differed by greater than 20, which is a common threshold when comparing percentages (Mapstone, 1995). Without complete mapping data across the biounits, it is difficult to provide a comprehensive comparison. However, there were still notable differences when limited to the shallower depth ranges where LiDAR data provides very good coverage across the state. In many cases, the MPAs protected a higher proportion of reef habitat than was available across the biounit. Due to the higher biodiversity often associated with reef habitats (Toohey et al., 2007; Rees et al., 2014), this indicates that, in some instances, important habitat for preserving biodiversity across the coast is overrepresented in MPAs compared with the biounits. On the other hand, MPAs often protect less of the sediment habitat, especially in the shallow zones, than the proportion occurring in their associated biounits. This could have implications for the protection of species found mainly in sediment habitats as they are not afforded as much protection within MPAs. Mapping habitats using seafloor data has been shown to be an important tool in evaluating the placement of MPAs (Jordan et al., 2005; Malcolm et al., 2010; Young and Carr, 2015), and these comparisons can be refined as more seafloor habitat mapping data becomes available.

The comparison of representation of the biotope complexes inside the MPAs and in their associated biounits found that most of the biotope complexes within the biounits were also found within their associated MPAs. Despite the overall good representation, different classes were present in different proportions in the biounit and associated MPAs. In most cases, the differences were greater than 20, suggesting that representation in the MPAs does not adequately reflect proportions in the biounits. Some of these differences could be a result of the incomplete mapping across the state, as seen in the substrate representation. Rarer classes (e.g. Non-reef epibiota and Rhodolith beds) tended to not be captured within the MPAs. In many biounits, the reef-associated biotope complexes were over-represented compared to sediment habitats, which were generally under-represented; however, this was not always the case. Some sediment biotope complexes were well or over-represented compared to biounits in some in some MPAs (e.g. Twelve Apostles, Cape Conran, Point Hicks, and Gabo), and reef biotope complexes were under-represented in Twelve Apostles MNP. This study used broad biotope mapping from existing efforts undertaken for the VEAC because our focus was on products with broad spatial coverage. Future work could investigate the value of using the ground truth data products to better understand the representativeness of MPA biotopes at more detailed hierarchical levels, including rare classes (e.g. BC5 or BC6).

We also looked at how hydrodynamics varied in the MPAs compared to their surrounding biounits. In most cases, currents tended to follow the same patterns inside the MPAs as in the biounits. Divergent patterns in the MPAs usually occurred in the smaller marine sanctuaries, which are often found in shallow, nearshore areas where currents are more impacted by the seabed and coastline features. In these marine sanctuaries, the currents were usually faster than those found throughout the biounit. Ocean current patterns and characteristics are important in determining the larval dispersal patterns in most marine taxa (Cowen and Sponaugle, 2009) as their pelagic larvae often have poor swimming capacity relative to the velocity of currents. Therefore, patterns of ocean currents are important for understanding the dispersal capacity in regions of interest.

Evaluation of wave energy patterns showed that, as with currents, wave orbital velocities inside the MPAs had similar patterns to those in the biounits. However, as the error bars indicate, there is a lot more variability in wave orbital velocities than other variables, both across the biounits and in some of the marine national parks. This is likely because seafloor habitat and depth alter patterns of wave orbital velocities as the waves reached shallower areas. The higher mean orbital velocities in the smaller, shallow marine sanctuaries are indicative of the impact of greater seafloor complexity and shallower depth in increasing velocities. Wave energies are expected to increase with climate change in the future, especially in this region (Young et al., 2011). A 5 increase in significant wave height has already been observed in the Southern Ocean over the past 30 years using satellite altimetry data (Morim et al., 2019), so understanding the variation in wave patterns across the MPAs is important for future management. It is also important to note that model outputs for the hydrodynamics had limited data for model validation, and current modelling efforts and validation data from Victoria's wave buoy network (www.vicwaves.com.au) are likely to enhance these products.

The patterns of SST inside the MPAs across both summer and winter were shown to be a good representation of the biounits, although with less variability. The reduced variability is likely a result of the coarser resolution of the SST data, causing the means to be computed across fewer pixels. However, SST varied a lot across the state, especially in the seasonal analyses. SST shows an obvious gradation across the state, with cooler temperatures in west increasing as you move east and become influenced by the East Australian Current (EAC). The strengthening of the EAC has caused warming in eastern Victorian waters and has impacted species ranges (Lough and Hobday, 2011). Understanding patterns of SST across the state and inside the MPAs can help with future management as climate change continues to heat the oceans. These patterns can help pinpoint MPAs that are changing at faster rates than others, potentially impacting the biodiversity they are meant to protect. In the eastern portion of the state and within Port Phillip Bay, we are observing greater increases in temperature and greater differences between summer and winter temperatures. For example, Port Phillip Heads biounit and Ninety Mile Beach biounit are showing a widening of the gap between summer and winter temperatures. These changes

could have implications if either temperature extreme gets close to the tolerance of the species within them. Continuing to assess biodiversity in these areas where we are seeing larger changes could help with managing biodiversity into the future and tracking distributional changes.

Finally, the connectivity analyses showed strong geographic patterns across the state and that the patterns of connectivity were similar within the MPAs and their associated biounits. Although there is some uncertainty about several of the biological and physical parameters (e.g. larval mortality, maximum occupancy, reproductive output, stratified current speeds) across all life history types, these connectivity patterns give some idea of the dispersal of these species across the state. These models also showed differences in patterns of connectivity across the different species and life history types. Purple Sea Urchins tended to have the largest amount of inflow, or greatest larval supply from upstream sites, with the highest inflow occurring in the western portion of the state. Blacklip Abalone have the highest levels of self-recruitment, which was highest towards the centre of the state. For abalone, previous studies have shown key clusters in the western zone and in the west section of the central abalone zone (primarily west of Port Phillip Bay). These large, productive abalone subpopulations may be responsible for seeding easterly reefs and MPAs with potential recruits. (lerodiaconou et al., 2018a). Making sure that these source populations are protected within MPAs will help to preserve biodiversity both inside this region and along the state where the larvae are exported. The remaining species experienced similar levels of self-recruitment across the state with the highest levels to the east of Wilsons Promontory. The analyses of in-degree showed that Snapper populations were the most connected and Purple Sea Urchins the least. To function and sustain populations, MPAs require both local larval replenishment and importation of larvae from other reserves (Planes et al., 2009). Further analyses should look at how well MPAs are connected to each other but, overall, the rates of inflow across all the MPAs suggests that they are fairly well connected and that MPAs are representative of the connectivity of their biounits.

Overall, these analyses show that the MPAs along the Victorian coast represent the ecological and environmental conditions in the biounits. We found that most habitat classes, both substrate/depth and biotope complexes, were represented inside the MPAs, but the proportional representation of those classes differed. However, more mapping data are needed to complete a comprehensive analysis to assess true representation. A good portion of the discrepancies between habitats in MPAs and biounits can be linked to the lack of complete seafloor mapping data across entire biounits. To provide a better understanding of habitat representation across Victorian MPAs, more complete habitat mapping data are required. These additional data would allow for more coverage of substrate and depth classifications and would let us extend the biotope complex classification across entire biounits. On the other hand, environmental conditions were represented well within the MPAs when compared to their associated biounits. Areas that

differed in their physical characteristics tended to be the smaller marine sanctuaries, demonstrating that larger marine national parks are required to representatively capture the characteristics of the biounits. Physical conditions are likely to continue to change in the future, which could potentially threaten the effectiveness of MPAs (Bruno et al., 2018). Assessing these changes and their resultant effects on species populations will allow better management of MPAs by anticipating potential changes in species composition. These results can also help to pinpoint gaps in protection that could potentially be captured if more MPAs are designated in the future.

# Part 2 – Richness and diversity patterns across Victorian marine protected areas

## 5. Introduction

Across the 2,000 km coastline of Victoria, 5 of coastal waters are protected within no-take marine national parks and marine sanctuaries (Wescott, 2006). These marine protected areas (MPAs) were designed to include a comprehensive, adequate, and representative (CAR) sample of marine habitats (Ferns, 2003). The coastal waters of Victoria are unique due to the convergence of cooler waters in the west and warmer waters in the east, which creates a mix of habitats and results in a high level of species endemism (Wescott, 2006). Assessments of the efficacy of these MPAs in protecting the diverse and distinctive species inhabiting Victorian marine ecosystems is critical for understanding whether MPAs are achieving the purpose for which they were designed, which is to protect biodiversity along the coast.

Multiple long-term monitoring programs have sampled marine communities within and outside Victorian MPAs with the aim of understanding how well they protect the biodiversity found within state waters. Long-term monitoring datasets are essential for achieving quantitative assessments of protected area effectiveness in maintaining diversity and condition of ecosystems (Tierney et al., 2009) because they provide information on both contemporary status and how the ecosystems change through time (Magurran et al., 2010; Sergeant et al., 2012). Monitoring programs in Victoria have been observing marine communities since 1998 and provide information on fish, invertebrate and macroalgae abundance and distribution.

To understand how marine communities are changing through time and across different habitats and status of protection, we used the Victorian long-term datasets to examine associations between the marine communities, environmental conditions and MPA protection through time. We first collated observation data across 3 monitoring programs and extracted information about the environment and protection status at each site surveyed. We then used a machine learning approach (boosted regression trees) to analyse temporal, spatial, and environmental dynamics associated with fish richness and diversity and fish functional groups; invertebrate richness and diversity, invertebrate groups, and invertebrate fishery species; urchins; and canopy-forming macroalgae. We also developed species distribution models for the urchins and stacked species distribution models for the macroalgae to predict the distribution and abundance of species across the state based on their responses to environmental variables. The results from these analyses tell us how marine communities are responding to the environment and in marine protected areas across Victoria, which can inform management actions aimed at the protection of these communities. Additionally, this information can be used to determine which characteristics

of the environment should be captured within MPAs to maximise biodiversity protection and which are associated with decreases in biodiversity.

## 6. Methods

## 6.1 Collating observation data

Time series observation data of fish, invertebrates and macroalgae were collated across the state of Victoria. These datasets were collected across 3 different sampling programs: Parks Victoria's Subtidal Reef Monitoring Program (SRMP), Reef Life Survey (RLS), and fishery independent abalone surveys by the Victorian Fisheries Authority (VFA). These datasets were all collected using scuba in the coastal zone of Victoria. To combine these data for analyses, all datasets were processed and standardised to matching units. The sampling methods for RLS and SRMP are similar but slightly different to the VFA methods. However, converting them all to the same units allowed methods to be combined. A brief overview of each method is given below.

## 6.1.1 Subtidal Reef Monitoring Program

Parks Victoria established the SRMP for the purpose of monitoring the status of reef-associated macroalgae, macroinvertebrates and fish within the coastal waters of Victoria. Through long-term surveys, the SRMP tracks the trends in species abundances, species diversity and reef community structure through time. The sites surveyed for the SRMP include sites within Victorian MPAs and in areas adjacent to them. These datasets allow for comparison between highly protected areas (e.g. marine national parks and marine sanctuaries) and unprotected reefs (Edgar and Barrett, 1997, 1999). The visual census methods used in these surveys were developed by Edgar and Barrett (Edgar and Barrett, 1997, 1999; Edgar et al., 1997). Each site is located using a global positioning system (GPS) unit, and a 200 m transect line is laid along the 5 m contour with its centre on the GPS point. Three different methods are used for each transect to collect information on mobile fishes and cephalopods; invertebrates and cryptic fishes; and macroalgae and sessile invertebrates.

Mobile fishes and cephalopods are counted as the diver swims up one side of a 50 m section of the transect and then back along the other. Within 5 m of each side of the transect, all fish and their estimated size class are recorded. These counts are repeated across each of the remaining 50 m transect sections, resulting in four 50 m by 10 m areas surveyed. The methods used to capture the abundances of invertebrates and cryptic fishes are similar, but the area is restricted to within 1 m of one side of the transect line. Therefore, there are four 50 m by 1 m transects. To quantify macroalgae and sessile invertebrates,  $0.25 \text{ m}^2$  quadrats are placed at 10 m intervals along the transect line. These quadrats are divided into a grid of  $7 \times 7$  perpendicular wires to provide 49 points plus one corner, making 50. The cover of macroalgae and invertebrates is then estimated by counting the number of times a species

intersects with one of the points. This method provides a total area surveyed of 1.25 m<sup>2</sup> for each of the 50 m transect lines.

## 6.1.2 Reef Life Survey (RLS)

RLS is citizen science program that trains volunteer scuba divers to conduct visual surveys of underwater reefs. RLS started surveying along the Victorian coast in 2008 and continues to extend the time series of observations of fish, invertebrates and macroalgae in the region. Detailed methods for acquiring RLS data are described in Edgar and Stuart-Smith (2009). Briefly, each site is surveyed using a 50 m line transect along a selected depth contour with 2 or more depth contours targeted at each site. Fishes within 5 m of either side of the 50 m transect line are counted and their lengths estimated. Invertebrates and cryptic fishes are counted within 1 m of either side of the transect and all cryptic fish are sized. Additionally, at 2.5 m intervals along the transect line, digital photo quadrats are acquired. These photos are taken downward from a 50 cm height above the seabed. These photo quadrats are then classified into 16 functional or morphological categories of algae using the Collaborative and Annotation Tools for Analysis of Marine Imagery and video (CATAMI) classification scheme (Althaus et al., 2015), which is a standard image classification system for Australia.

## 6.1.3 Victorian Fisheries Authority (VFA)

To supplement the macroalgae data from the RLS and SRMP datasets, we used estimates of percentage cover of 2 macroalgae species, Golden Kelp (*Ecklonia radiata*) and Crayweed (*Phyllospora comosa*), and densities of 2 urchin species, Purple Sea Urchin (*Heliocidaris erythrogramma*) and Longspined Sea Urchin (*Centrostephanus rodgersii*), from fishery independent diver surveys conducted by the VFA at 195 monitoring sites along the coast of Victoria. At each of these sites, the divers estimated percentage cover of *E. radiata* and *P. comosa* and counted the urchins within six 30 m by 1 m transects at random cardinal directions from the central site coordinates. We divided the urchin counts by the area surveyed to provide density estimates per metre squared for both species at each site.

#### 6.1.4 Combining datasets

Once all datasets were collated, we calculated the density of fish and invertebrates per metre squared and the biomass of fishes per metre squared by dividing the counts and biomass by area surveyed in each method. We also calculated the richness and diversity (Shannon–Wiener diversity index) of fishes and invertebrates within each transect and then calculated an average per site. These calculations were done for each year in the time series. Percentage cover does not require standardisation and therefore was used as percentage cover in all analyses. The standardised datasets were combined into a single dataset for analyses. This final dataset includes a time series from 1998 to 2020.

## 6.2 Extracting environmental information

We extracted environmental information from each site for inclusion in statistical analysis to understand associations between the abundance and distribution of species, assemblages and communities. First, we calculated additional variables describing the structure of the seafloor using the Benthic Terrain Mapper toolbar (Wright et al., 2005) and Spatial Analyst within ArcGIS (ESRI, 2011). All derivatives extracted for each site and their descriptions are shown in Table 6.1. These variables were chosen based on their use in past studies to help explain the distribution and abundance of marine species (e.g. Wines et al., 2020; Young and Carr, 2015; Young et al., 2016b). Variables with a temporal component (wave orbital velocity, current speed, SST) were extracted for the matching year in the biological sampling.

## 6.3 Statistical analyses

To complete all the analyses described below, we used boosted regression trees (BRTs). Rather than providing a single 'best' model, such as in traditional regression methods, the BRT method uses a large number of relatively simple tree models to develop associations between response and explanatory variables and allows for more robust predictions (Elith and Leathwick, 2009; Leathwick et al., 2006). To reduce overfitting the data and optimise model parameters, we used the BRT tuning functions in the gbm package prior to running each model. These tuning functions provided us with the learning rate, interaction depth and number of trees to optimise model performance without overfitting the data. We also used a 10 k-fold cross-validation method to further reduce instances of overfitting (Leathwick et al., 2006). The BRT models were run using R statistical software (R Core Team, 2014) and the gbm package (Ridgeway, 2007). For each response variable outlined below, we ran a series of BRTs with varying combinations of explanatory variables until we developed a model with high variance explained and accurate predictive ability. Each BRT was trained using 70 of the observations while the remaining 30 were held in reserve for evaluating the predictive ability of the resulting best model. The final BRT model was used to predict from the evaluation dataset, and those predictive values were compared to the observed values using a Pearson correlation analysis.

Table 6.1: Descriptions of derivatives used in the boosted regression trees

Derivative	Software	Description
Depth	ArcGIS Pro 2.2 (Base)	Elevation of seafloor relative to the Australian Height Datum
Rugosity	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	Incorporates the heterogeneity of both slope and aspect using 3-dimensional dispersion of vectors. See Sappington et al., (2007) for more details
Slope	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	Change in elevation over designated neighbourhood size. tan-1(Rise/Run)
Northness	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	The cosine of the angle of slope in the analysis window. Equation: cos(aspect)
Eastness	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	The sine of the angle of slope in the analysis window. Equation: sin(aspect)
Standard deviation of bathymetry	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	Calculates the standard deviation of the depth values within a $3\times 3$ moving window to provide an indication of the relief of the benthic terrain
Bathymetric position index (fine, moderate and broad)	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	BPI, which is a measure of the relative elevation of the terrain
Annual mean sea- surface temperature (daytime)	IMOS	Annual mean sea-surface temperature (°C) sourced from the Integrated Marine Observing System (IMOS) 1995–2019
Summer sea-surface temperature (daytime)	IMOS	Summer (December to February) sea-surface temperature (°C) sourced from the Integrated Marine Observing System IMOS 1995–2019
CBiCS BC2	Deakin Marine Mapping Group	Broad habitat classification modelled statewide coverage created for the Victorian Environmental Assessment Council (VEAC)
CBiCS BC3	Deakin Marine Mapping Group	Habitat complex classification modelled statewide coverage created for the VEAC
CBiCS BC4	Deakin Marine Mapping Group	Biotope complex classification modelled statewide coverage created for the VEAC
Longitude	ArcGIS Pro 2.2 (Spatial Analyst)	Raster calculator. Increasing in value from west to east
Winter max wave orbital velocity mean	Water Tech	25-year hindcast model of wave orbital velocities from 1990 to 2015
Annual average current speed	Water Tech	25-year hindcast model of annual current speeds from 1990 to 2015

#### 6.4 Fishes

#### 6.4.1 Richness and diversity

Using a BRT with a Poisson distribution for richness and Gaussian for diversity, we modelled the relationship between fish richness and diversity and the environmental variables. Multiple models with different combinations of the variables Table 6.1 were run until the best model for each response variable was chosen based on the variance explained and the predictive performance.

## 6.4.2 Functional feeding groups

In addition to richness and diversity, we also assigned each fish observed to its functional feeding group. Fishes were split into these functional feeding groups using a table adapted from Stuart-Smith et al. (2013), which used FishBase (Froese and Pauly, 2010) and dietary studies to classify species into trophic groups. Species that were not present in the 2013 study were assigned into groups based on their closest relatives resulting in 4 functional feeding groups: benthic invertivores, browsing herbivores, higher carnivores and planktivores. Although invertivores are technically carnivores, the invertivores were classed separately due to the likely differences in habitat associations of species that feed on benthic invertebrates compared to species that feed on more mobile prey. We ran BRTs for each functional feeding group to determine their environmental associations and patterns through time.

#### 6.5 Invertebrates

#### 6.5.1 Richness and diversity

Using a BRT with a Poisson distribution for richness and Gaussian for diversity, we modelled the relationship between invertebrate richness and diversity and the environmental variables. Multiple models with different combinations of the variables in Table 6.1 were run until the best model for each response variable was chosen based on the variance explained and the predictive performance.

#### 6.5.2 Species groupings

In addition to richness and diversity, we also assessed the relationship between invertebrate species densities and densities of species groupings and their environment using BRTs. The invertebrates with significant observations across the time period were classified into 3 groups: sea stars, snails and crabs. Table 6.2 shows the species included in each group. All these groupings had greater than 300 observations in total, allowing us to develop robust models across several environmental variables. We also ran separate models for the important invertebrate fisheries species along the Victorian coast: abalone (*Haliotis rubra* and Greenlip Abalone, *H. laevigata*) and Southern Rock Lobster (*Jasus edwardsii*).

Table 6.2: Species in each invertebrate grouping

Group	Species	Common name
Sea stars	Cenolia trichoptera	Orange Feather Star
	Coscinasterias muricata	Eleven-Arm Star
	Fromia polypora	Many-Spotted Sea Star
	Meridiastra gunnii	Gunns Six-Armed Star
	Nectria macrobrachia	Large-Plated Seastar
	Nectria ocellata	Ocellate Seastar
	Nectria pedicelligera	Seastar
	Pentagonaster duebeni	Fire-Brick Star
	Petricia vernicina	Velvet Star
	Plectaster decanus	Mosaic Seastar
	Pseudonepanthia troughtoni	Troughton's Seastar
	Tosia australis	Southern Biscuit Star
	Uniophora granifera	Granular Seastar
Snails	Dicathais orbita	Dog Whelk
	Lunella undulata	Turban Shell
	Scutus antipodes	Elephant Snail
Crabs	Guinusia chabrus	Red Bait Crab
	Plagusia chabrus	Chabrus Crab
Abalone	Haliotis laevigata	Greenlip Abalone
	Haliotis rubra	Blacklip Abalone
Lobsters	Jasus edwardsii	Southern Rock Lobster

# 6.6 Urchins and macroalgae

Due to the more extensive spatial coverage of the urchin and macroalgae datasets, we expanded the application of the BRT models to also make spatial predictions of urchins and macroalgae across the state.

## 6.6.1 Urchins (Heliocidaris erythrogramma and Centrostephanus rodgersii)

Using BRTs with Gaussian distributions, we modelled the relationship between *H. erythrogramma* and *C. rodgersii* and a selection of environmental variables from Table 6.1. In addition to the environmental variables introduced across the previous models, we also incorporated the species-specific connectivity variables described in Part 1 (Section 2.8). We used measures of in-degree, self-recruitment, total inflow and local retention across the models, but only retained variables that had a large impact on and improved the models in the final model. The best model for each species was chosen based on the

variance explained and the predictive performance. Once we had suitable models, they were used to predict and extrapolate density estimates across the coastal zone within Victorian state waters. We did this by creating a raster stack of the variables found to be influential using the raster package in R (Hijmans and van Etten, 2014) and then predicting densities from the raster stack using the gbm package (Ridgeway, 2007). Unlike other species examined in this part of the report, very high densities of both *H. erythrogramma* and *C. rodgersii* are generally considered undesirable, as this can lead to the creation of urchin barren areas and declines in macroalgal cover. Our driver for examining urchin densities was thus to identify environmental variables that increase the risk of urchins reaching high densities.

# 6.6.2 Macroalgae (Phyllospora comosa and Ecklonia radiata)

Using BRTs with Gaussian distributions, we modelled the relationship between *P. comosa* and *E. radiata* percentage cover and different combinations of environmental variables outlined in Table 6.1, including the connectivity variables for macroalgae from Part 1 (Section 2.8). In addition to the environmental variables explored in the other BRTs in this study, we also included the predictions of *C. rodgersii* and *H. erythrogramma* from the previous analysis to help predict the distribution of macroalgae, also known as stacking SDMs. This was done because of the well-known relationship between macroalgal cover and population of urchins, both *H. erythrogramma* (Ling et al., 2010) and *C. rodgersii* (Ling and Johnson, 2009). Large populations of urchins can drastically reduce the cover of macroalgae and we wanted to capture that in our models. Again, we used the relationships in the BRT to extrapolate percentage cover of both *P. comosa* and *E. radiata* across the state of Victoria, applying the same methods outlined for the urchin models.

#### 7. Results

## 7.1 Fishes

## 7.1.1 Richness and diversity

The model attributes for the final BRT models for fish richness and diversity are shown in Table 7.1 with the results from the cross-validation. The BRT model for richness used 1,250 trees across 9 explanatory variables, while the BRT model for diversity used 1,300 trees, also across 9 variables. The performance statistics outlined in Table 7.1 show that the model performed relatively well at explaining variation in fish species richness and diversity across the study area and time period. The *R*-squared of the fitted model shows that the richness BRT explains 82 and the diversity BRT explains 84 of the spatial and temporal variation. Additionally, when we used the BRT models to predict richness and diversity from the evaluation datasets and compared those predictions to the observed values, we found that the BRT model was fairly accurate in predicting richness and diversity across both space

and time with statistically significant Pearson correlations of 0.74 (P < 0.001) and 0.76 (P < 0.001), respectively.

Table 7.1: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate fish richness and diversity with spatial and temporal explanatory variables. The error distribution, learning rate, interaction depth and number of trees parameters are all optimised prior to running the models to prevent overfitting. The performance of each model is assessed using the training data correlation, the *R*-squared and the Pearson correlation

BRT model parameters	Explanation of parameter	Fish richness	Fish diversity
Error distribution	Distribution of the response data (e.g. richness or diversity)	Poisson	Gaussian
Learning rate	The contribution of each tree to the final model – lower values indicate a smaller contribution, resulting in a greater number of trees	0.01	0.001
Interaction depth	Tree complexity or the number of nodes in each tree – greater complexity in the trees results in fewer trees being needed	5	5
Number of trees	Total number of trees used in the final model	1,250	1,300
Mean residual deviance	How well a response is predicted by a model with predictors included	0.762	0.051
Training data correlation	A measure of how well the model predicts within the 70 of the data used to develop the model	0.908	0.917
R-squared (fitted model)	The amount of variation explained by the model	0.825	0.840
Pearson correlation with evaluation data ( <i>P</i> value)	The correlation between the predictions from the model and the actual observations in the 30 of the data set aside to assess the predictive performance of the model	0.742 ( <i>P</i> < 0.001)	0.764 ( <i>P</i> < 0.001)

The nature and relative magnitude of influence of the explanatory variables used in the final BRTs for richness and diversity are shown in Figures 7.1 and 7.2, respectively. The same 9 variables were found to be influential across both models, and the patterns with those variables were very similar. However, the orders of importance for the variables differed slightly between models. Year was found to be one of the most influential variables; richness and diversity oscillated through time and both showed a downward trend in the most recent years. Although year is not producing a clear pattern, its incorporation in the model allows the model to account for any interannual variation in the response variable and reduce temporal correlation (i.e. where years closer to each other are more similar than

years further apart). Longitude shows that there is a general increase in richness and diversity moving from west to east along the Victorian coast. Both richness and diversity decrease as depths get shallower. There is a mostly positive relationship between both richness and diversity and average current speed up until the speed increases to around 1.0 m/s. As currents exceed that value, richness and diversity decrease. Sea-surface temperature begins to have a negative effect on fish richness and diversity once average summer SST reaches values about 20 °C. Two measures of complexity of the seafloor were also found to be influential across both models: bathymetry standard deviation and rugosity. The relationship with bathymetry standard deviation shows a slight increase in richness and diversity as relief increases, and the relationship with rugosity shows a peak in richness and diversity in areas of moderate rugosity followed by a slight decrease as rugosity increases. Richness and diversity showed different relationships with max winter wave orbital velocities. The richness BRT shows highest richness occurs in moderate orbital velocity values and lower richness at both lower and higher extremes. In contrast, diversity increases with increases in orbital velocity up to around 0.4 m/s and then remains relatively stable with no further increases. Protection gained from MPA designation was the least important variable in the model, but there is a slight increase in richness inside the MPAs compared to outside.

These results help to indicate what conditions are required in MPAs to increase species richness and diversity. The BRT models for fish species richness and diversity show that MPAs located in the east of the state protect greater fish richness than those in the west. Also, to improve fish richness, MPAs should be located in areas with higher complexity, deeper reefs, temperatures not exceeding 20 °C and lower wave energy.

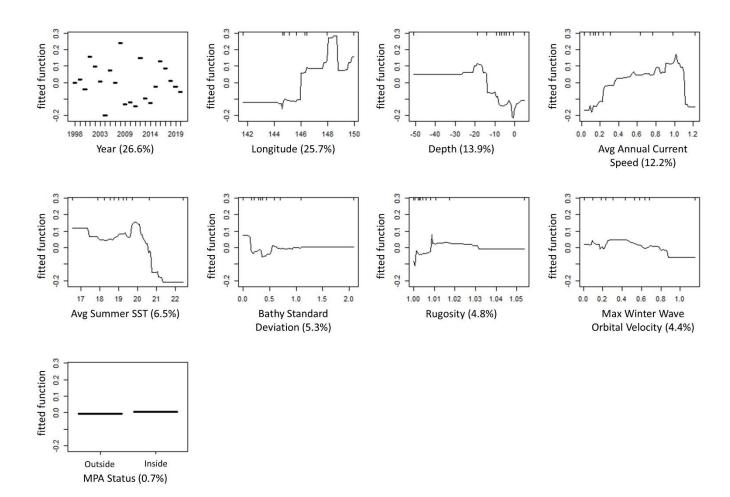


Figure 7.1: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for fish species richness. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for fish species richness. Increases in y-values indicate an increase in species richness and decreases in y-values indicate a decrease in species richness. All relationships are shown for median values of the other variables in the model

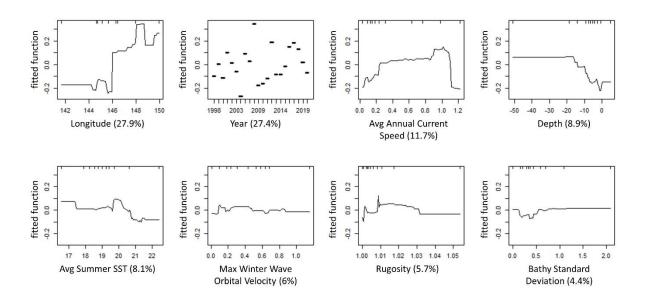


Figure 7.2: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for fish species diversity. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for fish diversity. Increases in y-values indicate an increase in species diversity and decreases in y-values indicate a decrease in species diversity. All relationships are shown for median values of the other variables in the model.

# 7.1.2 Fish functional groups

The parameters for the final BRT models for biomass across 4 fish functional feeding groups are shown in Table 7.2 with the results from the cross-validation. The BRT models for browsing herbivores, benthic invertivores and planktivores did relatively well, explaining between 81 and 95 of the variation in biomass and predicting with accuracies of 69 to 82. The model for higher carnivores had much lower performance, only explaining 25 of the biomass variation and predicting with an accuracy of 45.

Table 7.2: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate fish functional feeding groups with spatial and temporal explanatory variables

BRT model parameters	Browsing herbivore	Benthic invertivore	Higher carnivore	Planktivore
Error distribution	Gaussian	Gaussian	Gaussian	Gaussian
Learning rate	0.01	0.01	0.001	0.001
Interaction depth	5	5	5	5
Number of trees	800	700	2,450	7,800
Mean residual deviance	15.049	24.223	162.48	13.527
Training data correlation	0.902	0.941	0.496	0.977
R-squared (fitted model)	0.814	0.886	0.246	0.954
Pearson correlation with evaluation data (P value)	0.790 ( <i>p</i> < 0.001)	0.688 ( <i>p</i> < 0.001)	0.450 ( <i>p</i> < 0.001)	0.815 ( <i>p</i> < 0.001)

**Note:** See Table 7.1 for an explanation of model parameters

#### **Browsing herbivores**

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for browsing herbivore biomass are shown in Figure 7.3. Average current speed was the most influential variable: it showed that biomass increases with increasing current speeds. Browsing herbivore fishes are also found in higher biomass in high-relief areas, shown by the relationship with the standard deviation of bathymetry. Browsing herbivore biomass decreases as waters become shallower, and abundance has seen an overall increase from 1998 to 2017. Biomass also decreases with increasing average summer SST and increases with increasing wave orbital velocities. We also see a greater biomass of browsing herbivores as you move from west to east along the coast. Although MPA status was the least influential variable in the model, there is a slight increase in biomass within MPAs compared to outside.

These results indicate that browsing herbivores have highest biomass in areas with high current speeds, higher complexity reefs, deeper depths and lower summer temperatures, and in the eastern section of the state. Additionally, they tend to have lower biomass at very low wave energies, so MPAs located in calmer regions along the coast may not be as successful at protecting this group. The positive relationship with MPA protection also shows that the current MPAs are supporting larger densities of browsing herbivores than are areas outside the MPAs.

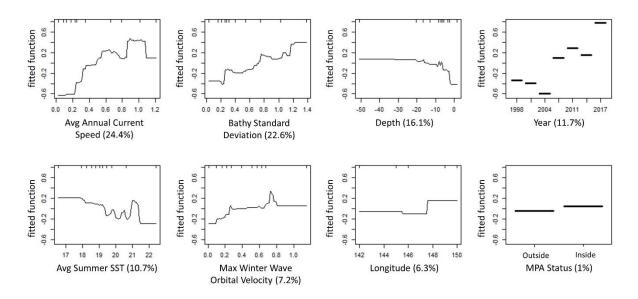


Figure 7.3: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for browsing herbivore fish biomass. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for browsing herbivore fish biomass. Increases in y-values indicate an increase in fish biomass and decreases in y-values indicate a decrease in fish biomass. All relationships are shown for median values of the other variables in the model

#### Benthic invertivores

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for benthic invertivore biomass are shown in Figure 7.4. The bathymetry standard deviation, a measure of terrain relief, was the most influential variable in the BRT for benthic invertivore biomass: biomass increases substantially in areas of high relative relief. Depth, the second most influential variable, shows biomass is slightly greater in the deeper end of the depth range. Benthic invertivore biomass also increases as you move east along the coast, through the years and as current speed increases. However, biomass decreases slightly as average summer SST increases. Biomass is lowest at low values of winter wave orbital velocity but then increases slightly and stays relatively stable as velocities increase. As with the BRT for browsing herbivores, the protection afforded by MPAs has a slightly positive effect on benthic invertivore biomass.

The strong relationship between benthic invertivore biomass and reef complexity indicates that MPAs with high-complexity reef are likely to support a greater biomass of benthic invertivores. Also, MPAs with greater depths and in the east of the state are likely to have a larger biomass of benthic invertivores. The general negative trend with temperature also indicates that MPAs located in areas with lower temperature are likely to have higher biomass, while positive trends with current speeds indicate MPAs with faster current speeds also support higher biomass. Weak relationships between wave orbital velocity and benthic invertivore biomass indicate that biomass will not differ greatly among MPAs with different

wave conditions, though there was a slight trend for MPAs with calmer wave condition to support slightly higher biomass. Currently, the MPAs are supporting a greater biomass of benthic invertivores than those areas outside.

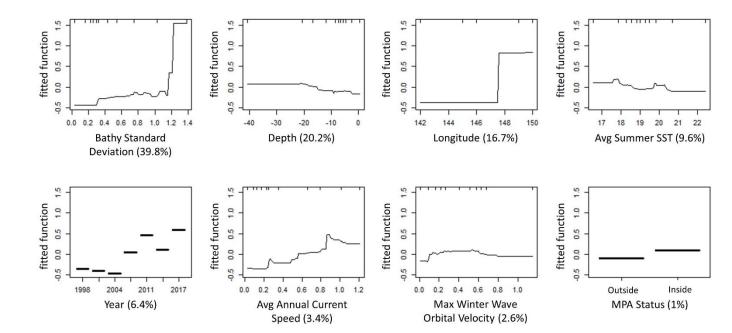


Figure 7.4: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for benthic invertivore fish biomass. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for benthic invertivore fish biomass. Increases in y-values indicate an increase in benthic invertivore fish biomass and decreases in y-values indicate a decrease in benthic invertivore fish biomass. All relationships are shown for median values of the other variables in the model

## **Higher carnivores**

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for higher carnivore biomass are shown in Figure 7.5. Longitude was the most influential variable: the greatest higher carnivore biomass is found in the eastern section of the state. Biomass also tends to increase with summer SST up to around 17.5 °C and then stay relatively stable with increasing temperatures. Biomass of higher carnivores is greater in areas of greater sloping terrain (bathymetric position index) and in deeper areas of the surveys. The relationship with the BPI shows that slightly higher biomass occurs in lower areas of the terrain. Higher carnivore biomass has also increased slightly since 1998, peaking in 2017 followed by a decrease in recent years. The relationship with current is relatively neutral with a slight peak in biomass around current speeds of 0.6 m/s.

As with the previous fish models, MPAs in the eastern portion of the state are likely to contain higher carnivore biomass than those in the west. Average annual SST do not seem to negatively impact these species as much as others with lower biomass found in the cooler temperatures but there is a relatively neutral relationship with temperatures above 7 °C. Carnivore biomass tends to be greatest in areas of high slope but is not associated with higher complexity reef like the other species groups, so MPAs with higher complexity habitat are not necessarily more effective for these species. MPAs with deeper depth ranges are also likely to be more successful than shallow MPAs at protecting carnivores. However, no relationship between MPA status was found for higher carnivores, indicating that their biomass is not strongly influence by the protection offered by MPAs.

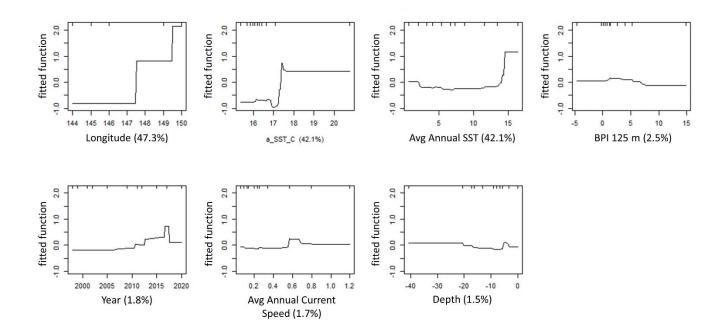


Figure 7.5: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for higher carnivore fish biomass. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for higher carnivore fish biomass. Increases in y-values indicate an increase in higher carnivore fish biomass and decreases in y-values indicate a decrease in higher carnivore fish biomass. All relationships are shown for median values of the other variables in the model

#### **Planktivores**

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for planktivore biomass are shown in Figure 7.6. Depth and longitude were the most influential variables: the highest biomass was found on the deeper end of the depth range surveyed and in the east of the state. Standard deviation of bathymetry was also very influential, showing planktivore biomass increasing with increased relief. The relationship

with average summer SST varies: the highest biomass is found around 17 °C, followed by a sharp decrease and then a gradual increase as temperatures increases. We also see a general increase in planktivore biomass through time with the highest biomass in the most recent surveys. Currents and waves are also influential, showing higher biomass at lower wave orbital velocities and a gradual increase in biomass as current speed increases. Higher planktivore biomass is also found in areas of greater sloping terrain. Finally, although MPA status is not very influential at only 0.1, there is slightly higher planktivore biomass inside MPAs than outside.

The relationship between planktivore biomass and depth indicates that MPAs with extensive regions in the 20 m depth range are likely to have higher biomass of planktivores, as biomass decreases in shallower depths. Eastern MPAs are again more likely to protect greater biomass of this functional group. Planktivores also seem to do better in MPAs with higher relief reef. Relationships between temperature, wave energy and currents indicate planktivore biomass will be higher in MPAs with lower wave energy and currents and will not be negatively affected in MPAs with higher temperatures. The relationship with MPA status also shows that there is currently higher biomass of planktivores within the MPAs.

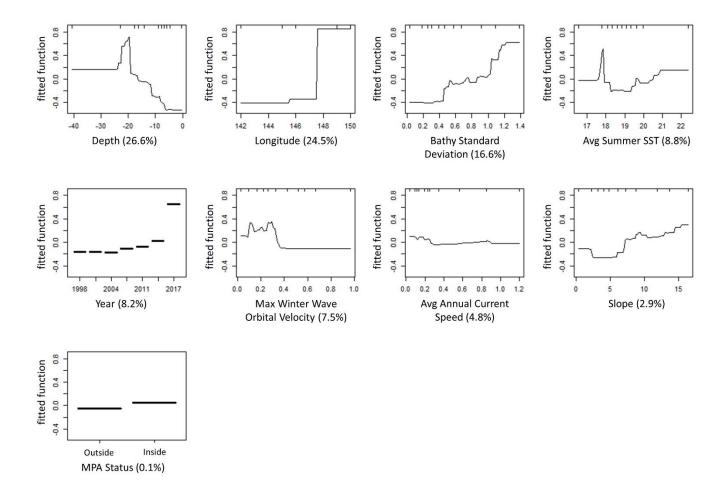


Figure 7.6: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for planktivore fish biomass. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The *y*-axis represents the fitted function from the model for planktivore fish biomass. Increases in *y*-values indicate an increase in planktivore fish biomass and decreases in *y*-values indicate a decrease in planktivore fish biomass. All relationships are shown for median values of the other variables in the model

## 7.2 Invertebrates

## 7.2.1 Richness and diversity

The parameters for the final BRT models for invertebrate richness and diversity are shown in Table 7.3 with the results from the cross-validation. The BRT model for richness used 2,050 trees across 10 explanatory variables, and the BRT model for diversity used 1,550 trees, also across 10 variables. The performance statistics outlined in Table 7.3 show that the model performed relatively well at explaining variation in invertebrate species richness and diversity across the study area and time period. The *R*-squared of the fitted model shows that the richness BRT explains 87 and the diversity BRT explains 84 of the spatial and temporal variation. Additionally, when we used the BRT models to predict richness and

diversity from the evaluation datasets and compared those predictions to the observed values, we found that the BRT model was fairly accurate in predicting richness and diversity across both space and time with statistically significant Pearson correlations of 0.62 (P < 0.001) and 0.60 (P < 0.001), respectively.

Table 7.3: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate invertebrate richness and diversity with spatial and temporal explanatory variables

BRT model parameters	Invertebrate richness	Invertebrate diversity
Error distribution	Poisson	Gaussian
Learning rate	0.01	0.001
Interaction depth	5	5
Number of trees	2,050	1,550
Mean residual deviance	0.392	0.046
Training data correlation	0.933	0.915
R-squared (fitted model)	0.871	0.837
Pearson correlation with evaluation data (P value)	0.619 ( <i>P</i> < 0.001)	0.598 ( <i>P</i> < 0.001)

**Note:** See Table 7.1 for an explanation of model parameters

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for invertebrate species richness and diversity are shown in Figures 7.7 and 7.8, respectively. Although the same variables were used across both models, the relative influence and relationships with those variables differ slightly. In both models, year was the most influential variable, but there is not a clear pattern with richness and diversity. Longitude showed that richness is greater in the eastern portion of Victoria, but diversity is greater towards the west. There is a positive relationship between richness and bathymetry standard deviation, showing that higher invertebrate species richness is found in areas of higher relief. Invertebrate diversity and relief is higher at lower values of relief followed by a slight increase with increasing relief. Average current speed generally has a positive relationship with both invertebrate richness and diversity. Biotope complex was also found to be influential. The highest richness and diversity tend to be found in infralittoral reef with low exposure, and high values are also found in the other categories for infralittoral and circalittoral rock. Invertebrate species richness and diversity tend to be higher at intermediate depths and in higher areas of the terrain (BPI). Rugosity has a relatively neutral influence on richness; the highest diversity is found in areas of lower rugosity. Wave orbital velocity has differing effects on richness and diversity: invertebrate species richness increases slightly with orbital velocity values while invertebrate diversity tends to decrease with increased velocities. Both invertebrate richness and diversity decrease with increasing average summer SST.

These results show that MPAs extending from a longitude of 144° east (near Point Addis MNP) to 149° east (near Point Hicks MNP) contain greater invertebrate species richness and diversity than those outside that range. This indicates that MPAs placed in these regions are likely to preserve higher invertebrate diversity than MPAs in areas outside. In addition, MPAs that contain a large area in the 20 m depth range, have higher complexity reef, faster current speeds, moderate wave energy and lower temperatures are likely to protect greater invertebrate diversity. However, the results show that invertebrate richness and diversity are similar inside and outside MPAs, as MPA status is not an explanatory factor in the final BRT.

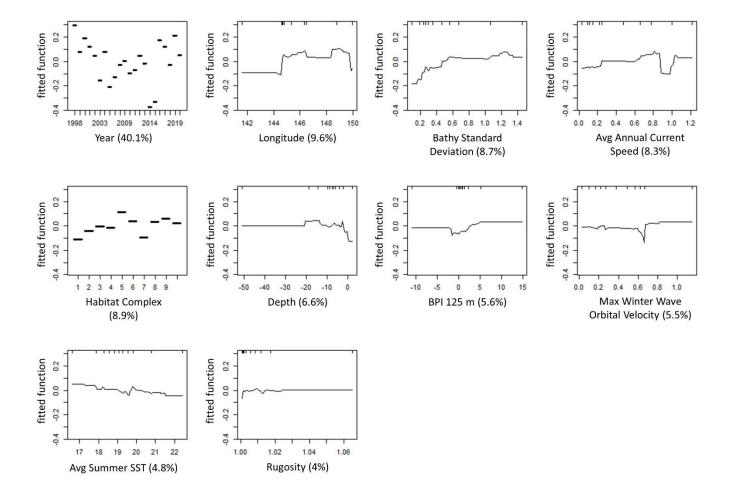


Figure 7.7: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for invertebrate species richness. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for invertebrate richness. Increases in y-values indicate an increase in invertebrate species richness and decreases in y-values indicate a decrease in invertebrate species richness. All relationships are shown for median values of the other variables in the model

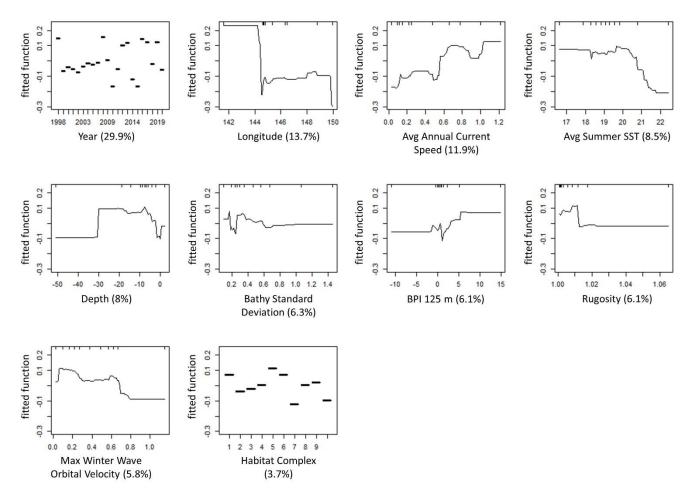


Figure 7.8: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for invertebrate species diversity. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for invertebrate diversity. Increases in y-values indicate an increase in invertebrate species diversity and decreases in y-values indicate a decrease in invertebrate species diversity. All relationships are shown for median values of the other variables in the model

## 7.2.2 Sea stars, crabs and snails

The parameters for the final BRT models for the densities across the 3 invertebrate groupings are shown in Table 7.4 with the results from the cross-validation. The BRT models for crabs did relatively well, explaining 64 of the variation in density and predicting with an accuracy of 74. On the other hand, the models for sea stars and snails have much lower performance. They only explained 31 to 34 of the biomass variation and predicted with accuracies of 39 to 45.

Table 7.4: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate invertebrate groups with spatial and temporal explanatory variables

BRT model parameters	Sea stars	Crabs	Snails
Error distribution	Gaussian	Gaussian	Gaussian
Learning rate	0.001	0.001	0.001
Interaction depth	5	5	5
Number of trees	3,000	3,900	1,700
Mean residual deviance	6.475	0.007	0.083
Training data correlation	0.557	0.800	0.580
R-squared (fitted model)	0.310	0.640	0.336
Pearson correlation with evaluation data ( <i>P</i> value)	0.451 ( <i>P</i> < 0.001)	0.741 ( <i>P</i> < 0.001)	0.389 (P < 0.001)

**Note:** See Table 7.1 for an explanation of model parameters.

#### Sea stars

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for sea star density are shown in Figure 7.9. Bioregional unit (biounit) was the most influential variable in the BRT. It showed a slight increase in densities in the eastern biounits with Cape Conran having the highest densities of sea stars. Average summer SST was also influential, showing increasing sea star densities with increasing temperatures. We are also seeing an increase in densities in more recent years. The relationship between sea star density and bathymetric position shows that density is slightly higher in lower parts of the terrain. Winter wave orbital velocities and slope have almost neutral relationships with sea star density, but show some increase in densities as they increase. Biotope complex was the least influential variable in the sea star model; it showed the highest densities on high energy infralittoral and circalittoral rock.

These relationships show that MPAs in the eastern biounits, with warmer average temperatures and greater habitat complexity tend to support greater densities of sea stars and that these densities have increased overtime. Lower densities of sea stars are also likely to be found in MPAs with lower wave velocities, flatter slopes and lower elevations across the terrain, though the magnitude of these effects is small. Sea star densities did not differ within and outside MPAs. Because BRT models only explained a moderate amount of variation in sea star density, these results should not be interpreted with a high level of certainty.

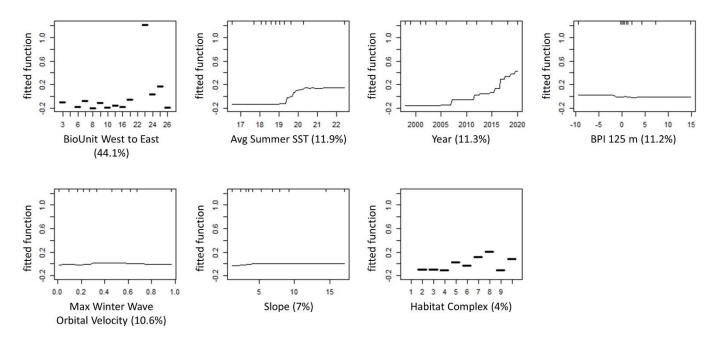


Figure 7.9: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for sea star densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The *y*-axis represents the fitted function from the model for sea star densities. Increases in *y*-values indicate an increase in sea star density and decreases in *y*-values indicate a decrease in sea star density. All relationships are shown for median values of the other variables in the model

#### Crabs

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for crab density are shown in Figure 7.10. Except for high density in the Cape Nelson biounit in the west of the state, most of the high-density biounits are found in the east from Gippsland to Cape Howe. There is a positive relationship between crab density and year, showing a general trend of increasing density in more recent years. Depth was the third most influential variable in the crab density BRT, showing an increase in crab density towards shallower depths. The relationship with average annual SST shows a slight increase in density up to around 17 °C and then a levelling off. Both currents and waves have a subtle negative effect: crab density decreases with increases in current speed and wave orbital velocity. Slope and standard deviation of the bathymetry were also found to be important. The highest densities are found at lower slope values but there is not much variation in density across different areas of relief. MPA protection was the final influential variable in the model, showing a slightly higher crab density outside MPAs than inside.

These results show that MPAs in the east of the state, encompassing areas of shallower depth (<10 m), with average annual SSTs greater than 16.5 °C, of lower energy (i.e. lower current speeds and wave velocities) and higher sloping terrain support greater densities of crabs. However, crab densities were also lower inside MPAs than outside, indicating that areas with these features outside MPAs are likely to support higher crab densities.

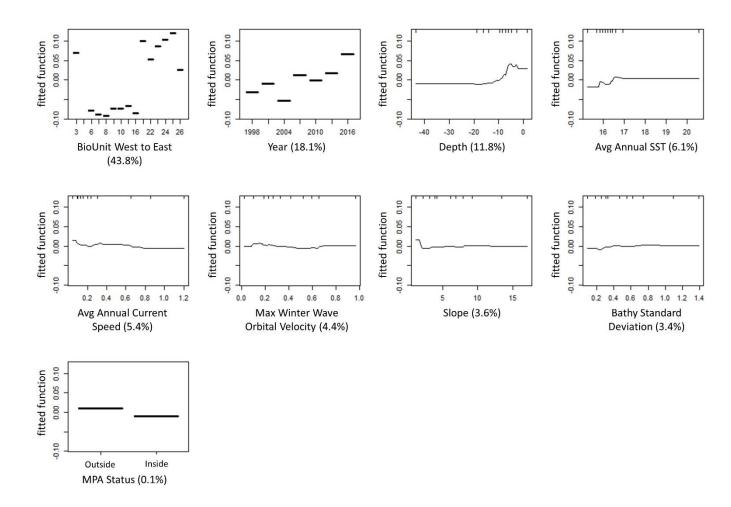


Figure 7.10: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for crab densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for crab densities. Increases in y-values indicate an increase in crab density and decreases in y-values indicate a decrease in crab density. All relationships are shown for median values of the other variables in the model

#### **Snails**

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for snail density are shown in Figure 7.11. The highest snail densities are found in both the far west and far east of the state based on the relationship with biounits. There is also a slight increase in snail densities through time. The impact of the structure of the seafloor shows that snail densities increase with higher relief, but higher densities are found in the lower points of the terrain over a 125 m scale. Snail density also tends to increase in the shallower portion of the depth range. Finally, except for a small initial increase in snail densities up to temperatures of 17 °C, the relationship with average annual SST is relatively neutral. These results show that MPAs in the west and east of the state (but not central

regions), and those with higher relief, low-lying terrain and shallow depth ranges, are likely to support the highest snail density. However, there was a high degree of uncertainty associated with these patterns compared to the results for other taxa.

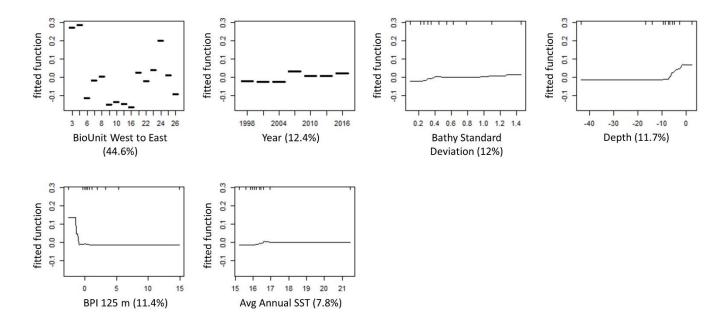


Figure 7.11: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for snail densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for snail densities. Increases in y-values indicate an increase in snail density and decreases in y-values indicate a decrease in snail density. All relationships are shown for median values of the other variables in the model

## 7.2.3 Rock lobster and abalone

The parameters for the final BRT models for Southern Rock Lobster (*Jasus edwardsii*) and abalone (*Haliotis* spp.) densities are shown in Table 7.5 with the results from the cross-validation. The BRT models for both rock lobster and abalone performed well, explaining 63 to 83 of the variation and predicting with 61 to 69 accuracy.

Table 7.5: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate invertebrate fishery species with spatial and temporal explanatory variables

BRT model parameters	Southern Rock Lobster	Abalone
Error distribution	Gaussian	Gaussian
Learning rate	0.001	0.001
Interaction depth	5	5
Number of trees	9,250	5,750
Mean residual deviance	0.001	0.159
Training data correlation	0.912	0.793
R-squared (fitted model)	0.832	0.629
Pearson correlation with evaluation data (P value)	0.610 ( <i>P</i> < 0.001)	0.690 ( <i>P</i> < 0.001)

**Note:** See Table 7.1 for an explanation of model parameters.

## Southern Rock Lobster (Jasus edwardsii)

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for rock lobster density are shown in Figure 7.12. Biounit was the most influential variable, and the highest densities were in the western and eastern biounits and lower densities in biounits towards the middle of the state. Increased densities are also seen in more recent years, peaking in 2007 and again in 2016. Average summer SST is also influential: rock lobster densities peak around 18.5 °C, and the lowest densities are found in warmer temperatures. There is a general increase in rock lobster density with increases in wave orbital velocities and current speeds. Higher densities are also found in areas of higher relief and greater slope. Finally, inclusion of MPA protection in the BRT shows that there are slightly higher densities inside protected areas than outside.

These results can help to assess how the habitats and environmental conditions captured within MPAs are likely to have a positive impact on Southern Rock Lobster populations. The biounits in the west and the east of the state tend to have higher abundances, indicating that MPAs in the central regions may not protect high densities. MPAs in regions between 18 °C and 19 °C would be more successful than those outside that temperature range. In addition, higher complexity reefs, moderate wave energy and faster current speeds within MPAs have positive effects on increased densities. The current MPAs seem to be placed well for protecting Southern Rock Lobster densities, as higher densities are found within MPAs than outside.

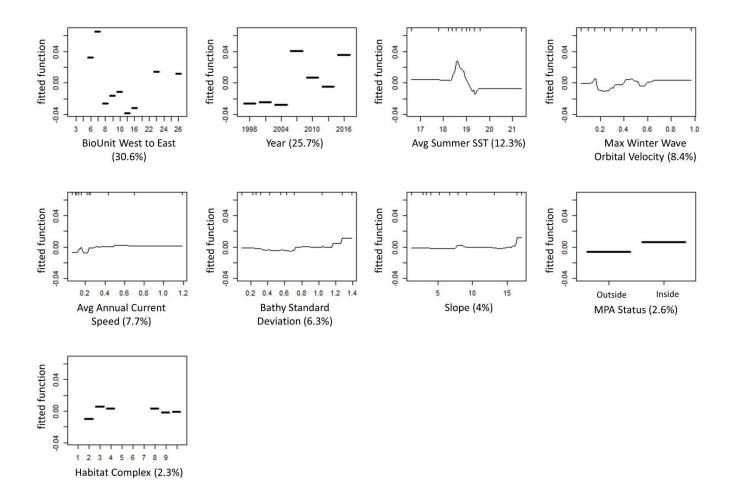


Figure 7.12: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for Southern Rock Lobster (SRL) densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for SRL densities. Increases in y-values indicate an increase in SRL density and decreases in y-values indicate a decrease in SRL density. All relationships are shown for median values of the other variables in the model

#### Abalone (Haliotis rubra and Haliotis laevigata)

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for abalone density are shown in Figure 7.13. Biounit is the most influential variable in the BRT, and abalone densities are highest in the eastern part of the states with a smaller peak in the far west. Year, the second most influential variable, shows that abalone densities tend to oscillate through time without a straightforward pattern. The relationship between abalone density and winter wave orbital velocities shows an increase in density as orbital velocity increases. Average current speed, the fourth most influential variable, shows highest abalone densities at lower current speeds and then a relatively neutral effect with increasing speeds. Increases in relief and slope tend to show increases in abalone density. Abalone are also found at higher densities in shallower depths. The relationship between

abalone density and average annual SST is relatively neutral above around 17 °C. The final variable, MPA protection, shows a greater density of abalone inside MPAs than outside.

These results indicate that MPAs in the far western and far eastern biounits protect greater abalone densities. The relationships with the environmental variables show that abalone are most abundant in areas of higher wave energies, slower current speeds, more complex rocky reef and shallower depths. The current MPAs seem to capture the habitat and conditions favouring high abalone density, with larger densities found within the MPAs than outside.

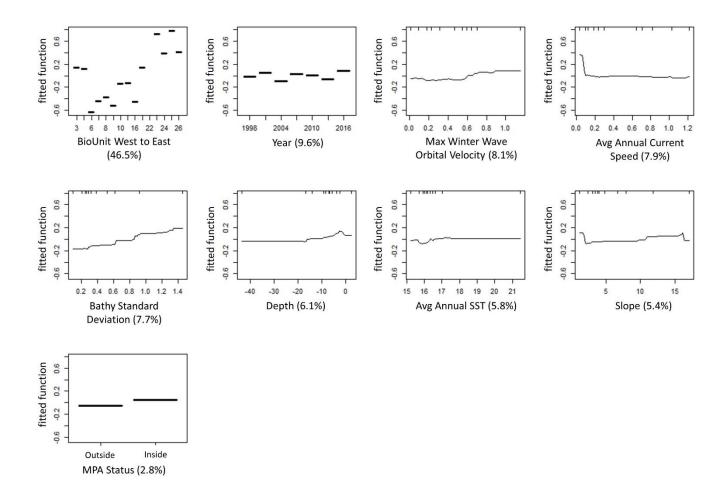


Figure 7.13: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for abalone densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The *y*-axis represents the fitted function from the model for abalone densities. Increases in *y*-values indicate an increase in abalone density and decreases in *y*-values indicate a decrease in abalone density. All relationships are shown for median values of the other variables in the model

#### 7.2.4 Urchins

The parameters for the final BRT models for the Longspined Sea Urchin (*Centrostephanus rodgersii*) and Purple Sea Urchin (*Heliocidaris erythrogramma*) densities are shown in Table 7.6 with the results from the cross-validation. The model for *C. rodgersii* performed relatively well using 8,000 trees across 5 variables; it explained 64 of the variation and predicted with 82 accuracy. However, the model for *H. erythrogramma* performed better with 5,350 trees across 9 variables. This model explained 95 of the variation in *H. erythrogramma* density and predicted with an accuracy of 93.

Table 7.6: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate urchin species with spatial and temporal explanatory variables.

BRT model parameters	Centrostephanus rodgersii	Heliocidaris erythrogramma
Error distribution	Gaussian	Gaussian
Learning rate	0.001	0.01
Interaction depth	5	5
Number of trees	8,000	5,350
Mean residual deviance	3.791	3.470
Training data correlation	0.798	0.973
R-squared (fitted model)	0.636	0.947
Pearson correlation with evaluation data (P value)	0.820 ( <i>P</i> < 0.001)	0.933 ( <i>P</i> < 0.001)

**Note:** See Table 7.1 for an explanation of model parameters.

## Longspined Sea Urchin (Centrostephanus rodgersii)

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for *C. rodgersii* density are shown in Figure 7.14. Longitude is by far the most influential variable in explaining the variation in the density of *C. rodgersii* (84.8 influence). This species is mainly found in the far east of the state past a longitude of 148° east. The other variables sharing the remaining influence on the model include BPI, slope, current speed and depth. The relationship with BPI shows that *C. rodgersii* tend to be found in higher areas of the terrain. Also, their density increases slightly as slope increases. There is a negative relationship with annual current speed: densities decrease as current speed increases. *C. rodgersii* density also decreases towards shallower depths. Overall, these results indicate that MPAs in the east of Victoria, with higher areas of terrain and greater sloping terrain, encompassing areas of deeper water and with lower current speeds are more at risk of higher densities of *C. rodgersii*. The predicted distribution and changes in cover of *C. rodgersii* density in response to these environmental variables are shown across Victoria in Figure 7.16.

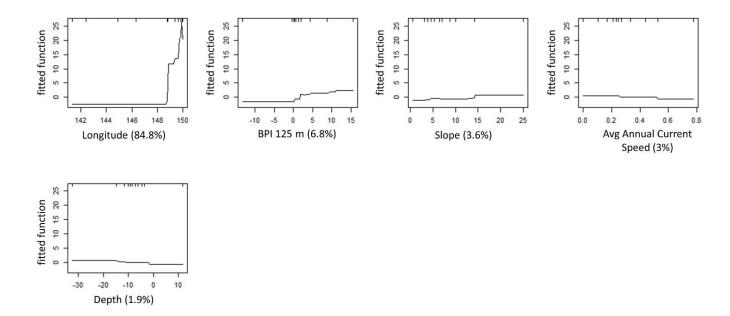


Figure 7.14: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for *Centrostephanus rodgersii* densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for *C. rodgersii* densities. Increases in y-values indicate an increase in *C. rodgersii* density and decreases in y-values indicate a decrease in *C. rodgersii* density. All relationships are shown for median values of the other variables in the model

#### Purple Sea Urchin (Heliocidaris erythrogramma)

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for H. erythrogramma density are shown in Figure 7.15. Average annual SST was the most influential variable in the model; H. erythrogramma density decreases as SST increases. Slope follows closely behind in influence, and density decreases with increasing slope. Two of the connectivity variables were also found to be influential: local retention and in-degree. Local retention is a measure of the proportion of released larvae that settle back to the source site; H. erythrogramma density decreases as local retention increases. Indegree, the total number of 'significant' connections coming into a destination site, has a relatively neutral relationship with H. erythrogramma density except for a spike in density at lower values of in-degree. H. erythrogramma density decreases with areas of increasing wave orbital velocity and increasing rugosity. Density decreases in deeper depths but remains relatively stable from 30 m to the shallowest depth sampled. Average annual current speed has a slight negative relationship with *H. erythrogramma* density but then density increases substantially around current speeds of 1 m/s. Finally, the relationship between density and BPI shows that H. erythrogramma are consistently found in higher areas of the terrain.

The relationships suggest that MPAs in water with lower average SST (<16 °C), with flatter, higher and rougher terrain, lower connectivity but higher local retention of larvae, lower wave energy, depths shallower than 30 m and with lower current speed until currents exceed 1 m/s are at higher risk of supporting higher density of *H. erythrogramma*. The predicted distribution and changes in cover of *H. erythrogramma* density in response to these environmental variables are shown across Victoria in Figure 7.17.

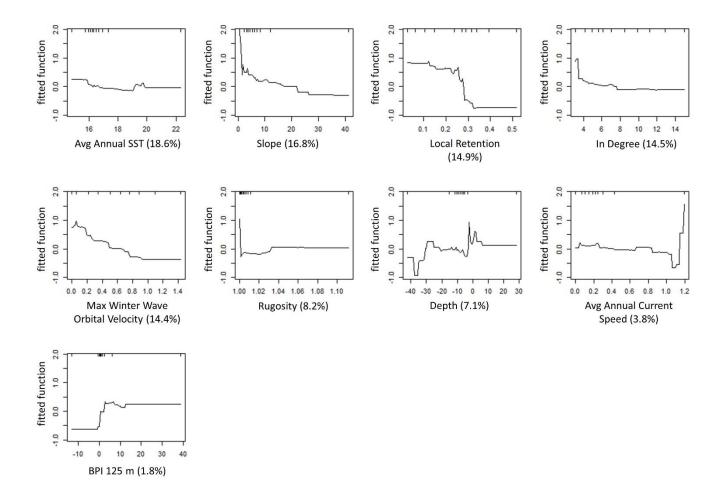


Figure 7.15: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for *Heliocidaris erythrogramma* densities. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The y-axis represents the fitted function from the model for *H. erythrogramma* densities. Increases in y-values indicate an increase in *H. erythrogramma* density and decreases in y-values indicate a decrease in *H. erythrogramma* density. All relationships are shown for median values of the other variables in the model

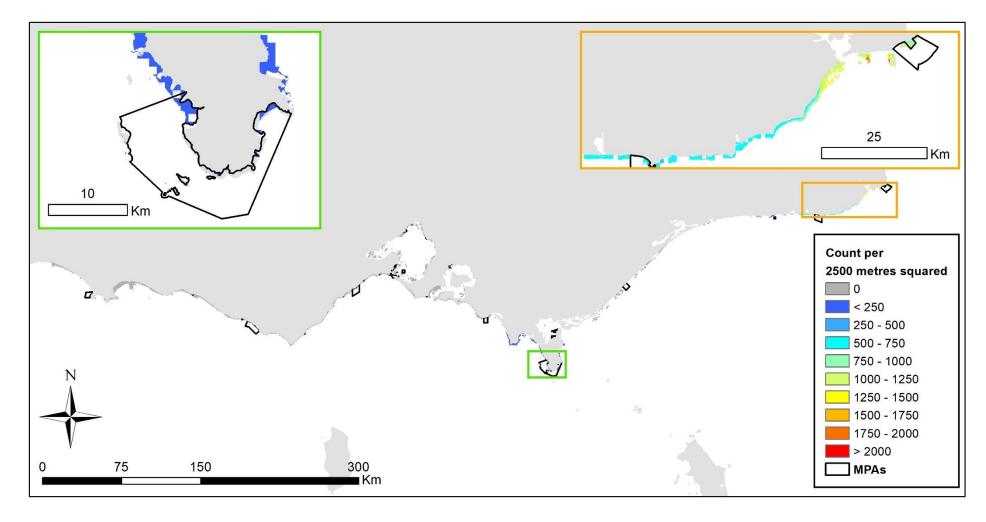


Figure 7.16: Predictive distribution map of *Centrostephanus rodgersii* densities across the coast of Victoria based on the location of suitable habitat. These maps were predicted based on the relationship with urchin density and the environmental variables in the boosted regression tree models. The marine protected areas are outlined in black

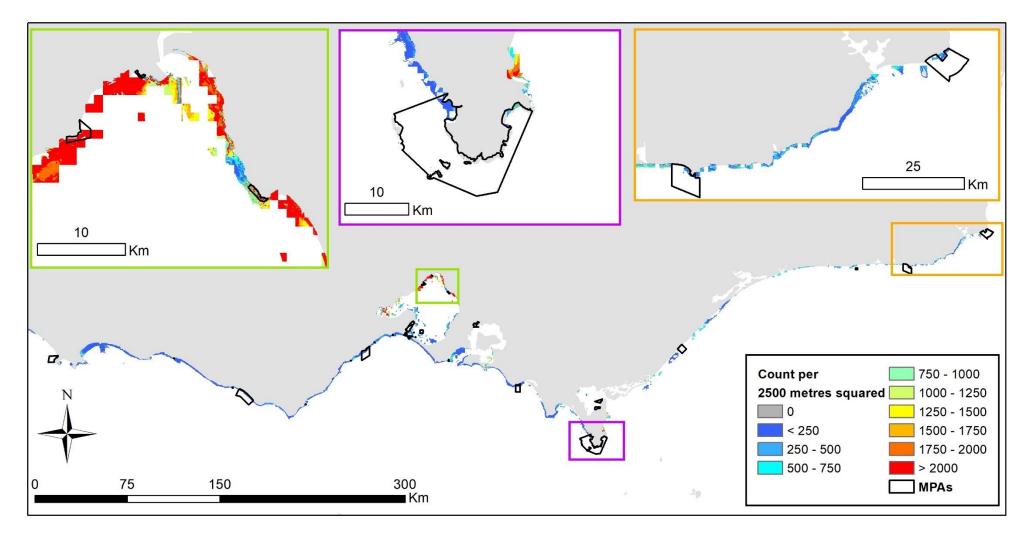


Figure 7.17: Predictive distribution map of *Heliocidaris erythrogramma* densities across the coast of Victoria based on the location of suitable habitat. These maps were predicted based on the relationship with urchin density and the environmental variables in the boosted regression tree models. The marine protected areas are outlined in black

# 7.3 Macroalgae

The parameters for the final BRT models for *Ecklonia radiata* and *Phyllospora comosa* densities are shown in Table 7.7 with the results from the cross-validation. Both models used 14,000 trees; 11 variables were found influential in the *E. radiata* model and 12 in the *P. comosa* model. The *E. radiata* model explained 63 of the variation in percentage cover and predicted with 74 accuracy while the *P. comosa* model explained 60 of the variation and predicted with 78 accuracy.

Table 7.7: Model parameters and performance statistics from the final boosted regression trees (BRTs) to associate macroalgae percentage cover with spatial and temporal explanatory variables.

BRT model parameters	Ecklonia radiata	Phyllospora comosa
Error distribution	Gaussian	Gaussian
Learning rate	0.001	0.01
Interaction depth	5	5
Number of trees	14,000	14,000
Mean residual deviance	0.091	0.082
Training data correlation	0796	0.772
R-squared (fitted model)	0.633	0.596
Pearson correlation with evaluation data (P value)	0.744 ( <i>P</i> < 0.001)	0.782 ( <i>P</i> < 0.001)

**Note:** See Table 7.1 for an explanation of model parameters.

## 7.3.1 Golden Kelp (*Ecklonia radiata*)

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for E. radiata percentage cover are shown in Figure 7.18. Winter wave orbital velocity was the most influential variable in the model, and *E. radiata* percentage cover decreases with increasing wave velocities. There was also a positive relationship with rugosity; the highest E. radiata percentage cover occurs at the higher rugosity values. Year was another influential variable, showing a decrease in percentage cover as years increased. Average current speed was associated with an increase in percentage cover of E. radiata up to around 0.7 m/s followed by a subtle decrease and a steadier relationship. Both in-degree, the number of significant connections coming into a site, and self-recruitment, the relative proportion of settlers at each site that originated from that site, were connectivity variables found to be important in the E. radiata BRT. E. radiata percentage cover increases with both in-degree and self-recruitment. The relationship with depth shows that there is an increase in percentage cover towards the shallower portion of the depth range. The densities of both urchin species, C. rodgersii and H. erythrogramma, were also influential and show that E. radiata percentage cover is highest at lower densities of urchins. Standard deviation of bathymetry has a positive relationship with E. radiata percentage cover, as percentage

cover increases with increasing relief. Finally, the relationship with average annual SST shows that *E. radiata* percentage cover is relatively stable with increasing SST until around 20 °C when it drops off.

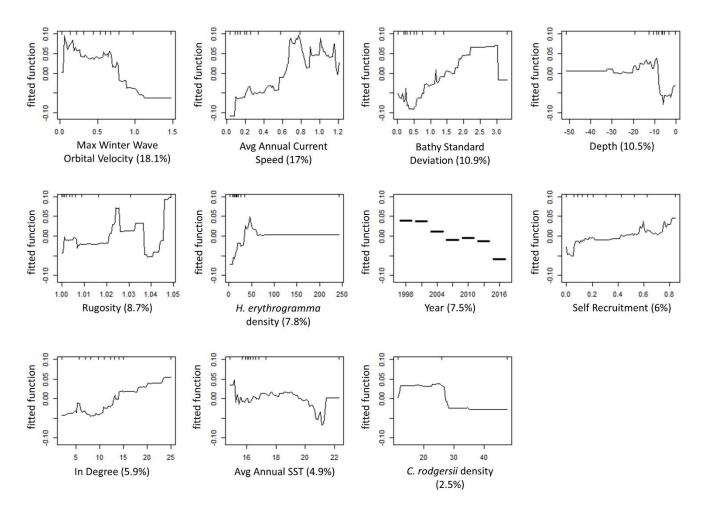


Figure 7.18: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for *Ecklonia radiata* percentage cover. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The *y*-axis represents the fitted function from the model for *E. radiata* percentage cover. Increases in *y*-values indicate an increase in *E. radiata* percentage cover and decreases in *y*-values indicate a decrease in *E. radiata* percentage cover. All relationships are shown for median values of the other variables in the model

Overall, these relationships indicate that MPAs in areas with lower wave velocities, higher current speeds, temperatures below 20 °C, higher surface roughness and shallower habitat, and that are well connected with higher self-recruitment and have low urchin densities, will support the highest percentage cover of *E. radiata*. *E. radiata* cover has declined significantly over time and no differences in cover within and outside MPAs were identified.

The predicted distribution and changes in cover of E. radiata in response to these environmental variables are shown across Victoria in Figure 7.20a.

## 7.3.2 Crayweed (Phyllospora comosa)

The nature and relative magnitude of influence of the explanatory variables used in the final BRT for *P. comosa* percentage cover are shown in Figure 7.19. Year was the most influential variable with decreasing percentage cover through the years. Average summer SST was the second most influential variable; it showed a slight negative relationship with percentage cover up until 20 °C followed by a sharp decrease. *P. comosa* percentage cover tends to increase with complexity of the seafloor as shown by its positive relationship with rugosity, standard deviation of bathymetry (relief) and bathymetric position index. *P. comosa* percentage cover has a relatively neutral relationship with current speed until around 1 m/s when cover drops off substantially. Connectivity variables in-degree and self-recruitment were also found to be important. Percentage cover is highest at the lowest values of indegree, and it also has a negative relationship with self-recruitment. Both urchin species also impact *P. comosa* percentage cover, which decreases at higher densities of urchins. The relationship with depth shows a peak in percentage cover around the 10 m depth.

Combined, these relationships indicate that MPAs in areas with summer sea-surface temperatures below 20 °C, higher complexity of the seafloor, current speeds below 1 m/s, lower self-recruitment and connectivity, lower urchin densities and habitat at depths of 10 m or greater will support the highest cover of *P. comosa*. The distribution and changes in cover of *P. comosa* in response to these environmental variables are shown across Victoria in Figure 7.20b.

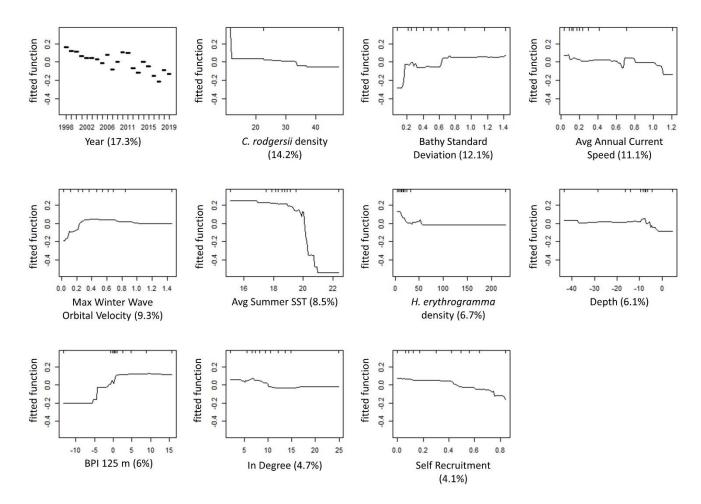


Figure 7.19: The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for *Phyllospora comosa* percentage cover. The variables are in order of decreasing influence on the fitted relationship. The percentage influence is given in parentheses. The *y*-axis represents the fitted function from the model for *P. comosa* percentage cover. Increases in *y*-values indicate an increase in *P. comosa* percentage cover and decreases in *y*-values indicate a decrease in *P. comosa* percentage cover. All relationships are shown for median values of the other variables in the model

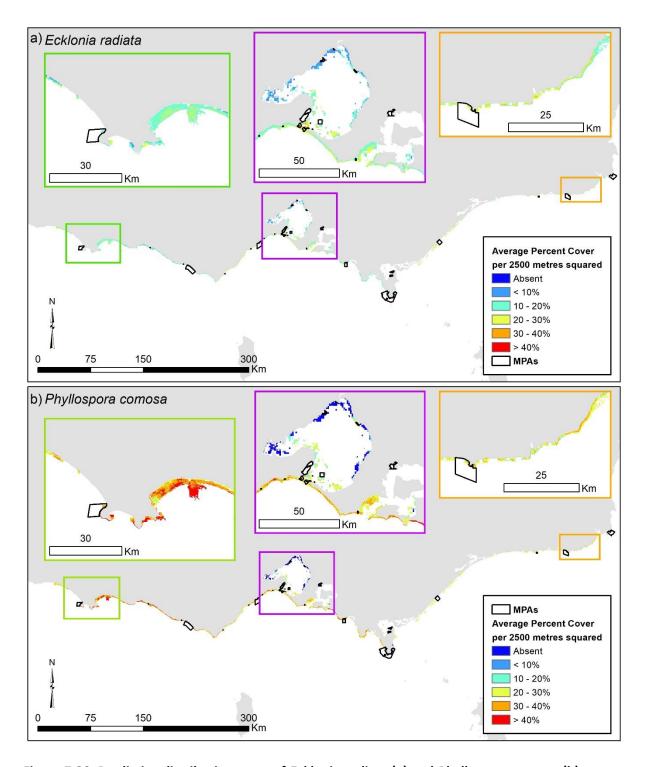


Figure 7.20: Predictive distribution maps of *Ecklonia radiata* (a) and *Phyllospora comosa* (b) densities across the coast of Victoria. These maps were predicted based on the relationship with macroalgae percentage cover and the environmental variables in the boosted regression tree models. The marine protected areas are outlined in black

## 8. Discussion

One of the main focuses of marine conservation, and one of the goals of Victoria's marine national parks and sanctuaries, is the preservation of biodiversity. Thus, a region's biodiversity is directly linked to its ecological value. Changes in patterns of biodiversity can have ecosystem-level consequences as functional roles can be lost (Chapin, et al. 2000). In this study, we looked at variations in assemblages, groups and species across a network of MPAs off the coast of Victoria, Australia, to determine how they change through time and with different environmental conditions and levels of protection. The models for the different aspects of the marine communities across the state waters environmental associations change depending on the species, functional groups or assemblage structure. Despite the variations in relationships, the machine learning approach employed in this study produced informative and accurate models in most cases, explaining the majority of the variation and predicting with fairly high accuracy for ecological models.

Understanding the relationships between these biological patterns and the environmental processes that drive them can be very informative for MPA management. They provide information about the types of conditions that will best support a given species and thus the conditions that should be represented in an MPA if conservation of that species is a goal. Through most of these models, it is clear that several species and assemblages follow similar patterns, showing greater diversity, abundance and biomass in the eastern portion of the state. Higher diversity, abundance and biomass are also often associated with higher complexity reef habitats, deeper depths, cooler sea-surface temperatures, higher current speeds and moderate wave energies. Although these patterns are common, patterns do differ somewhat between species, assemblages and communities.

# 8.1 Fish assemblages and functional groups

Using the combined dataset from the multiple scuba observation methods applied across the state of Victoria to monitor marine communities, we looked at how fish assemblages and fish functional feeding groups were responding to environmental conditions along the coast. Those models for assemblage structure, including fish richness and diversity, performed well in explaining a large portion of the variation (83 to 84) and predicting with relatively high accuracy when testing on a reserved subset of the data (74 to 76). When broken down into functional feeding groups, the models continued to perform well or better for browsing herbivores, benthic invertivores, and planktivores ( $R^2$  values of 0.81 to 0.95, and prediction accuracy from 69 to 82). However, the model for higher carnivores was one of the lowest performing models in this study. It only explains around 50 of the variation and predicts with 25 accuracy. The lower performance of the carnivore model is likely due to the highly mobile behaviour of many carnivore species (Chapman and Kramer, 2000). Carnivorous fish are usually relatively large and travel across a wide range of habitats in search of prey (Andradi-Brown et al., 2016; Ward-Paige et al., 2010), resulting in difficulty associating them to environmental conditions at relatively small scales.

One of the goals of this study was to determine how marine communities are performing within the Victorian MPAs compared to the areas outside. MPA status (i.e. protected area or not) was included as a variable across all the models but was only retained in those where it had some influence on the results. Through these analyses, we found that species richness, browsing herbivore density, benthic invertivore density and planktivore density all had higher values within the MPAs than outside, although the influence of MPA status on the model was low for all groups. The low influence of MPA status in the model could be due to a number of conditions. First, much of the habitat represented within the MPAs is found throughout the regions, as was evident in the Part 1 of the report. The availability of suitable habitat and the fact that many of the fish species making up these assemblages are not targeted recreationally or commercially could explain why MPA status is not very influential.

On the other hand, MPA status had no influence in the models for fish diversity or higher carnivore density. Throughout the world, studies on MPA effects have shown a similar variety of responses from fish communities, including showing population increases within MPAs through time (Claudet et al., 2006; Thompson et al., 2017; Young and Carr, 2015), little change through time (Denny and Babcock, 2004) or variable responses (Dufour et al., 1995). MPAs also tend to have more pronounced affects on species that are targeted by fisheries compared to those that are not (Côté et al., 2001). In Victoria, the most targeted fishery species are found in the higher carnivore group, which tend to have greater home ranges and are less likely to benefit from protection within MPA boundaries. It could also be the case that these species are under-represented in diver surveys, and alternative approaches such as baited cameras could be more effective. The models developed in this study also incorporated a range of environmental conditions including seafloor structure. From the previous assessment of habitat representation (see Part 1), we found that MPAs tend to incorporate more structurally complex habitat than is found outside the reserves.

Across all the fish models, depth was an influential variable: richness, diversity and density were all greatest around the deepest range of the survey depths (about 20 m) and then decreased as the depths got shallower. These results are supported by other studies that have found depth to be an important correlate with fish assemblages (Harvey et al., 2013; Hyndes et al., 1999; Malcolm et al., 2010; Moore et al., 2010; Schultz et al., 2014). For example, Moore et al. (2010) found that temperate fish species richness increases with depth. Depth is often correlated with changes in light attenuation, wave energy and temperature, resulting in less light, more protection from wave energy and cooler temperatures as you move deeper (Brito and Newton, 2013; Hill et al., 2014). Also, moving from algal dominance to dominance of sessile invertebrates increases the number of functional feeding groups. The marine national parks across Victoria tend to capture the full depth range of the state waters (out to 3 nautical miles), suggesting that these larger MPAs are likely to contain higher diversity. In contrast, the marine sanctuaries tend to be smaller and closer to shore, only covering a small depth range, usually in shallower waters. It is

likely that, if the goal is to protect fish diversity and abundance, including deeper depth ranges within the MPA is optimal.

In our models we used several measures of the complexity of the seafloor, including rugosity, slope, standard deviation of bathymetry (relief) and bathymetric position index. In most cases, fish richness, diversity and functional group biomass increase with seafloor complexity. This result is consistent with other studies that have found both fish diversity and abundance tend to increase in marine habitats with more structural complexity (Galaiduk et al., 2017a; Wines et al., 2020; Young and Carr, 2015). Because of the strong effect of structural seafloor complexity on the diversity and abundance of marine fish, it is important to account for variation in complexity when comparing fish assemblages inside and outside marine protected areas (Monaco et al., 2007). To increase fish diversity and abundance within MPAs, the MPAs should capture more complex habitat.

Longitude was another influential variable in all fish diversity and abundance models except for the model for browsing invertivores. Models where longitude was influential show greater richness, diversity and abundance in the eastern portion of the state. This pattern is likely driven by the effects of temperatures and the incursion of the East Australian Current in the east of the state, which is increasing the occurrence of tropical fish further south across south-eastern Australia (Booth et al., 2007). This interface, where temperate and tropical species converge, helps to explain the increase in fish richness and diversity and abundances in some of the functional feeding groups as you go further east. This pattern could have implications for MPA management. If more MPAs were to be placed within eastern state waters, greater fish diversity could be protected. However, focusing only on the eastern region would exclude many of the species found in the cooler waters in the most western regions of the state.

Although somewhat related to temperature, the longitudinal patterns we are seeing across fishes are likely not a *direct* relationship with temperature. Except for the higher carnivore and planktivore models, fish richness, diversity and abundance have a negative relationship with temperature. These models show that fish diversity and abundance tend to decrease with increasing temperature, especially around 20 °C. This pattern could be a result of the more temperate species towards the west of the state being negatively impacted by increasing temperatures while those in the east are benefiting. Therefore, it is important to include multiple factors that could be affecting fish distributions. For example, increases in temperature that near or surpass the thermal tolerance are well known to have deleterious effects on fish species as warming waters reach a point where the fish experience reduced growth, reduced reproductive output and death (Neuheimer et al., 2011; Wang and Overgaard, 2007). Increasing temperatures are expected to reduce the resilience of temperate fish communities, especially those made up of endemic species (Galaiduk et al., 2017a). These negative relationships with temperature could also be due to decreases in macroalgae cover (Galaiduk et al., 2017a), which is known to occur with increasing

temperature (Wernberg et al., 2011). The more positive relationship with temperature in the higher carnivore and planktivore groups could be a result of the differences in adaptations to temperature of the species making up those groups.

Year of survey was important in many of the models as well, although this interannual variation was not due to patterns of increase or decrease through time. Temporal variation in fish assemblages is known to occur and is expected, so this was not a surprising finding (Charton and Ruzafa, 1999). These temporal variations could be the result of oceanographic processes (e.g. temperature fluctuations, current variation, El Niño, pacific decadal oscillation), alterations to sampling design across years, or impacts of protection (Wines et al., 2020). Fish richness and diversity vary across sampling years, showing an overall decrease in the more recent years while the abundances of each of the functional feeding groups are showing an increase in recent years. It is unclear what is causing the variation between years, but the importance of year shows the benefit of collecting data over longer temporal scales to capture the temporal variation in fish assemblages. These interannual variations show the importance of designing long-term monitoring programs to better understand the impacts of MPAs on marine biodiversity.

In our models we looked at 2 measures of water motion: average current speed and winter wave orbital velocities. Oceanographic current patterns are known to affect the structure and distributions of marine communities (Cetina-Heredia et al., 2014; Davis et al., 2020). Many of the fish species making up the assemblages across Victoria rely on larval dispersal, which requires current flow. As a result, currents have been shown to influence abundance patterns through the recruitment processes they drive (Gaylord and Gaines, 2000). Across our models, we found a mostly positive relationship between fish assemblages and current speeds. Wave energy, on the other hand, had varying relationships with the fish assemblage response variables. Many studies have shown links between wave exposure and variations in fish assemblages (Davis et al., 2020; Friedlander et al., 2003; Fulton and Bellwood, 2004, 2005). Wave energy has been shown to affect the swimming performance of fishes (Webb, 2004), which can have cascading effects on their ability to forage and use habitat (Fulton and Bellwood, 2005). Therefore, the response of fishes to wave energy can vary based on their swimming biomechanics (Fulton and Bellwood, 2004; Fulton et al., 2005). The variety of fishes in each group in our models helps to explain the varying responses to wave energy the models are showing. Understanding these relationships can help to further evaluate the representativeness of Victorian MPAs. Rather than looking just at the habitat present on the seafloor, assessing how well the MPAs represent different wave energies and current speeds can give an indication of how well the MPAs are likely to protect certain groups of fish. The patterns outlined in Part 1 show that the Victorian MPAs do a fairly good job of protecting representative areas of wave energies and current speeds in relation to their associated biounits, with the exception of the smaller marine sanctuaries that do not extend across the range of conditions experience throughout the entire biounit.

# 8.2 Invertebrate assemblages, groups and species

Models for invertebrate species richness and diversity performed well, explaining 84 to 87 of variation, respectively, and predicting both with around 60 accuracy. When grouped into organisms with similar habitat usage (sea stars, crabs and snails), the models mostly reduced in performance. The models for sea stars and snails were the lowest performing, only explaining 31 to 34 of the variation and predicting with accuracies of 39 to 45. These lower performances could be explained by the more generalist behaviour of sea stars and snails, which are found across almost all habitats surveyed in Victoria. On the other hand, the BRT for crabs performed better by explaining 64 of the variation in densities and predicting with 74 accuracy. The 2 important fishery groups we modelled, Southern Rock Lobster and abalone, also performed well. The model for Southern Rock Lobster explained 83 of the variation and predicted with 61 accuracy, while the abalone model explained 63 of the variation and predicted with 69 accuracy. These models likely perform well due to the strong habitat associations of these species as shown in other habitat mapping studies ((Young et al., 2020) for abalone and (Young et al., 2016b) for Southern Rock Lobster).

Marine protected area status (inside or outside) was only important across a few of the invertebrate models. Crabs were found more often outside MPAs than inside; however, the 2 fisheries groups, Southern Rock Lobster and abalone, had higher abundances inside MPAs than outside. This result is promising as abalone and rock lobster are the most valuable fisheries along the coast of Victoria and it appears that the MPAs are affording some amount of protection. Additionally, the larval duration and connectivity across both species (lerodiaconou et al., 2018a) suggest that the MPAs can serve as source populations to potentially replenish fished stocks outside the MPAs.

We also tested the importance of biotope and habitat complexes across the different models for invertebrate diversity and abundance. However, the variable for biotope complex was not influential, and habitat complex was only influential within a few models (invertebrate diversity, invertebrate richness and sea star densities). For models where habitat complex was found to be influential showed that invertebrates are more commonly found in low- to moderate-exposure reef environments. This result is not surprising as most of these invertebrates are predominantly associated with reefs. However, this information can be used in MPA management by targeting those low- to moderate-energy reef areas for either protection or increased monitoring.

Across most the models, year of survey was an influential variable explaining both invertebrate diversity and densities. Many studies have shown that dispersal and recruitment of marine invertebrates drives variations in abundance, richness, and diversity (Caley et al., 1996). Because of the strong impacts of oceanographic processes on reproduction, settlement and recruitment, which tend to vary annually (Bourne et al., 2013; Keough and Downes, 1982), it is expected that there will be an impact of year as seen in our

models. Interannual variation can be expected both inside and outside MPAs, and there was no evidence that patterns of variation differed as a result of MPA protection.

Location along the coast, defined as either longitude or biounit, was also found to be influential in the invertebrate models. We saw opposite patterns with longitude for richness and diversity. Richness is higher in the east while diversity is higher in the west. These patterns show that, although more species of invertebrates are found in the east, potentially caused by the influence of the East Australian Current (Sunday et al., 2015), many of those additional species occur in low abundances so do not significantly alter diversity. Across the different group densities, patterns with longitude vary. Sea stars have slightly higher densities in the east compared to the rest of the coast, while snails and crabs see increases in densities both in the west and the east compared to the central portion of the state. Southern Rock Lobster and abalone follow similar patterns as those for snails and crabs, having slightly higher densities in the western and eastern extremes. These patterns could be driven by larval dispersal. Connectivity patterns for abalone show strong west to east connectivity with additional inputs in the east from Tasmanian populations and strong source populations in the western portion of the state (lerodiaconou et al., 2018a). The longer larval duration of Southern Rock Lobster (Villacorta-Rath et al., 2016) likely results in non-local recruitment conditions driving their distributions. Changes in upwelling patterns and resulting reductions in temperatures can have an impact on the growth rate and size of maturity of Southern Rock Lobster (Gardner et al., 2006; Linnane et al., 2008). It is expected that settlement of larvae will become even more variable with time as climate change alters the oceanographic environment at higher rates in the future (Linnane and Crosthwaite, 2009).

The relationships with temperature show that species richness and diversity of invertebrates tend to decrease around 20 °C, while the relationship is relatively stable at lower temperatures. Temperature is recognised as an important determinant in the distribution and abundance of marine invertebrates (Newell and Branch, 1980; O'Connor et al., 2007; Pörtner, 2008, 2005), especially at early stages of their life cycles (Pörtner, 2008; Przeslawski et al., 2008). Increasing temperatures with climate change are having negative effects on invertebrates (Przeslawski et al., 2008). Because most invertebrates are sessile in their adult life stages, they are unable to move far when temperature extremes are reached, causing mortality and reducing species abundances and richness (Hiddink et al., 2015). However, the thresholds of temperature that cause decreases in density seems to vary by species according to our models. Sea stars increase in density around 20 °C and then densities remain relatively stable at higher temperature. In echinoderms, increased temperatures can cause faster progression through the embryonic and larval phases of their life cycle (Hardy et al., 2014; Pecorino et al., 2013), potentially increasing their abundances in warmer temperatures and explaining the pattern we are seeing in our models. Crabs and snails had relatively neutral relationships with temperature and only saw decreases in density at low temperatures. Southern Rock Lobsters, however, have a positive relationship

with temperature up to around 19 °C where densities peak and then decrease at warmer temperatures. This is consistent with Thomas et al. (2000), who found that optimal temperatures for growth and survival of Southern Rock Lobster occurred between 19 and 21 °C. The BRT model for abalone in this study showed a slightly negative relationship between abalone density and increasing temperature. These results are consistent with other studies that have looked at abalone abundance along the Victorian coast (Jalali et al., 2018; Young et al., 2020). Haliotids experience fitness reductions when they are exposed to chronic or acute thermal stress (Raimondi et al., 2002; Rosenblum et al., 2005; Vilchis et al., 2005).

Understanding these varying patterns in response to temperature can help us better manage and monitor the Victorian MPAs. Species that respond negatively to increased temperature are at most risk along this coastline and may require more comprehensive monitoring to assess their population conditions as temperatures increase. Alternatively, management actions may be required to further protect populations in areas along the coast that are more buffered from the effects of increasing temperatures. Less emphasis on temperature changes is needed in the monitoring and protection of species that are not negatively impacted by temperature. The general pattern observed – that invertebrate richness, diversity and abundance decrease at temperatures above 20 °C – highlights the risk to Victoria's MPAs from an increase in sea-surface temperature. MPAs in areas that are likely to experience cooler sea-surface temperature (e.g. Wilsons Promontory MNP and Discovery Bay MNP) may become important climate refuges in future.

Water motion variables, including current speed and winter wave orbital velocities were also influential in the distributions of invertebrate diversity and densities of most of the groups analysed. Waves and water flow (currents) are known to influence the distributions of invertebrates (e.g. Arribas et al., 2014; Dayton, 1971; Denny, 1995, 1987; Hammond and Griffiths, 2004; Tuya and Haroun, 2006). Too much water flow can dislodge individuals or limit feeding time and success (Sebens, 2002), explaining the mostly negative relationship with wave energy across most of the models. However, dislodgment of prey can be beneficial to predators. Invertebrates also rely on larval dispersal (Kinlan and Gaines, 2003; Robinson et al., 2011), and flow from currents can have a positive effect on invertebrate assemblages by increasing recruitment potential and increased delivery of nutrients, such as drift algae, a primary food source for abalone. This pattern explains why invertebrate richness and diversity and most of the species groups are positively associated with current speed. It highlights the importance of protecting habitat exposed to high current within MPAs to support these taxa. Part 1 of this study showed that Victorian MPAs capture a full spectrum of current speeds, although marine sanctuaries tend to be more representative of areas of higher currents.

Depth was also influential in the models for invertebrate species richness and diversity and some of the species groups. Diversity and richness show a positive relationship with increasing depth: the highest richness and diversity are found at the deepest depths

sampled (about 20 m). This pattern could be related to wave energy since many of the invertebrates are sessile and could become dislodged in shallower depths (Sebens, 2002). On the other hand, densities of crabs, snails and abalone increase in shallower depths. These patterns could be a result of the habitat provided by macroalgae, which becomes light limited at deeper depths. It is well known that macroalgae provide habitat and food for many marine subtidal species (Kendrick et al., 2004; Robertson and Lucas, 1983). Because of these varying relationships with depth, it is important that the MPAs represent a range of depth values within their borders. As shown in Part 1, this is the case for most of the marine national parks, which capture most of the depths within their associated biounits. In contrast, marine sanctuaries are much smaller and are often located in the very shallow depths close to shore. When assessing the change in populations within these different MPAs, it is important to consider the depth ranges represented and the species associated with those depth ranges. For example, a marine sanctuary is more likely to adequately capture suitable depths for crabs, snails and abalone, but may have lower diversity than a marine national park because it does not contain the deeper depths associated with higher diversity values.

Finally, the structure of the seafloor terrain was influential to the diversity, richness and abundance of marine invertebrates across the coast of Victoria. Richness, diversity and abundance of invertebrates tend to increase with increases in structural complexity. Habitat complexity is known to influence the distributions of species by providing more refuge space for species to inhabit (Kovalenko et al., 2012). Studies in coral reefs have shown that reductions in reef complexity due to ocean acidification have drastically reduced invertebrate densities (Fabricius et al., 2014), indicating that loss of complexity results in loss of available habitat area. Other studies have also shown that the more complex the habitats are, the greater number of microhabitats they contain (Alexander et al., 2014; McGuinness and Underwood, 1986). More available habitat usually results in more species in an area, as seen with the results of our models. Part 1 of this study found that Victorian MPAs contain a good representation of habitat types, but they often over-represent more structurally complex reef, which provides good habitat for the invertebrate species examined in this study.

## 8.3 Urchins

## 8.3.1 Longspined Sea Urchin (Centrostephanus rodgersii)

The model for *C. rodgersii* only found 5 variables to be influential in explaining their density across Victoria. Longitude was by far the most influential variable, explaining 84.8 of the variation. The relationship with longitude shows that there are no or very few *C. rodgersii* individuals across most of the longitude values of the state until you reach just past 148° east in the far eastern portion of the state. The east—west distribution of *C. rodgersii* is important for understanding the risks associated with this habitat-altering species and can help to target areas where they are possibly present but not yet observed. The historical

range of C. rodgersii extends into eastern Victoria (Byrne and Andrew, 2020); however, the warming waters off Victoria are extending their distributions further to the west. This range expansion is likely a consequence of climate change and the strengthening of the East Australian Current (Ling and Johnson, 2009; Ling et al., 2009; Ridgway, 2007), and temperatures have already increased 0.8 °C since the 1960s (Lough, 2009). As waters off the coast continue to warm, it is expected that C. rodgersii will continue to expand their range westward (Jalali et al., 2018) as has been seen in eastern Tasmania (Ling, 2008; Ling and Keane, 2018). Complexity of the reef habitat was also found to be influential, and C. rodgersii density increases with increasing reef complexity. These results are consistent with previous studies that have found habitat complexity to be an important driver in the abundance distribution of C. rodgersii (Jalali et al., 2015; Ling and Johnson, 2012). More complex benthic structure provides shelter and protection from predators as well as more suitable feeding and breeding habitats for benthic invertebrates (Alexander et al., 2014). For example, Ling and Johnson (2012) found that access to refuge from predators in more complex habitats resulted in higher abundances of C. rodgersii. Additionally, habitat complexity has been shown to be a reliable predictor of C. rodgersii distributions (Jalali et al., 2018). This suggests that MPAs in the east of the state with complex reef habitat, such as Cape Howe, Beware Reef and Point Hicks, are at the greatest risks of supporting overabundant *C. rodgersii* populations.

Current speed also had an influential relationship on *C. rodgersii* density in our BRT but the model shows that densities have a relatively neutral relationship with increasing current speed. Previous studies have shown that oceanic currents are integral in shaping the dispersal of *C. rodgersii* across its range (Banks et al., 2007). With the majority of the *C. rodgersii* population occurring in the very eastern section of the state, it is likely that there is not enough variability in current conditions to pick up clear patterns. Incorporating populations across their entire range into New South Wales would help to clarify the impact of currents on their distribution.

Depth was the final variable found to be influential to the density distribution of *C. rodgersii* in our model, which showed densities increasing along the deeper edge of the surveyed range. These results are consistent with findings from Jalali et al. (2018), who showed the same pattern along the Victorian coast, and Johnson et al. (2005), who found *C. rodgersii* densities significantly decrease in shallow reefs at depths less than 9 m. However, studies in New South Wales show that high densities of *C. rodgersii* occur in less than 10 m of water (Hill et al., 2003). These differences in observations across their range could be due to greater wave exposure along the southern coast of Australia and Tasmania or to variations in cover of algal species (Johnson et al., 2005). Marine national parks that encompass deeper habitats, such as Cape Howe MNP, are therefore likely to be more vulnerable to high densities of *C. rodgersii*.

When we used the above relationships to predict the distribution of *C. rodgersii* across the state of Victoria, our results were as expected. The highest abundances occur in the eastern section of the state with low abundances around Wilsons Promontory. Further west than Wilsons Promontory, the model shows an absence of *C. rodgersii*. These types of models can help to manage *C. rodgersii* across its range. They can help predict where the urchins are likely to occur in the future under climate change and also the habitat areas they are more likely to expand into (i.e. deeper depths). Using these relationships, risk maps of potential expansion areas could be developed based on habitat suitability and how those risk areas may affect MPAs. Because of the strong negative influence of *C. rodgersii* on macroalgae communities, it is important to have a detailed understanding of their distributions.

## 8.3.2 Purple Sea Urchin (*Heliocidaris erythrogramma*)

The BRT model for *H. erythrogramma* found more variables to be influential than were found for C. rodgersii, possibly due to the more extensive distribution of H. erythrogramma along the Victorian coast and the resulting increase in environmental conditions experienced. Annual average SST was the most influential variable in the model (influence of 18.6); temperature increases have a slightly negative effect on H. erythrogramma densities and the lowest densities were found at temperatures greater than 22 °C. This result is consistent with findings from other studies showing that higher temperatures can have deleterious effects on H. erythrogramma (Carey et al., 2016). Increased temperature can increase energetic demands on *H. erythrogramma* by changing metabolic rates, which most individuals cannot compensate for with increased feeding (Carey et al., 2016). Also, prolonged exposure to higher temperatures (about 3 months) can increase mortality (Harianto et al., 2018). Despite these negative effects of temperature, previous studies have also shown that H. erythrogramma might adapt to higher temperatures since individuals in the higher intertidal zone experience a large range of temperature fluctuations, including highs up to the expected increase in SST with climate change (Byrne et al., 2010). This relationship may go some way to explaining why marine sanctuaries in the north of Port Phillip Bay, where water temperatures tend to be warmer, have experienced higher densities of *H. erythrogramma*.

Unlike the other invertebrate species explored in this study, the relationship between *H. erythrogramma* and the structural complexity of their reef habitat was negative. Higher densities tend to be found in areas of lower structural complexity as shown by the relationship between density and slope and rugosity. However, the relationship between density and bathymetric position index is positive, indicating that greater densities are found in higher areas of the terrain. Other studies that have evaluated the distributions of *H. erythrogramma* across reef habitats have also found that higher densities occur on flatter reefs or rock faces. This contrasts with other urchins, which tend to be found on more structurally complex reefs (Vanderklift and Kendrick, 2004).

The third and fourth most important variables in the BRT for *H. erythrogramma* density were the connectivity variables local retention and in-degree. Local retention is the proportion of larvae released from a site that settles in that focal patch, while in-degree provides the total number of significant connections coming into a site. Local retention can be achieved when larvae remain close to their natal site, or are transported away, but return through an oceanographic or behavioural mechanism. If a site has high local retention, the local population has strong self-replenishment potential, where large populations can potentially persist through many generations (Burgess et al., 2014) but only if these larvae are of good or high quality. A site with a large in-degree will have many options for population replenishment as many sources supply larvae. The larval duration of *H. erythrogramma* is around 3 weeks and they are able to settle after 5 days if they come into contact with suitable habitat (Williams and Anderson, 1975). This shorter larval precompetency period increases the likelihood of local retention, whereas the longer competency window also increases the likelihood of downstream connectivity.

Increase in wave energy has a negative influence on the density of *H. erythrogramma*. Surveys of habitat associations of *H. erythrogramma* show they are often found in sheltered to moderate-energy sites and are absent from very exposed sites (Dix, 1977). In areas where there is more wave exposure, *H. erythrogramma* occupy deeper depths, buffering themselves from the waves (Keesing, 2020). These patterns are consistent with our findings.

Depth had a 7.1 influence on the BRT for *H. erythrogramma* density; the lowest densities occur in deeper depths and densities increase towards the shallow edge of the survey zone. This pattern is corroborated by findings from other studies that show *H. erythrogramma* are most abundant at depths less than 10 m (Dix, 1977; Underwood et al., 1991; Wright and Steinberg, 2001). However, in areas with greater wave exposure, *H. erythrogramma* are found more commonly in deeper depths (around 20 m) where they are more sheltered from wave action (Keesing, 2020).

Because of the role of *H. erythrogramma* in structuring macroalgae communities, it is important to understand their distribution across the state (Carnell and Keough, 2016; Livore and Connell, 2012; Reeves et al., 2018). The species distribution model for *H. erythrogramma* shows that densities are patchy across the state, as found by Vanderklift (2002) and Vanderklift and Kendrick (2004). The highest densities occur in Port Phillip Bay and generally on the leeward side of points along the open coast. The hotspots in density in more protected areas are likely due to the decreased wave action and the availability of reef habitat in the northern portion of Port Phillip Bay. As with *C. rodgersii*, understanding the habitat associations of *H. erythrogramma* can help managers define areas that are likely to be at risk of supporting *H. erythrogramma* population increases or expansions to then target management action. For example, entire MPAs, or areas within those MPAs, with strong connectivity to current populations, high self-retention of larvae, lower temperatures, shallower depths, higher areas in the terrain, and low wave exposure could be monitored

more consistently to determine if populations are expanding or overabundant and requiring management.

## 8.4 Macroalgae

The BRTs associated *E. radiata* and *P. comosa* with environmental conditions along the coast and both found 11 variables to be influential. One of the variables with the most influence, average annual current speed, has a mostly positive relationship with *E. radiata* and *P. comosa* percentage cover. As current speeds increase, percentage cover of macroalgae along Victoria tends to increase as well. Water motion is often beneficial to macroalgae in marine environments as it can increase nutrient uptake (Hurd, 2000; Wheeler, 1988), increase irradiance by pushing the fronds in different directions (Leigh et al., 1987) and remove waste from the vicinity of the plants (Díez et al., 2003). Therefore, areas with faster current speeds are likely helping the survival of *E. radiata* and *P. comosa* along Victoria, resulting in increased percentage cover.

Not all water motion has a positive influence on macroalgae, however. Wave orbital velocity has a negative relationship with *E. radiata* and *P. comosa* percentage cover, following an initial positive effect at very slow velocities in both models. Wave forces are often responsible for tearing out macroalgae and is one of the main factors affecting their distributions throughout the world (Reed et al., 1988; Wernberg et al., 2005; Wernberg and Thomsen, 2005). Disturbance from waves is potentially reducing percentage cover in areas along the Victorian coast.

Water depth, which is one of the main factors driving the distribution of macroalgae (Goldberg and Kendrick, 2004; Kirkman, 1989; Novaczek, 1984), was influential in the models for both *E. radiata* and *P. comosa* percentage cover. Percentage cover tends to increase in shallower depths, peaking at around 10 m followed by a decrease. Light attenuation in deeper waters is likely responsible for the decrease in percentage cover in deeper depths since algal productivity is directly linked with light levels (Connell, 2003; Graham, 1996; Reed and Foster, 1984). Increased wave action in the shallower waters (<5 m) could also be increasing disturbance (Wernberg et al., 2005), resulting in the lower percentage cover we see in our models.

Measures of substrate complexity were also found to be influential in both models: percentage cover of *E. radiata* and *P. comosa* tends to increase with increases in complexity. Both species tend to be found in higher abundance on more complex, higher areas of the terrain. These patterns are consistent with other studies that have associated macroalgae with the complexity of the seafloor terrain (Young et al., 2016a; Young et al., 2015). Higher complexity reef substrate provides a greater variety of microenvironments, and higher areas of the terrain are less likely to experience sediment inundation (Toohey et al., 2007).

Increases in SST had a mostly negative influence on the percentage cover of macroalgae, with a more pronounced negative impact on *E. radiata*. Global analyses of kelp distributions

have shown that kelps are decreasing in abundance in areas of increased temperatures and increasing in abundance in areas of decreased temperature (Krumhansl et al., 2016). As cooler water species, kelps are physiologically stressed by temperature increases (Kirkman, 1984). Elevated temperatures also reduce kelp's resilience to other perturbations such as pollution or increased wave energy (Wernberg et al., 2010). Predictive models incorporating future conditions under climate change forecast large contractions of kelps along the southern coast of Australia, including the local extinction of some species such as *P. comosa* (Martínez et al., 2018).

Year of survey was also influential in the models for *E. radiata* and *P. comosa* percentage cover, showing a general overall decrease in the cover of these species since 1998 and reflecting patterns found in global analysis. Many studies have shown that variations in temperature (Wernberg et al., 2013), the occurrence of extreme storms (Smale and Vance 2015), and changes in nutrients (Tuya et al., 2012) over annual time periods can cause changes in abundances among years. Understanding the relative influence of these processes on kelp abundance in Victoria is important to distinguish persistent long-term declines in kelp abundance from declines due to annual variability in environmental conditions that kelp are likely to recover from (Pinho et al., 2016). In Victoria, the causes of declines in kelp appear to differ among regions. On the eastern coast and Port Phillip Bay, declines have been associated with overabundant urchin species (see below), whereas on the west and central coast, the cause of decline is not associated with overabundant urchins but may be linked to changes in water temperature and nutrients.

The connectivity variables found to be influential across the models for *E. radiata* and *P. comosa*, in-degree and self-recruitment, varied slightly with their influence on percentage cover. *E. radiata* has a positive relationship with both in-degree and self-recruitment while *P. comosa* has highest percentage cover at both low and high values of in-degree and a negative relationship with self-recruitment. In-degree, as described above, is the number of incoming connections to a site. At high in-degree values, many sources likely supply propagules to the site. Self-recruitment, as opposed to local retention described above, is the proportion of all incoming propagules that originated from the site.

Finally, we found density of both *H. erythrogramma* and *C. rodgersii* had influential negative effects on the abundance of *E. radiata* and *P. comosa*. Both species of kelp do well at lower densities of urchins but then see a large decrease in percentage cover as urchin densities increase. Evidence from previous studies have shown that both *H. erythrogramma* (Keesing, 2020) and *C. rodgersii* (Filbee-Dexter and Scheibling, 2014) establish and maintain barren habitat, drastically affecting the coverage of macroalgae in areas where the urchins occur in large abundances. Caging and removal experiments, and experiments following mass mortality events of *C. rodgersii*, have shown that macroalgae increases in their absence (Andrew and Underwood, 1989, 1993; Hill et al., 2003; Ling, 2008). As *C. rodgersii* expands its range south and to the west along the Victorian coast, it is likely that new barrens will

form and persist (Flukes et al., 2012; Ling and Johnson, 2012). Studies on the impact of *H. erythrogramma* in Victoria have shown that, although *H. erythrogramma* do not always form barrens, they do limit the growth of macroalgae canopy when present (Keesing, 2020). Furthermore, increases in *H. erythrogramma* abundance have been shown to cause removal of the entire kelp canopy in an area (Carnell and Keough, 2016; Kriegisch et al., 2016; Livore and Connell, 2012; Reeves et al., 2018).

E. radiata and P. comosa are important habitat-forming species that support communities along the coast. Understanding their relationships with habitat and environmental conditions is essential for helping managers to determine if these foundation species are adequately protected. The analyses in Part 1 show that many of the MPAs represent the habitat well by over-representing reef habitat, which is important to the distribution of these species. In addition, the shallower distribution of these species means that both the marine national parks and the marine sanctuaries are likely protecting important habitat for these populations. Because of the negative effects of temperature on the cover of these species, continuing to monitor these species through time will allow for better management and assessment of which MPAs may be at risk of losing their macroalgae cover due to increased temperatures. Finally, the effects of urchins on macroalgae are likely to increase in the future with the expansion of urchin populations along the coast. Therefore, understanding the thresholds in urchin abundance that are associated with decreasing macroalgae percentage cover can help managers determine if management action, such as the culling of sea urchins within (and outside) MPAs, is needed.

The influential relationships across all of these variables allowed us to predict the distribution of both E. radiata and P. comosa across the marine environment of Victoria. As with urchins, the distributions of both species are patchy across the state. Many previous studies have shown that multiple environmental variables are correlated with the distribution of kelp (e.g. Martínez et al., 2018; Young et al., 2015), which is what we have shown occurring across the state of Victoria. Understanding how these variables are affecting the abundance of macroalgae can help to better manage them into the future. With significant declines in kelp forests already occurring in Victoria (Carnell and Keough, 2019; Kriegisch et al., 2016), it is important to understand the drivers of those declines. For example, the impact of urchins on declines in kelp cover is increasing across the state; severe impacts are occurring in MPAs in Port Phillip Bay and on the far east coast of Victoria (e.g. Cape Howe MNP and Beware Reef MS). Although Victoria has not yet seen the great losses in kelp coverage that is being experienced in New South Wales (Andrew, 1993; Andrew and O'Neill, 2000) and Tasmania (Johnson et al., 2011; Ling, 2008), the strengthening of the East Australian Current, which brings warmer waters, could bring that about. The species distribution maps provided in this study can be used to understanding the habitat association, environmental relationships and spatial distribution of macroalgae to inform the better management of these species. For example, they can be used to

identify areas within MPAs that support high cover of these species, or have favourable conditions that can act as refuges, to be targeted for better protection or rehabilitation.

# Part 3 – Fish species and fish community distribution models

### 9. Introduction

Species distribution models are used to predict the distributions of a variety of characteristics (e.g. species abundance, species presence, species richness, species diversity) by linking observation data with environmental variables (Guisan and Thuiller, 2005). In both terrestrial and marine environments, species distribution models have been in use for over 2 decades to gain insights into the relationships between environmental conditions and species occurrences and to predict and map expected distributions (Ready et al., 2010). The purpose of this study is to investigate the ability of using a benthic habitat map, classified into biotopes, in combination with bathymetric and oceanographic variables and observations from baited remote underwater video systems (BRUVS) to predict statewide fish species richness using machine learning and develop species distribution models. The best model for fish richness will then be used to model the abundances of several species of fish observed in the BRUVS data. These resulting models will be used to create seamless maps of fish richness and species abundance across the coastal region of Victoria, Australia, and provide an assessment of species richness within marine protected areas (MPA) in comparison to their respective biogeographic regions (biounits).

Mapping species distributions requires knowledge of how habitats and conditions vary throughout the range of interest. Remote sensing provides efficient methods for collecting environmental variables at broad scales using technologies such as satellite, multibeam echosounders (MBES) and light detection and ranging (LiDAR). Satellites provide oceanographic variables such as sea-surface temperature and net primary productivity from ocean colour data, while LiDAR and MBES provide high-resolution bathymetric data, which reveal the structural characteristics of the seafloor.

Structural characteristics of the seafloor, specifically topographic complexity and depth, are key drivers in fish distribution (Friedlander and Parrish, 1998; Pittman et al., 2007). Typically, higher demersal fish biodiversity is found over areas with high topographical complexity (e.g. reef) (Mellin et al., 2010; Wines et al., 2020), and species richness often decreases as depth increases (Kendall and Haedrich, 2006; Sousa et al., 2006). Previous descriptions of this pattern may be due to a limitation in sampling techniques (e.g. a lot of sampling was previously focused on shallow reefs); however, mesophotic reefs (low-light reefs in the transition zone between well-lit shallower waters and dark deep water) have gained prominence in recent years in terms of their importance for biodiversity. Some studies report higher species richness values in mesophotic reefs than in reefs in the photic zone (Hollarsmith et al., 2020; Lindfield et al., 2016; Williams et al., 2019). Previous studies have also shown that species richness varies with reef classes (Bax et al., 1999; Davis et al., 2020; MacDonald et al., 2016; Rees et al., 2014); for example, photic reefs contain higher species

richness for herbivorous fish due to the presence of macroalgae, while mesophotic reefs have relatively higher species richness for invertivores and carnivorous fish (Williams et al., 2019; Wines et al., 2020).

Despite the importance of reef type, these classifications are usually missing additional information on the biological habitat they provide. Habitat classes are often defined by their geological characteristics (abiotic), and species distribution models successfully link observations with high-resolution habitat maps (Elith et al., 2005; Johnson and Gillingham, 2005; Laman et al., 2018). Few studies have incorporated biotic components into these habitat maps to predict species distributions due to a lack of full-coverage environmental data. In Victoria, Australia, data from a variety of high-resolution acoustic and optical remote sensing methods and ground truth surveys were combined, producing a highresolution statewide classified habitat map identified to the biotope level (the biological community or species assemblage consistently associated with a particular habitat) (VEAC, 2019). Many studies have compared fish communities between biotopes (Bax et al., 1999; Hollarsmith et al., 2020; Kulbicki and Bozec, 2005; MacDonald et al., 2016), but few have been able to model fish diversity distributions, mainly due to the lack of biotope maps. Terrestrial studies have demonstrated that including biotopes as a predictor in species distribution models improves overall model accuracy (Austin and Van Niel, 2011; Cord and Rödder, 2011; Giannini et al., 2013) because distributions of many taxa are closely correlated with particular biotopes (Dimitrakopoulos and Schmid, 2004; Kivinen et al., 2006). Some marine studies have demonstrated their importance in assessing invertebrate populations (Young et al., 2016b), and based on known relationships between fish and biological habitat, we can apply similar methods to understanding distributions in fish richness.

Species distribution models predicting fish—environment relationships are critical for informing environmental policy and marine spatial planning and are applicable to a wide variety of applications (Barrett et al., 2007; Ferrari et al., 2018). They can be used to generate maps of the most suitable habitat for supporting populations within MPAs, which can inform targeted management and monitoring priorities. Species distribution models that predict the occurrence and abundance of species across a broad spatial scale (e.g. a state) let managers compare species richness within established MPAs against their respective biogeographical regions (biounits) to assess the MPA's effectiveness at conserving representative fish biodiversity. The models can be used to identify previously unknown hotspots across seascapes, which is critical for future marine spatial planning. This study uses random forest models to map out fish species richness across the state, allowing for comparisons of richness within and outside Victorian MPAs. Additionally, applying these same methods to map out the distributions of individual species provides further insight into where along the coast are hotspots that support high diversity and abundance of fish.

### 10. Methods

Our study site assesses fish species richness and fish species abundances for coastal marine Victoria at depths from 0 to 107 m. The study area is approximately 2,512 km long and covers an area of approximately 4,064 km². LiDAR coverage is available for the whole state, which extends from 0.5 to 1.5 km offshore. MBES coverage, where available, extends roughly 5 km offshore to the state water limit. The Victorian coastline is generally considered an exposed high-energy coastline, and the littoral zone contains many rocky headlands separated by sandy beaches (Parks Victoria, 2006). In the sublittoral zone, large areas of unconsolidated sediment are separated by rocky reefs. Infralittoral reef supports a wide variety of canopy-forming brown algae species such as Crayweed (*Phyllospora comosa*) and Golden Kelp (*Ecklonia radiata*) occasionally with mixed red algal understorey. Circalittoral reefs primarily support sponge garden communities. Communities found in both the infralittoral and circalittoral reefs are key habitats for many fish species because they provide a source of food and shelter (Davis et al., 2020). Physical variables, such as wave exposure, depths and currents, vary considerably across the state (Parks Victoria, 2014).

## 10.1 Environmental variables

Bathymetry was collected using a combination of LiDAR and MBES. Bathymetric LiDAR provides depth information of the nearshore environment and has a limited survey depth due to light attenuation within the water column (Lecours et al., 2016). MBES provides coverage at greater depths where LiDAR is limited and was combined with bathymetric LiDAR to provide a complete map of nearshore coastal Victoria. Data were collated across numerous MBES surveys which spanned from 2006 to 2018, using a variety of vessels and echosounders, including Kongsberg 2040C and Reson SeaBat 8101 (Ierodiaconou et al., 2007, 2011, 2018b). LiDAR data were provided by the then Victorian Department of Environment and Primary Industries and collected across multiple surveys using a LADS Mk II system. Both the LiDAR and MBES bathymetric data were collated and merged, resulting in a 2.5 m horizontal resolution surface covering 4,064 km² of the state's coastal waters within 3 nautical miles of shore.

Bathymetric derivatives were created using the Benthic Terrain Mapper toolbox (v3.0) for ArcGIS Pro 2.2 (Table 10.1) (Walbridge et al., 2018) at an analytical scale of 3 × 3 pixels. Bathymetric position index (BPI) was calculated at multiple scales including fine, moderate and broad, with an inner and outer radius of 8–16 m, 25–50 m and 100–500 m, respectively, by following methods outlined in a broadscale survey conducted by Novaczek et al. (2019). Distance to reef was calculated using ArcGIS Pro Euclidean distance tool with raster cells classified as reef receiving a distance value of 0 m. Oceanographic variables, including seasurface temperature (50 m resolution), net primary productivity (10 m resolution) and chlorophyll concentration (10 m resolution), were sourced from Australia's Integrated Marine Observing System (IMOS) (IMOS, 2020a, 2020b, 2020c). They are downloaded as

NetCDF's at daily intervals and are converted in R into rasters for analysis in ArcGIS Pro. Max winter wave orbital velocity data were obtained using a 25-year hindcast model developed by Water Tech (lerodiaconou et al., 2018a) at a 50 m resolution. Due to the variety of datasets, oceanographic variable resolution varied, so those variables were resampled to 2.5 m to match the resolution of the bathymetric variables. Biotopes were classified according to the Combined Biotope Classification Scheme (CBiCS) (Edmunds and Flynn, 2018a). CBiCS surfaces were created for the Victorian Environmental Assessment Council by the Deakin Marine Mapping Group using a supervised random forest classifier across the state (VEAC, 2019). For more information on how these biotopes were classified across the state, see Section 2.5 in Part 2. Using ArcGIS Pro's 'extract-multi values to points' tool, all variables were extracted for each BRUVS site to be used as training and validation within the species distribution models.

Table 10.1: List of derivatives tested in the random forest model. Variables not retained for analysis are shown in italics

Derivative	Software	Description
Depth	ArcGIS Pro 2.2 (Base)	Elevation of seafloor to the Australian Height Datum
Rugosity	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	Incorporates the heterogeneity of both slope and aspect using 3-dimensional dispersion of vectors and provides a measure of terrain complexity. See (Sappington et al., 2007) for more details
Slope	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	Change in elevation over designated neighbourhood size. tan <sup>-1</sup> (Rise/Run)
Curvature	ArcGIS Pro 2.2 (Spatial Analyst)	Steepest curve of convexity for a pixel over designated neighbourhood size and provides a measure of terrain complexity. $K(x) =  e^x /(1 + e^{2x})^{3/2}$
Northness	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	The cosine of the angle of slope in the analysis window, providing northness orientation of the feature or aspect. Equation: cos(aspect)
Eastness	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	The sine of the angle of slope in the analysis window, providing eastness orientation of the feature or aspect. Equation: sin(aspect)
Distance to reef	ArcGIS Pro 2.2 (Spatial Analyst)	Reef layer was derived from previously collected bathymetry and backscatter data. Distance from observation to reef was found using ArcGIS Pro Euclidean distance tool. Observations on reef had a value of 0 m
Bathymetric position index (fine, moderate and broad)	ArcGIS Pro 2.2 (Benthic Terrain Mapper)	BPI, which is a measure of the relative elevation of features in the terrain including peaks and valleys

Derivative	Software	Description	
Annual mean sea- surface temperature (daytime)	IMOS	IMOS 2006–19	
Annual range sea- surface temperature (daytime)	IMOS	IMOS 2006–19	
CBiCS BC2	Deakin Marine Mapping Group	Broad habitat class including the depth and habitat class (rock or sediment). Modelled statewide coverage created for the Victorian Environmental Assessment Council (VEAC)	
CBiCS BC3	Deakin Marine Mapping Group	Habitat complex providing information of the wave energy associated with each of the habitat classes (BC2). Modelled statewide coverage created for the VEAC	
CBiCS BC4	Deakin Marine Mapping Group	Biotope complex provides some information on the biotic component of the seafloor with the wave energy environment and the habitat class. Modelled statewide coverage created for the VEAC	
Longitude	ArcGIS Pro 2.2 (Spatial Analyst)	Raster calculator. Increasing in value from west to east	
Net primary productivity	IMOS	IMOS 2002–20	
Chlorophyll concentration a	IMOS	IMOS 2002–20	
Winter max orbital velocity mean	Water Tech	25-year hindcast model developed by Water Tech from 2006 to 2015	
Winter max orbital velocity range	Water Tech	The velocity of water over the seafloor as a result of wave energy. 25-year hindcast model developed by Water Tech from 2006 to 2015	

# 10.2 Fish sampling

Fish sampling across the state was completed using baited remote underwater video systems (BRUVS). BRUVS is a popular technique for observing fish assemblages. BRUVS are structures with cameras (usually in stereo format so fish size can be observed) that are deployed to a stationary location on the seafloor for a set time period (e.g. an hour). They also contain a bait bag that attracts fish so that the fish assemblages in an area can be observed. All BRUVS used in this study have 2 cameras each to record video. BRUVS were baited with a 1 kg bait bag suspended in front of the 2 cameras, and 60 minutes of footage was collected for each drop. To reduce the chances of fish travelling between BRUVS, drops are separated by roughly 300 m. BRUVS data were collated from 14 different surveys across the state spanning from 2006 to 2019, resulting in 1,032 individual BRUVS drops. Survey site summaries can be found in (Table 10.2). BRUVS footage provides information on the maximum number of individuals per species, as well as species length. From this data, species richness was obtained for each BRUVS drop (Figure 10.1). Species richness for our study is defined as the number of unique species present over a 1-hour BRUVS surveying

period. A total of 86 unique families and 201 fish species were recorded across all BRUVS surveys.

Table 10.2: BRUVS survey sites, which had an overall mean depth of 33  $\pm$  22 m and range of 1 to 99 m

Location	Mean and standard deviation (m)	Range (m)
Point Addis	19 ± 11	3–50
Point Addis MNP	27 ± 15	4–55
Wilsons Promontory MNP	49 ± 17	13–91
Port Fairy	16 ± 11	3–30
Hopkins Point	33 ± 10	15–47
12 Apostles	37 ± 15	10–62
12 Apostles MNP	35 ± 17	4–61
Merri MS	10 ± 6	1–33
Discovery Bay	40 ± 23	9–76
Discovery Bay MNP	43 ± 18	7–68
Cape Howe MNP	50 ± 26	11–99
Port Phillip Heads MNP	9 ± 5	1–27

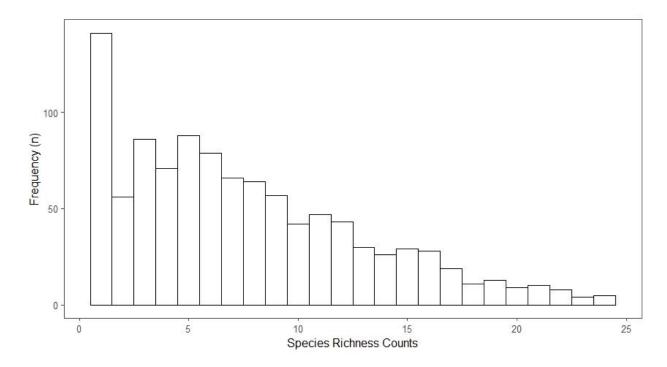


Figure 10.1: Species richness across the statewide dataset

## 10.3 Habitat classifications

Information on habitats and biotopes was provided by the Deakin Marine Mapping Group, which classified benthic communities using the CBiCS scheme (Edmunds and Flynn, 2018a). Ground truth data for the biotope classification were collected using a combination of towed video, quadrat and diver surveys and provided from state government archives. Predictor variables (bathymetric mean, vector ruggedness measure (VRM), eastness, northness, maximum curvature, slope and wave orbital velocity) were created from the same statewide bathymetric surface used in this study and included as predictor variables in the species distribution models. A supervised random forests model was used to predict classes across the state. Our study focuses on CBiCS's biotic hierarchy levels – broad habitat (BC2), habitat complex (BC3) and biotope complex (BC4) – and their impact on fish species richness. Classes and detailed descriptions can be found in Table 10.3.

Table 10.3: CBiCS hierarchy levels BC2, BC3 and BC4 and detailed descriptions of BC4 classes taken from the CBiCS Hierarchy Explorer<sup>a</sup>

BC2	вс3	BC4	Detailed description
Circalittoral rock and other hard substrata	High energy open-coast circalittoral rock	Sandy low profile reef wave surge communities	Deep communities on low profile, flat or sandy veneer reef adjacent to or affected by sand inundation and resuspension.  Considerable sand trapped around the base of sponge colonies and clumps
		Moderate to high complexity circalittoral rock with covering of small colonies and well-spaced erect sponges	Moderate to high complexity circalittoral rock with predominant covering of small colonies <10 cm and prominent but well-spaced erect sponges. Larger seabed covering sponges mostly absent
		High energy circalittoral rock with bushy branching and low erect sponges	High energy circalittoral rock with bushy branching and low erect sponges. <i>Pteronis</i> sea plumes and hydroids absent. Seawhips generally absent but may occur in low abundance in small patches
		Crustose coralline algal communities with combinations of thallose red algae and scattered sponges on high energy circalittoral rock	High energy open-coast circalittoral rock with a prominence of crustose coralline algae and various combinations of thallose red algae, trapped sand, bushy bryozoans and scattered low erect and small seabed covering sponges. Tall erect sponges uncommon. Occurs on sandy veneer, low complexity and high complexity reef

BC2	ВС3	BC4	Detailed description
		High energy circalittoral rock with seabed covering sponges	Moderate to high complexity circalittoral rock, including ramp/slope geoforms, with a predominance of seabed covering sponges and other cushion fauna. Erect forms may be common but mostly low in height, less than 40 cm. There is often trapped sand amongst the sponges but does not form veneer patches
		Moderate to high complexity circalittoral rock with prominent sea plumes, sea tulips and hydroid fans	Assemblages on moderate to high complexity circalittoral rock with prominence of sea tulips such as <i>Pyura spinifera</i> , sea plumes such as <i>Pteronisis</i> and hydroid fans such as <i>Solanderia fuscus</i> and <i>Clathrozoan wilsoni</i> . Sponges are the predominant substratum cover
		Low complexity circalittoral rock with non-crowded erect sponges	Low complexity circalittoral rock with predominant covering of small colonies <10 cm and occasional to prominent but well-spaced or non-crowded erect sponges. Larger seabed covering sponges mostly absent
		Bushy bryozoan- dominated communities	High complexity lower circalittoral reef with prominent rambling ridged sponges (grey and red) with coccoidal erect bushy branched and low tangled branched sponges present. Yellow bushy bryozoans prominent. The diversity of sessile invertebrates is low with the majority of the biomass occurring on the tops of reef outcrops. Thick lamellate ear sponges absent
		Sea whip and tall branching sponge communities on open coast circalittoral rock	Provision biotope complex from limited towed video imagery. Reef tops with sea plumes, sea whips and variously covering and rambling sponges. Slopes and gullies with large mounded and erect sponges, including flat branching, palmate but no flabellate sponges
		Centrostephanus grazed barrens	Deep sea urchin grazing barren by Centrostephanus rodgersii. Characterised by crustose coralline algae and low turfs with scattered sponges and soft corals
Infralittoral rock and other hard substrata	High energy infralittoral rock	High energy <i>Ecklonia-</i> <i>Phyllospora</i> communities	Mixed Ecklonia radiata and Phyllospora comosa dominated communities where both species have an appreciable proportion of the canopy structure but varying in relative dominance. Occurs in less than extremely exposed conditions. Often associated with sand-affected reef and behind surf breaks. Note: Ecklonia radiata may be a minor component in the Phyllospora biotope complex
		High energy lower infralittoral zone	Red algal dominated communities ranging from <i>Ecklonia</i> park to mixed red and browns to mixed reds and sessile invertebrates.  Excludes <i>Centrostephanus</i> grazed barrens

BC2	ВС3	BC4	Detailed description
		High energy <i>Phyllospora</i> communities	Phyllospora dominated communities, often associated with highly scoured substrata colonised by crustose coralline algae and with low to moderate abundance of thallose algal understorey species
		High energy <i>Ecklonia</i> Communities	Ecklonia radiata with abundant foliose red seaweeds on high energy rock
		High energy sandy veneer and scour turf communities	Seaweed communities on reef with sandy veneer or with considerable trapped sand and subject to scouring
		High energy sub-canopy brown seaweed communities	Mixed fucalean assemblages with multiple Cystophora species and typically with Seirococcus axillaris, Acrocarpia paniculata and Carpoglossum confluens. Typically on reefs affected by very strong ground surge (long period waves) and nearby sand patches
		Amphibolis stands on high energy rock	Seagrass Amphibolis antarctica assemblages on exposed rocky reef with sandy veneer. May be mixed with Cystophora species. On lower profile reefs in heavy surge reef and sometimes breaking conditions and with high sand influence
		High energy <i>Durvillaea</i> communities	Durvillaea dominated communities, usually associated with highly scoured substrata colonised by crustose coralline algae or intertidal biota if occurring in the swash zone
Sublittoral sediment	Sublittoral seaweed on sediment	Thallose red algae on sand with ground surge	Scattered thalli of predominantly red algae in tidal sediment channels, attached to objects in or on the sediment. Biotopes are differentiated by the nature of the sediments, including presence of coarse sand, fine sand, shelly sand, sandy shell, burrows, species of seaweed, and associated presence of sea pens, bivalves, sponges and corals. Occasional presence of <i>Caulerpa</i> and/or seagrass species
		Caulerpa beds on sediment	Caulerpa trifaria on shelly sand hummocks in the lower infralittoral zone on the open, exposed coast
	Non-reef sediment epibenthos	Erect octocorals on sediment	Epibiota characterised by erect octocorals (possibly covered in sponges) on sediment. sponge, ascidian and seaweed clumps may be present but not as a dominant epibiotic component

BC2	BC3	BC4	Detailed description
	Sublittoral sand and muddy sand	Circalittoral fine sand	Clean fine sands with less than 5 silt/clay in deeper water, either on the open coast or in tide-swept channels of marine inlets in depths of over 15–20 m. The habitat may also extend offshore and is characterised by a wide range of echinoderms, polychaetes, bivalves, and with occasional beds of rhodoliths. This habitat is generally more stable than shallower, infralittoral sands and consequently supports a more diverse community
		Infralittoral fine sand	Clean sands which occur in shallow water, either on the open coast or in tide-swept channels of marine inlets. The habitat typically lacks a significant seaweed component and is characterised by robust fauna, particularly amphipods and robust polychaetes
	Sublittoral mixed sediments	Circalittoral mixed sediments	Mixed (heterogeneous) sediment habitats in the circalittoral zone (generally below 15—20 m) including well mixed muddy gravelly sands or very poorly sorted mosaics of shell, cobbles and pebbles embedded in or lying upon mud, sand or gravel. Due to the variable nature of the seabed a variety of communities can develop which are often very diverse. A wide range of infauna polychaetes, bivalves, echinoderms and burrowing anemones often present in such habitat and the presence of hard substrata (shells and stones) on the surface enables epifaunal species to become established. The combination of epifauna and infauna can lead to species rich communities

Source: Australian Marine Ecology, Fathom Pacific and the State of Victoria, 'Exploring Biotic Component Hierarchy' webpage, Combined Biotope Classification Scheme. https://dev-tools.cbics.org/explore/biotic-component

# 10.4 Statistical analyses

Prior to running our statistical analyses, we checked for correlation between variables, as correlated variables are not independent of each other (see review by Dormann et al., 2013). To assess correlation among predictor variables, a Pearson Product-moment correlation matrix was generated (Figure 10.2). Correlated variables, below –0.7 and above 0.7, were removed by comparing variable importance and dropping the less important variable (Gregorutti et al., 2017; Strobl et al., 2007). The remaining variables were checked for collinearity using variance inflation factor (VIF) from R package 'car' (Fox and Weisberg, 2019), with all variables falling below a VIF of 2, well below the recommend value of 10 (Kennedy, 1992; Marquaridt, 1970; Neter et al., 1989). Maximum wave orbital velocity mean, maximum wave orbital velocity range, net primary productivity, longitude, chlorophyll α, BPI (broad) and BPI (fine) were highly correlated with better performing

variables and were therefore not retained for analysis. These correlated variables were replaced in the models by a variable that serves as a proxy for their characteristics (e.g. BPI medium was correlated with both BPI (broad) and BPI (fine), mean SST was correlated with primary productivity). Spatial autocorrelation between the BRUVS sites was tested using the 'ncf' package from R (Bjørnstad, 2016), which found autocorrelation present up to 22 m, which is less than the spacing between the majority of BRUVS deployments.

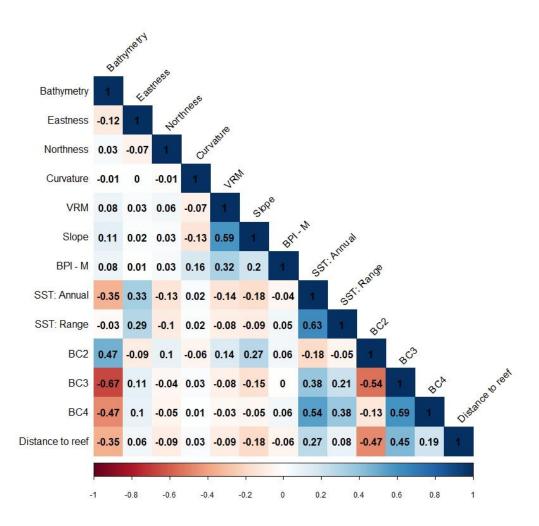


Figure 10.2: Pearson Product-moment correlation matrix for retained model variables. Colours indicate the correlation coefficient

Ground truth data were split, and we used 80 as training and 20 for model validation. CBiCS classifications were treated as factor variables, and the remaining variables were treated as continuous. We used root mean squared error (RMSE), mean absolute error (MAE) and pseudo- $R^2$ , to evaluate our models' performance (Dai et al., 2020; Li et al., 2017; Olaya-Marín et al., 2013). RMSE gives more weight to larger residuals, which means RMSE gives a relatively high weight to large errors. MAE gives equal weight to all residuals and thus to all

errors. The Akaike information criterion (AIC) is not applicable for RF, therefore was not assessed for comparison purposes across all models.

The machine learning technique random forests (RF) was selected because it provides good predictive performance with noisy data (Díaz-Uriarte and Alvarez De Andrés, 2006) and reduces the risk of over fitting (Breiman, 2001). Additionally, RF models have been used to model various species richness distributions, and they show high performance when compared to other machine learning methods (Dai et al., 2020; Li et al., 2017; Olaya-Marín et al., 2013). Our species richness ranged from 1 to 25 species per site. Although species richness values are count data, using the RF model to predict 25 classes across the state would result in low class accuracies for rare classes. To overcome this, species richness was treated as a continuous variable for the machine learning approach. RF models were created using the 'randomForest' package in R (Liaw and Wiener, 2002). Statewide predictive species richness maps were created in ArcGIS Pro using the spatial statistics package's 'Forest-based Classification and Regression' tool, which is based on the random forest algorithm from Breiman (2001). This is the same algorithm used in the 'randomForest' package in R.

These same methods were repeated for the relative abundances of 4 species of fish: Blue-Throat Wrasse (*Notolabrus tetricus*), Six-Spine Leatherjacket (*Meuschenia freycineti*), Senator Wrasse (*Pictilabrus laticlavius*) and Snapper (*Chrysophrys auratus*). These species were chosen based on each having an number of observations, and to provide a glimpse of the habitat associations of species with different life histories and home range sizes. For example, 2 species are very site attached (*N. tetricus* and *M. freycineti*), *P. laticlavius* is less site attached but is benthic associated, and *C. auratus* is less site attached and wider ranging. Also, all these species are found on or near reefs, making them easier to model.

# 10.5 Comparison of species richness in protected and unprotected areas

To determine if there was a significant difference in fish species richness between Victoria's marine protected areas and their respective biounits, a pairwise t-test with a 'Bonferroni' *P* value adjustment was conducted using the 'BSDA' package in R (Arnholt and Evans, 2017). Due to the large number of samples within each population, effect size was tested using Cohen's d to determine if the statistical results from the pairwise t-test are practically useful or trivial (Crutsinger et al., 2014; Matthews et al., 2014). Cohen hypothesised that any value below 0.2 was trivial even if statistically significant; meaning if 2 groups mean have a Cohen's d value of below 0.2, the difference is in practice trivial.

### 11. Results

## 11.1 Model performance

The final random forest model had a root mean square error (RMSE) and mean absolute error (MAE) of 3.69 and of 2.69, respectively. These values provide a measure of the error between observed values and those predicted from the model; lower errors indicate a more accurate model. These errors indicate that the model is performing well. The model also has a pseudo- $R^2$  of 0.54 using the following variables: bathymetry, BC2, BC3, BC4, BPI (medium scale), distance to reef, annual SST, SST range, slope, VRM, northness, eastness and curvature. Pseudo- $R^2$  is a measure of the variance explained by the model.

# 11.2 Variable importance

Variable importance for continuous variables can be measured by the percentage increase in RMSE when the variable is removed from the model (Table 11.1), with more important variables expected to cause a greater increase in RMSE. The most important variable for predicting species richness across the state is annual SST range. The highest performing CBiCS variable was BC4 (biotope classification at the biotope complex level), which is second in overall importance, followed by depth (bathymetry) (Table 11.1). Distance to reef and annual SST mean have similar variable importance. CBiCS BC2 (broad habitat classification) and BC3 (habitat complex) have the most-similar importance values of all retained variables. The best performing bathymetric derivative is VRM, followed by slope and BPI-M. Bathymetric derivatives, northness, eastness and curvature are the least important variables for predicting species richness (Table 11.1).

Table 11.1: Relative importance of retained model variables measured by percentage increase of RMSE error if the variable was absent

Variable	Increase in RMSE
Sea-surface temperature (SST) range	51.22
BC4	38.29
Depth	34.29
Distance to reef	29.18
SST mean	26.89
Vector ruggedness measure (VRM)	22.45
BC3	18.25
BC2	17.72
Slope	10.75
Bathymetric position index (BPI) (moderate)	6.76
Curvature	4.06
Eastness	3.45
Northness	1.09

Differences in fish species richness were well separated across the broad habitat classes (CBiCS hierarchy BC2) (Figure 11.1). Fish species richness was highest for the class containing circalittoral rock and lowest for the class sublittoral sediment. The overall dispersions are roughly even; however, this is mainly due to the presence of outliers of sampled habitat containing high species richness in infralittoral hard rock and sublittoral sediment. Even though richness was lower overall in sublittoral sediment and infralittoral rock than in circalittoral rock, the first 2 classes had more outlier samples with high species richness, which caused richness distribution to be more right skewed. Differences in fish species richness were well separated across CBiCS hierarchy BC3 classes with 2 exceptions: the classes Sublittoral sand and muddy sand and Non-reef sediment epibenthos had similar medians. High energy open-coast circalittoral rock had the highest species richness, and Sublittoral mixed sediments had the lowest. All dispersions overlapped and all boxplots were right skewed with the exceptions of Non-reef sediment epibenthos and Sublittoral seaweed on sediment. The greatest number of outliers were present in the class Sublittoral sand and muddy sand, and no outliers were present in Non-reef sediment epibenthos and High energy open-coast circalittoral rock. Differences in fish species richness were well separated in most CBiCS hierarchy BC4 classes; the highest species richness values were seen in Centrostephanus grazed barrens, Bushy bryozoan-dominated communities, and Moderate to high complexity circalittoral rock with covering of small colonies and wellspaced erect sponges. In addition to supporting Centrostephanus species, the class Centrostephanus grazed barrens is characterised by crustose coralline algae with scattered sponges. Circalittoral mixed sediments and Sea whip and tall branching sponge communities

on open coast circalittoral rock had the lowest species richness. Nine of the 24 classes had outliers, the greatest number being found in infralittoral fine sand (Figure 11.1).

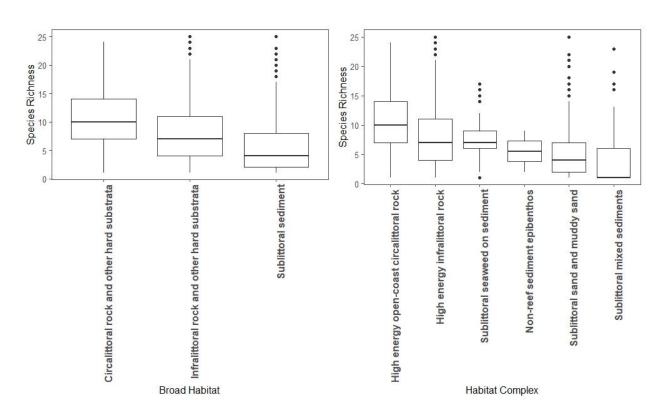


Figure 11.1: Species richness boxplots for CBiCS classes in hierarchy levels BC2 – Broad habitat, BC3 – Habitat complex and BC4 – Biotope complex (continued on next page)

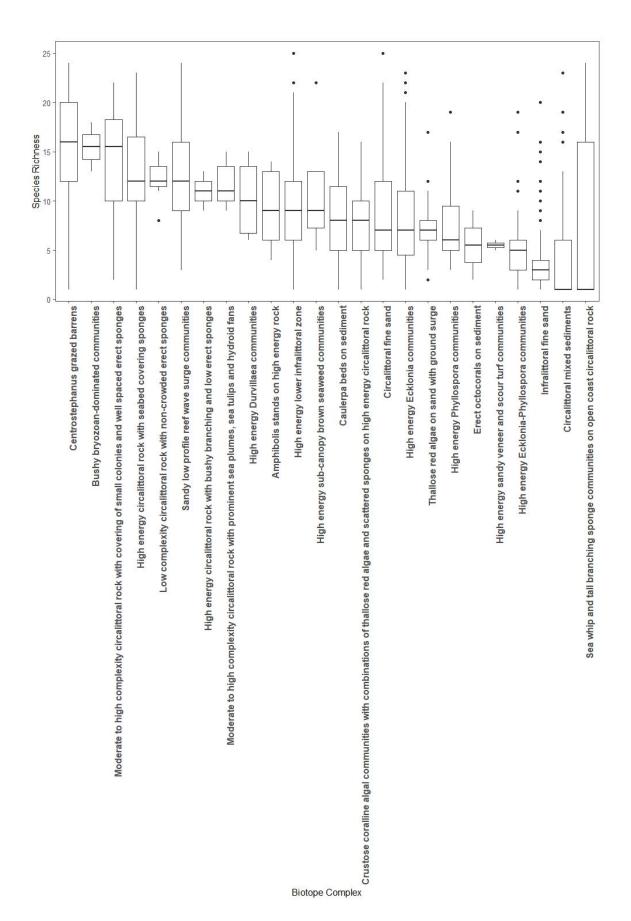


Figure 11.1 (continued): Species richness boxplots for CBiCS classes in hierarchy levels BC2 – Broad habitat, BC3 – Habitat complex and BC4 – Biotope complex

The relationships between fish species richness and the continuous variables differed (Figure 11.2). Species richness has asymptotic relationships with several variables including sea-surface temperature range, complexity of the seafloor habitat (VRM) and slope. With sea-surface temperature range, richness increases until a range of 6 °C and then levels off. Species richness is low in low-complexity and low-slope habitats but then increases and levels off once a moderate level of complexity (0.025 VRM) and moderate slope (5 degrees) is reached. The relationship between species richness and depth shows that highest richness occurs between 25 and 50 m depth, and richness decreases in deeper and shallower depths outside that range. Distance to reef was also influential and showed that species richness has a sharp decrease as distance to reef increases. The relationship with mean sea-surface temperature indicates that the highest fish species richness is found between 16.25 °C and 17.25 °C, and richness decreases in cooler and warmer temperatures. With the final variables, species richness decreases as curvature increases and is higher in moderate values of easting and northing (aspect). These results indicate that MPAs with higher ranges of temperature, moderate to high seafloor complexity and slope, a mean temperature between 16.25 °C and 17.25 °C, depth ranges between 25 and 50 m and lower curvature of the habitat are more likely to have higher species richness.

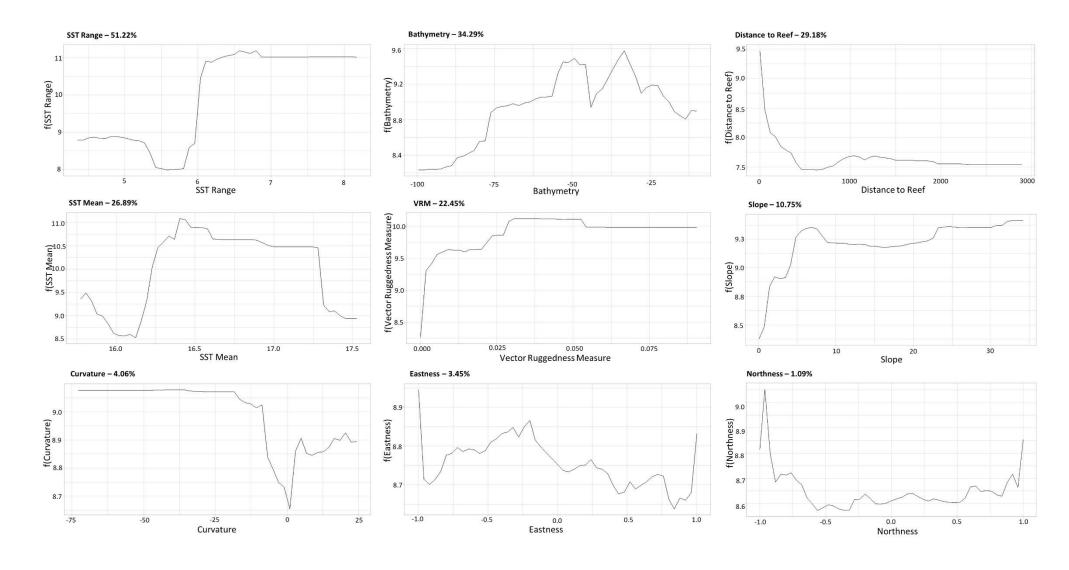


Figure 11.2: Partial dependence plots for the relationships between fish species richness (y-axis) and each of the continuous variables found in the final random forest model (x-axis)

# 11.3 Species richness map

The predictive species richness maps classified using the RF model display general trends across the state (Figure 11.3). Predicted species richness is higher in areas with complex reef and typically lower in areas with unconsolidated sediment (Figure 11.3). Within unconsolidated sediment areas, those closer to reefs have higher predicted richness, and predicted species richness decreases as distance from reef and depth increase (Figure 11.3). Reefs found in the mesophotic zone had higher predicted species richness values than their shallower counterparts (Figure 11.3). Generally, predicted species richness was highest in the Bellarine-Mornington biounit. Predicted species richness is relatively low from the Otways to Discovery Bay. There are very few reefs on the eastern coastline extending past Wilson's Promontory MNP, resulting in low predicted species richness until you reach the reefs of Mallacoota and Cape Howe MNP where predicted species richness increases (Figure 11.4).

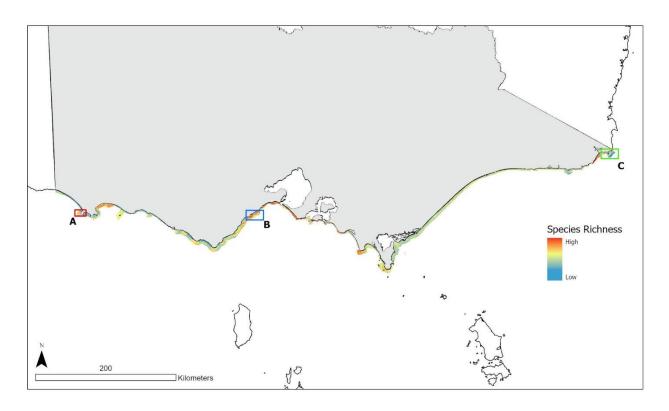


Figure 11.3: Predicted statewide species richness, for Victoria, Australia. Red (Discovery Bay), blue (Point Addis) and green (Cape Howe) boxes indicate the location of snapshots in Figure 11.4

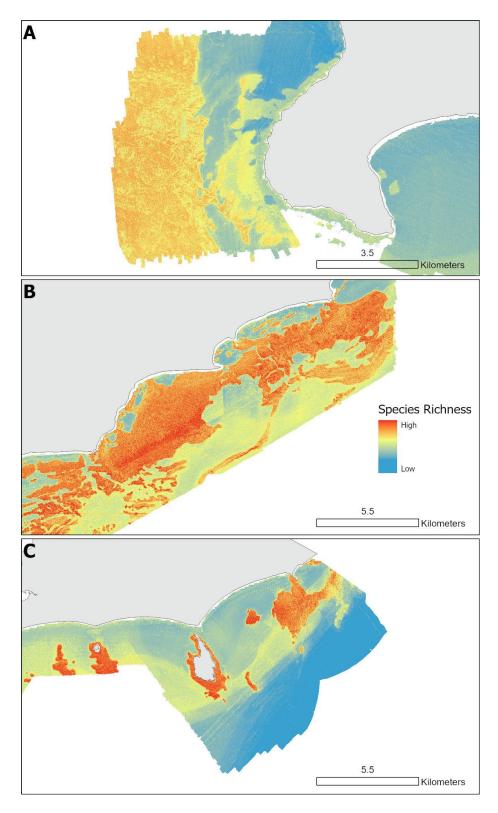


Figure 11.4: Snapshots of predicted species richness at Discovery Bay (a), Point Addis (b) and Cape Howe (c). See Figure 11.3 for the location of the snapshots

# 11.4 Species abundances

The models for relative abundance for the 4 species of fish analysed show that habitat associations vary between species. C. auratus, which has a larger home range and is found across a wider range of habitats than the other species, appears to have a more general association with habitats across the state. Temperature, both mean temperature and temperature range were the most important variables in the model for C auratus; abundance decreased with increasing temperatures but increased with greater ranges in temperature (Figure 11.5). The rest of the variables derived from the complexity of the reef including aspect (cosine and sine), vector ruggedness measure (VRM), slope and bathymetric position index followed. C. auratus abundance tends to decrease with increased complexity of the habitat but also decreases as distance to reef increases (Figure 11.5). This indicates that *C. auratus* tends to be found in flat, sedimentary habitats but in close proximity to reef. Depth (bathymetry) was the fifth most important variable in the model; it showed highest abundance in the 25 to 50 m depth range (Figure 11.5). C. auratus is predicted to be found across varying complexity of reefs, different biotope complexes and a wide depth range (Figure 11.6), more so than the other species. Due to the variation in response to different habitats, the model for C. auratus did not perform exceptionally well. The MSE of the final model was 27.4, and the model only explained 7.8 of the variance in C. auratus relative abundance.

Table 11.2: Variable importance from the random forest model for Chrysophrys auratus

Variable	Increase in mean square error (MSE) if removed
Annual mean sea-surface temperature	14
Annual range of sea-surface temperature	13
Cosine of aspect degrees	11
Vector ruggedness measure	11
Depth (bathymetry)	10
Slope	10
Sine of aspect degrees	9
Current	9
Distance to reef	7
Broad biotope class (BC2)	4
Bathymetric position index	1

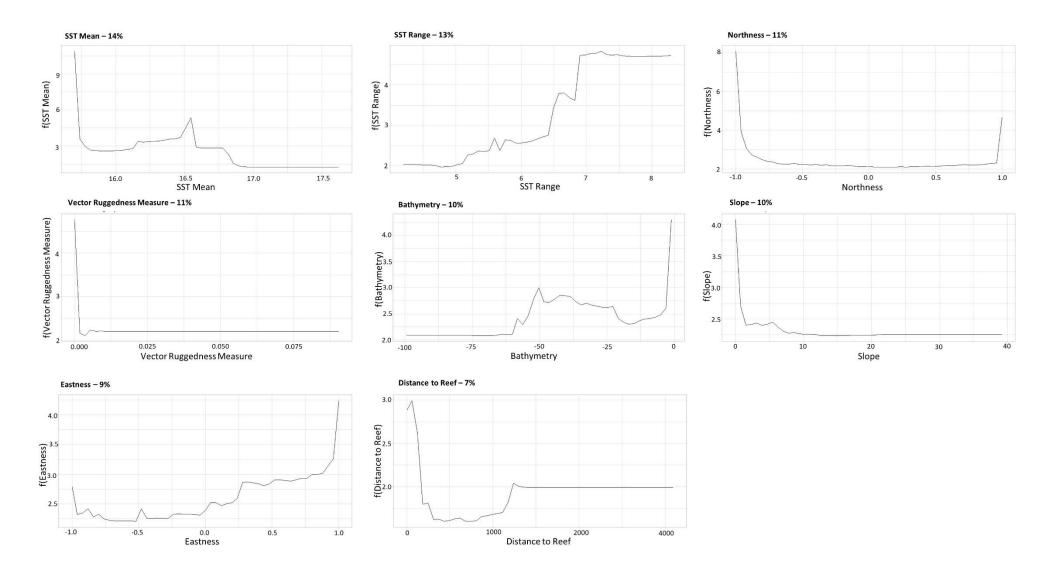


Figure 11.5: Partial dependence plots for the relationships between *Chrysophrys auratus* abundance (fitted values on the *y*-axis) and each of the continuous variables found in the final random forest model (*x*-axis)

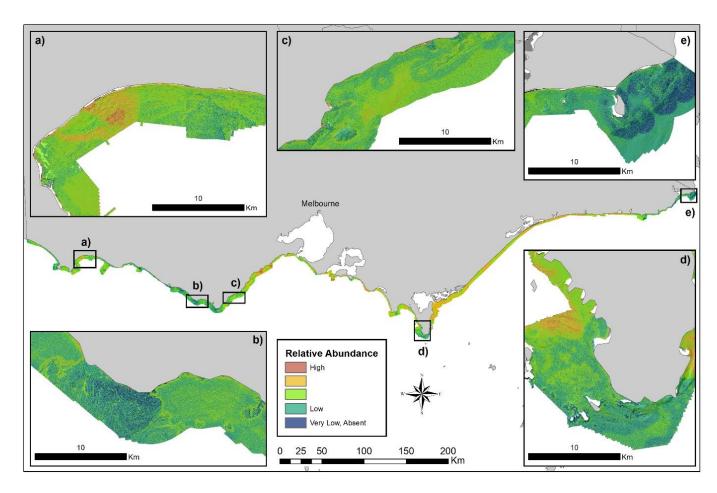


Figure 11.6: Predicted relative abundance of *Chrysophrys auratus* across the state waters of Victoria. These predictions are derived from the random forest model associating the relative abundance of *C. auratus* with environmental variables

Compared to *C. auratus*, *N. tetricus* and *P. laticlavius* have greater affinities for the rocky reef habitat across the state and the shallower depth range. The model for *N. tetricus* performed well with an MSE of 2.807 and 49.3 of the variance explained. Depth was the most important variable in the model followed by VRM and the broad biotope class (BC2) (Table 11.3). Abundance increases with shallower depths and higher complexity habitat with abundance decreasing with increasing distance to reef (Figure 11.7). Both temperature range and temperature mean were important. *N. tetricus* abundance was found to increase with a greater range of temperature, but overall increases in temperature resulted in lower abundance (Figure 11.7). The rest of the variables, ordered in importance can be found in Table 11.3. *N. tetricus* is rarely found in soft-sediment habitats. However, it is found in higher relative abundances across the entire state compared to the other species modelled (Figure 11.8). In contrast, *P. laticlavius* is mainly found in the areas west of Wilsons Promontory, and only very low abundances are predicted in the east of the state (Figure 11.9). As with the model for *N. tetricus*, the model for *P. laticlavius* found depth to be the most important variable and the broad biotope class was also important.

*P. laticlavius* abundance increases in shallower depths and in areas of higher complexity (Figure 11.10). Sea-surface temperature, both mean and range, were also important in the model, which showed increasing abundance in areas of greater temperature ranges and cooler temperatures (Figure 11.10). The rest of the variables can be found in Table 11.4, ordered by importance. The model for *P. laticlavius* performed had an MSE of 0.3 and 25 of the variance was explained.

Table 11.3: Variable importance from the random forest model for *Notolabrus tetricus* 

Variable	Increase in mean square error (MSE) if removed
Depth (bathymetry)	18
Vector ruggedness measure	17
Broad biotope class (BC2)	13
Annual range of sea-surface temperature	9
Slope	9
Curvature	8
Distance to reef	6
Annual mean sea-surface temperature	6
Sine of Aspect degrees	6
Bathymetric position index	4
Cosine of aspect degrees	4

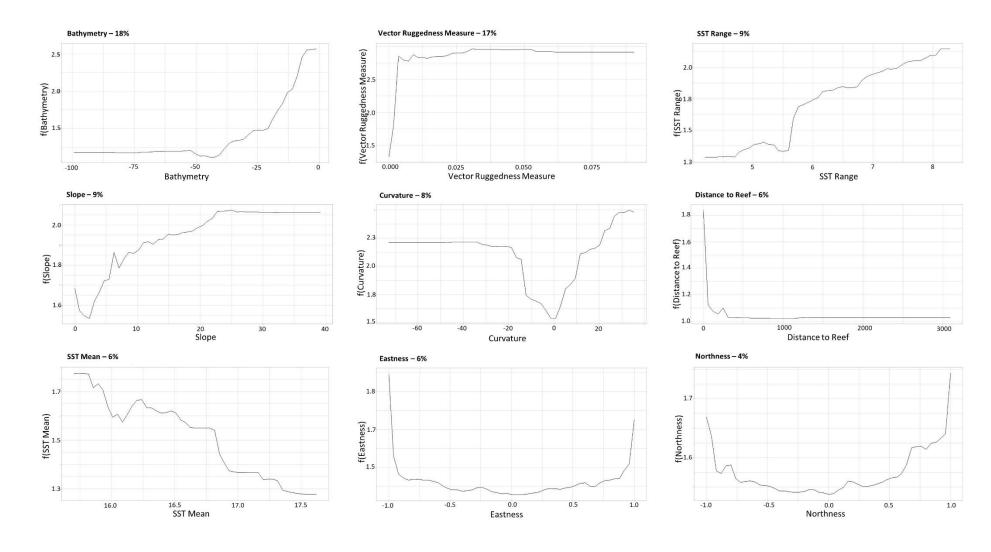


Figure 11.7: Partial dependence plots for the relationships between *Notolabrus tetricus* abundance (fitted values on the *y*-axis) and each of the continuous variables found in the final random forest model (*x*-axis)

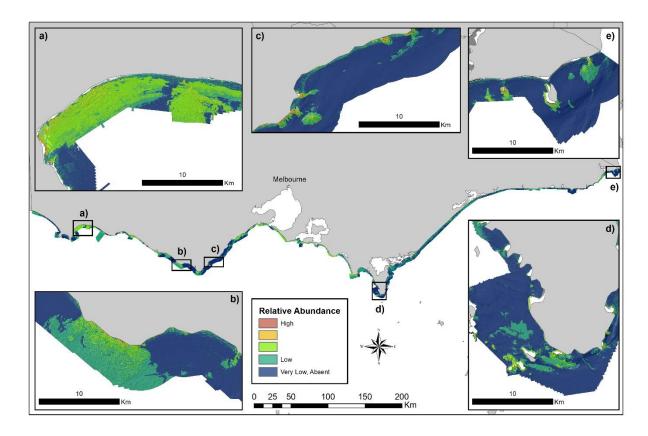


Figure 11.8: Predicted relative abundance of *Notolabrus tetricus* across the state waters of Victoria. These predictions are derived from the random forest model associating the relative abundance of *N. tetricus* with environmental variables

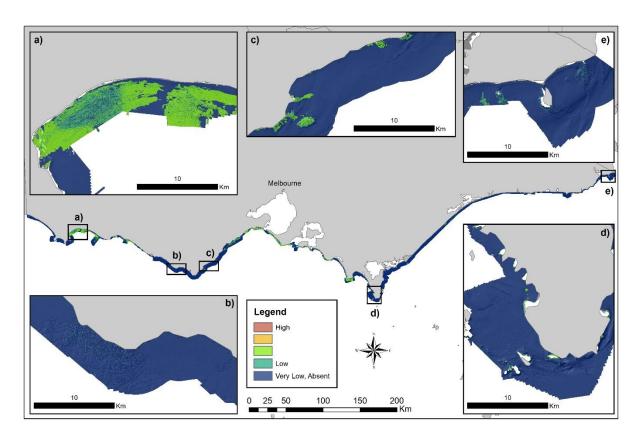


Figure 11.9: Predicted relative abundance of *Pictilabrus laticlavius* across the state waters of Victoria. These predictions are derived from the random forest model associating the relative abundance of *P. laticlavius* with environmental variables

Table 11.4: Variable importance from the random forest model for Pictilabrus laticlavius

Variable	Increase in mean square error (MSE) if removed		
Depth (bathymetry)	16		
Annual range of sea-surface temperature	15		
Broad biotope class (BC2)	13		
Annual mean sea-surface temperature	10		
Vector ruggedness measure	10		
Slope	8		
Cosine of aspect degrees	8		
Sine of aspect degrees	7		
Current speed	7		
Distance to reef	3		
Bathymetric position index	3		

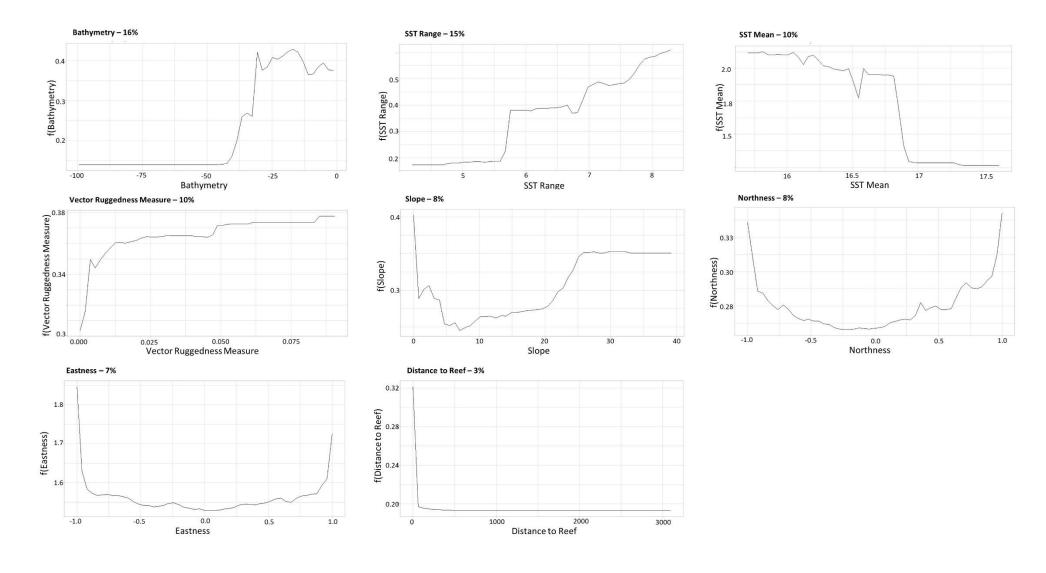


Figure 11.10: Partial dependence plots for the relationships between *Pictilabrus laticlavius* abundance (fitted values on the *y*-axis) and each of the continuous variables found in the final random forest model (*x*-axis)

Finally, the abundance distribution of *M. freycineti* was found to be driven by sea-surface temperature and the complexity of the reef. The abundance of *M. freycineti* increases with increases in both temperature mean and range and with increases in complexity (Figure 11.11). Their abundance also peaks around 50 m depth with decreases on the other side of that peak (Figure 11.11). The remaining variables are shown in Table 11.5, in decreasing order of importance from top to bottom. Overall, *M. freycineti* is mainly found in slightly deeper waters but over rocky reefs. The highest abundances tend to be associated with more complex rocky reef habitat, and moderate abundances are found across most areas of the reefs (Figure 11.12). This model explains 19.8 of the variance and has an MSE of 0.6.

Table 11.5: Variable importance from the random forest model for Meuschenia freycineti

Variable	Increase in mean square error (MSE) if removed		
Annual range of sea-surface temperature	17		
Annual mean sea-surface temperature	14		
Vector ruggedness measure	12		
Current speed	9		
Depth (bathymetry)	9		
Slope	9		
Cosine of aspect degrees	8		
Sine of aspect degrees	8		
Bathymetric position index	6		
Broad biotope class (BC2)	5		
Distance to reef	4		

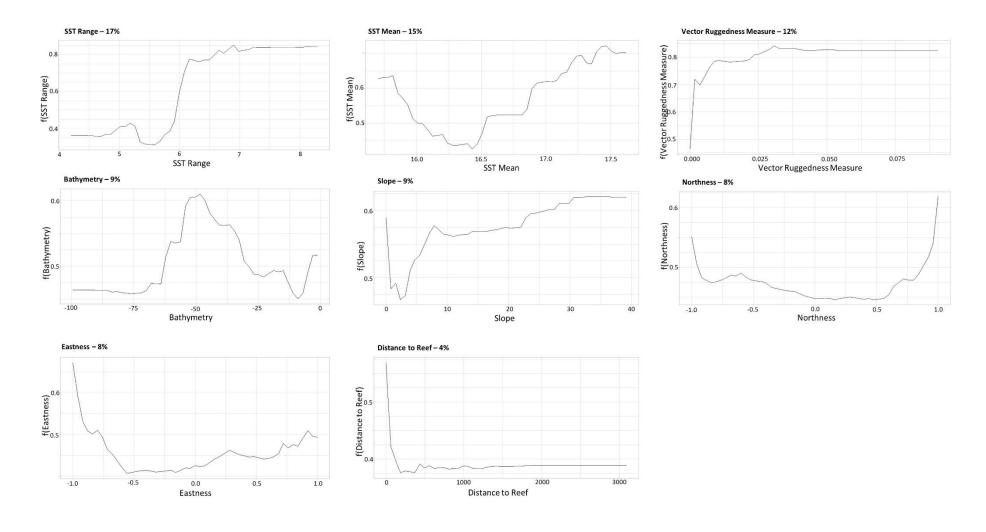


Figure 11.11: Partial dependence plots for the relationships between *Meuschenia freycineti* abundance (fitted values on the *y*-axis) and each of the continuous variables found in the final random forest model (*x*-axis)

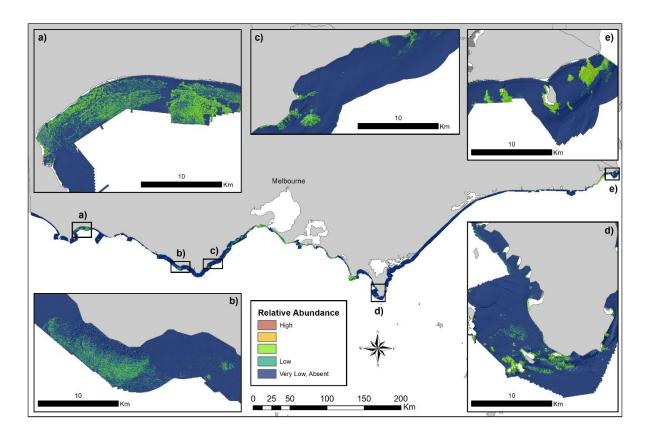


Figure 11.12: Predicted relative abundance of *Meuschenia freycineti* across the state waters of Victoria. These predictions are derived from the random forest model associating the relative abundance of *M. freycineti* with environmental variables

## 11.5 MPA comparison results

Of the 18 MPAs tested, 11 were predicted to have significantly higher number of species than their respective biounit (Table 11.6). Of these, Wilson's Promontory MNP had a Cohen's s value less than 0.2, indicating it had no practical difference when compared to Wilson's Promontory West. Six MPAs – Bunurong MNP, Wilson's Promontory MNP (compared to Wilson's Promontory East biounit), Point Danger MS, Eagle Rock MS, Mushroom Reef MS and Marengo Reefs MS – had large effect size differences (Cohen's d values > 0.8). Point Danger MS and Bellarine-Mornington biounit had the highest predicted species richness of all MPAs and biounits tested. The remaining 7 MPAs had significantly lower predicted species richness within the MPA than their respective biounit (Table 11.6). Of these 7, Cape Howe MNP, Point Hicks MNP, Port Philip Heads MNP and Ninety Mile Beach MNP have a Cohen's d value of less than 0.2, indicating that, although there were statistically fewer species, there is practically no difference in predicted species richness between the respective parks and their biounits.

Table 11.6: Mean predicted species richness of Victoria's marine protected areas compared to their respective biounits

Biounit	Species richness (± SD)	Marine protected area	Species richness (± SD)	P value	Cohen's	Effect size difference <sup>a</sup>
Gabo-Howe	5.7 ± 3.5	Cape Howe MNP	5.1 ± 3.9	P < 0.001	0.17	+
Point Hicks	6.2 ± 3.1	Point Hicks MNP	5.8 ± 2.2	P < 0.001	0.13	+
Cape Conran	7.5 ± 1.9	Beware Reef MS	9.7 ± 2.5	P < 0.001	0.68	++
Ninety Mile Beach	6.8 ± 1.4	Ninety Mile Beach MNP	6.6 ± 1.2	P < 0.001	0.14	+
Bunurong	8.8 ± 3.2	Bunurong MNP	12.3 ± 2.5	P < 0.001	1.09	+++
Wilsons Promontory West	8.1 ± 2.3	Wilsons Promontory MNP	8.5 ± 2.1	P < 0.001	0.17	+
Wilsons Promontory East	6.3 ± 1.3	Wilsons Promontory MNP	8.5 ± 2.1	P < 0.001	1.69	+++
Schanck- Woolamai	9.7 ± 3.5	Mushroom Reef MS	13.1 ± 1.3	P < 0.001	0.97	+++
Surf Coast	8.8 ± 3.2	Point Danger MS	13.1 ± 1.3	P < 0.001	1.53	+++
Surf Coast	8.8 ± 3.2	Point Addis MNP	10.0 ± 3.4	P < 0.001	0.38	++
Surf Coast	8.8 ± 3.2	Eagle Rock MS	12.0 ± 2.3	P < 0.001	1.00	+++
Bellarine- Mornington	11.4 ± 3.7	Barwon Bluff MS	12.7 ± 1.9	P < 0.001	0.35	++
Bellarine- Mornington	11.4 ± 3.7	Port Phillip MNP	10.9 ± 3.6	P < 0.001	0.14	+
Cape Otway	6.7 ± 2.4	Marengo Reefs MS	11.7 ± 2.3	P < 0.001	2.08	+++
Shipwreck Coast	6.5 ± 2.4	Twelve Apostles MNP	5.7 ± 2.4	P < 0.001	0.33	++
Shipwreck Coast	6.5 ± 2.4	The Arches MS	4.6 ± 1.2	P < 0.001	0.79	++
Shipwreck Coast	6.5 ± 2.4	Merri MS	5.6 ± 1.2	P < 0.001	0.38	++
Discovery Bay	5.3 ± 3.0	Discovery Bay MNP	7.5 ± 3.4	P < 0.001	0.73	++

**Note:** a + = trivial difference, ++ = moderate difference, +++ = large difference.

### 12. Discussion

In this study, we found that random forest models perform well at modelling species richness and species distributions for site-associated species across the coastal waters of Victoria, Australia, and that the incorporating biological habitat improved these models. More mobile species (such as *C. auratus*) proved harder to model accurately, but the models did give an indication of suitable habitats. We demonstrated how the resulting broadscale

fish species distribution models across a large region can be used to inform management on the value of existing MPAs for conserving fish biodiversity. For example, we showed that most nearshore MPAs in the state of Victoria have significantly higher predicted species richness values than their respective biounits, likely due to greater area of available reef habitat, and thus are valuable for conservation.

## 12.1 Variable importance

Annual SST range was the most important variable in the richness distribution model, reducing RMSE by 51 and showing higher richness in areas of greater SST. SST has been shown to have strong relationships that drive predicted fish species richness (Austin and Van Niel, 2011; Bradie and Leung, 2017; Mellin et al., 2010; Sequeira et al., 2016; Stuart-Smith et al., 2013). Temperature affects both the range and relative abundance of temperate fish species (Langlois et al., 2012; Simpson et al., 2011) and has been identified as an important variable for predicting fish species richness in past studies (Mellin et al., 2010). Annual SST range outranked annual SST mean, likely due to temperate fish having broader temperature tolerances; a wider range of temperatures supported more unique fish species (Guo et al., 2015; Payne et al., 2016). These results indicate that MPAs with higher average temperatures and a greater range in temperature are likely to have higher fish species richness and greater abundances for all species except for *M. freycineti*. Therefore, MPAs in the eastern portion of the state are likely to protect a greater variety of fish species and have greater abundances of fish than MPAs in the western portion.

Other variables of importance included biotope complex (CBiCS BC4), depth and distance to reef. CBiCS BC4 ranked second in variable importance, reducing RMSE by 38. Although past marine studies have used classified habitat maps as a predictor variable for species distribution models (Knudby et al., 2010a, 2010b), these are often limited to geological habitat classes (i.e. reef or sediment) identified using satellite imagery. Assessing the hierarchy levels captures how biotopes impact the prediction of fish species richness. Many demersal fish species are strongly associated with complex habitat (Dai et al., 2020; Francini-Filho and de Moura, 2008; Moore et al., 2010) and have been linked to specific reef biotopes (Nagelkerken et al., 2000; Sulak et al., 2007). Incorporating these biotope classifications into species distribution models can help to explain variation across reef habitats, as the change in biological habitat can increase or decrease habitat complexity, especially the diverse assemblages associated with mesophotic reefs. These relationships can also be used to assess how well the Victorian MPAs capture the habitats that support the greatest diversity and abundance of fishes. Overall, reef habitat is clearly important to fish richness and abundance, as higher richness and abundance are found in more complex reef habitats. Victorian MPAs capture large areas of reef habitat, in many cases an overrepresentation, and thus contain attributes that support higher fish species richness.

Due to higher costs and technological limitations, mesophotic reefs habitats are among the least surveyed in the marine coastal environment (Hollarsmith et al., 2020; Kahng et al.,

2010). Recent studies have demonstrated that mesophotic reefs can support a high biodiversity of marine fish due to having unique habitats such as rhodolith beds, soft corals, sponges and mesophotic algal communities (Hollarsmith et al., 2020). Fish species richness of mesophotic reefs can be comparable to that of the photic zone for fishery-targeted species (Williams et al., 2019). Our study supports these findings: the top 8 of the 24 classes by species richness came from circalittoral reef. Victorian MPAs tend to capture a good representation of both circalittoral reefs (see Part 1) and infralittoral reefs, and so protect important attributes for supporting high fish species richness.

Our highest-ranking BC4 class by mean species richness, *Centrostephanus* grazed barrens, has a complex substrate consisting of boulder fields that support crustose coralline algae and low turfs with scattered sponges (mesophotic reef). The *Centrostephanus* grazed barrens biotope complex is found in Victoria's eastern most biounit, Gabo-Howe, which is influenced by the East Australian Current (EAC). Temperate reef habitats influenced by the EAC typically support more fish species than others due to increased water temperatures and currents for transporting species (Church and Craig, 1998), which matches our findings. Schuster et al. (2021) identified Victoria's Cape Howe ecoregion as having a high sensitivity to urchin-driven tropicalisation – the temperate environment at Cape Howe could lead to areas for new colonisation of tropical fish species. The findings of Schuster et al. (2021) suggest that the high fish diversity supported by *Centrostephanus* grazed barrens may be a consequence of the habitat formed by urchin grazing, warmer ocean temperature and higher species transport from the EAC.

Although our study found that circalittoral reef supported the highest fish species richness, infralittoral reef classes still had relatively high values compared to sublittoral sediment. Of the infralittoral classes, we found that High energy *Durvillaea* communities supported the highest fish species richness. *Durvillaea* is a genus of brown algae, commonly referred to as bull kelp, whose complex canopies provide reef fish with a variety of habitats, resulting in high fish species richness (Cheminée et al., 2017; Pérez-Matus and Shima, 2010), and our findings support these studies. Of the 12 top classes for species richness, all are associated with complex seascape structure, which supports studies that demonstrated that higher fish species richness is related to substrate and habitat complexity (Dai et al., 2020; Francini-Filho and de Moura, 2008; Moore et al., 2010). These results could mean biotopes are acting as a proxy for habitat complexity and that they can be used to define relative importance for fish diversity, which is valuable when assessing the potential impact of coastal development and other marine functions.

Overall, our study shows that biotope complexes are important variables in predicting species richness, ranking higher than both depth and distance to reef. It demonstrates the importance of finer scale measurements of biotic habitat for effectively predicting species richness. Further studies on individual species and their relationship with biotopes as a predictor in species distribution models could provide greater understanding of these

relationships and enhance the predictive power of species distribution modelling approaches. Associating all these relationships with biotopes back to Part 1 can help to determine if MPAs represent these different biotopes associated with higher richness and abundance. Overall, these biotopes are well represented across Victorian MPAs, which is positive for the protection of the variety of fish species.

Depth ranked third for model variable importance in our study. Depending on the fish feeding group, different relationships between depth and species richness have been demonstrated. Herbivores tend to decrease with increasing depth (Logan et al., 2017), while both carnivore and invertivore numbers increase with increasing depth (Moore et al., 2010; Quimpo et al., 2019; Wines et al., 2020). These results indicate that MPAs that extend across greater depth ranges are likely to be more successful at protecting fish species. Therefore, it is likely that the marine national parks are more effective at protecting the fish diversity and abundance along the coast than are marine sanctuaries.

One limitation in this study is the sampling design of BRUVS, which were designed to sample at depths that diver surveys cannot. This, they have an average deployment depth of 33 m, which is below the infralittoral zone, resulting in fewer observations in shallow areas. Combining diver surveys and BRUVS could be one solution (Willis and Babcock, 2000). However, the relatively high cost of diver surveys means that BRUVS provide a more cost-effective method for monitoring fish assemblages (Langlois et al., 2010) and allow for greater spatial coverage needed for broadscale species distribution models.

Both depth and distance to reef are widely recognised as key variables for predicting fish species richness (Francini-Filho and de Moura, 2008; Moore et al., 2010; Quimpo et al., 2019; Sequeira et al., 2016). Studies have shown that distance to reef is an important predictor variable for defining fish assemblages. For example, Zavalas (2017) found that temperate reefs had a significant influence on fish assemblages in surrounding sediment habitats up to 75 m from the reef. Our study has similar results: predicted fish species richness decreases over sediment habitat as distance to reef increases (Harborne et al., 2012; Quimbayo et al., 2019; Schultz et al., 2012; Zavalas, 2017). Distance to reef ranked fourth in variable importance for our study, which observed the highest predicted species richness values over reefs. This was similar to a study conducted by Moore et al. (2011) who found that variable distance to reef ranked highest for explaining temperate fish assemblages. Additional studies have demonstrated that temperate fish assemblages (Schultz et al., 2012) and tropical fish assemblages (Olds et al., 2012) are better explained by distance to reef than by complexity measures such as rugosity.

## 12.2 Relative species abundances

Four species of fish were used to develop species-specific abundance distribution models across the mapped state waters of Victoria. First, *Chrysophrys auratus* is found across a wide range of habitats according to the predictive models developed in this study. This result is

expected as *C. auratus* is a mobile, higher order carnivore, which is often associated with a greater number of habitat types (Chapman and Kramer, 2000), and has a larger body size, indicating greater mobility (Kramer and Chapman, 1999). Previous studies have also shown the wide range of habitat associations of *C. auratus* (Wines et al., 2020). Despite a lack of strong associations with reef structure or depth range across this study area, *C. auratus* abundance tends to be higher in the central sections of the state and lower in both the far east and far west. It is unclear how much benefit this species, with a large home range and lower affinity for certain habitat types, receives from the MPAs.

Meuschenia freycineti is a commonly found species in the temperate regions of Australia and inhabits depths up to 145 metres, usually on reef habitat (Hutchins and Swainston, 1986). The predictive models developed in this study confirm these observations: higher abundances were found on reef habitats and there was little variation across the depth of the study area. Sea-surface temperature, both range and mean, were found to be the most important variables in this abundance model, signifying that temperature plays a large role in determining their distribution. Based on the relationships with these variables, it is clear that MPAs with wider depth ranges, in areas with warmer average temperatures and a greater temperature range, are likely to support higher abundances of *M. freycineti*.

Notolabrus tetricus is a common predator along the coast of Victoria that helps to shape the distribution and abundance of invertebrates (Shepherd and Clarkson, 2001). It has even been linked to the recruitment of abalone (Shepherd and Cannon, 1988). *N. tetricus* is also commercially targeted, so understanding its distribution can provide insights into the performance of MPAs. The distribution of *N. tetricus* observed with the BRUVS deployments and the subsequent predictions show that it is mostly found in close proximity to shallow reefs (Figure 11.8). This pattern is expected due to the species' dependence on reefassociated invertebrates as a food source (Shepherd and Cannon, 1988). The predictive map also shows that the relative abundance of *N. tetricus* is greatest in areas of reef near the coast and surrounding the offshore islands. The over-representation of reef habitat in the Victorian MPAs likely benefits this species.

*Pictilabrus laticlavius* is commonly found in shallow (3 to 40 m depth) coastal zones along southern Australia. It is often found in either macroalgal beds or sponge gardens, and it feeds on a range of invertebrates (Bray, 2020). *P. laticlavius* is also very site attached and has a small home range (Bray, 2020). The models from this study show that its distribution is as expected, having larger abundances on the shallow reefs. *P. laticlavius* is also more common in the western section of the state.

Overall, these species distribution models can help to understand how species are distributed across the coastal waters of Australia. They can also be used to determine how well MPAs are protecting areas where these species are present.

## 12.3 Management implications

By collating multiple BRUVS surveys across the state of Victoria, we were able to create a statewide species distribution model, predicting species richness and relative species abundances past sampled locations through the use of environmental variables (Harborne et al., 2012; Mellin et al., 2010; Moore et al., 2010; Sequeira et al., 2016). With predicted statewide coverage, we are able to assess the predicted species richness within 17 of Victoria's MPAs. We found that most MPAs have significantly higher predicted fish species richness values than their respective biounits. The Merri MS, 12 Apostles MNP and The Arches MS have significantly lower predicted species richness values, but these areas are designed to protect a variety of other species (e.g. algae and birds) under the comprehensive, adequate, and representative (CAR) principles. Lower predicted species richness values within these parks could also be explained by being located in shallow water, which has reduced BRUVS coverage (i.e. Merri MS), having unique geological features with high predicted species richness surrounded by large areas of sediment, thus lowering their mean predicted species richness (i.e. 12 Apostles MNP and The Arches MS). Our predicted species richness maps provide additional validation of MPA function in regard to conserving fish biodiversity and create an opportunity to predict high value areas that can be further explored or prioritised.

In addition to providing critical information for MPAs, our study provides data which could be important for marine spatial planning. Marine and coastal ecosystems play important roles, including protecting juvenile fish species, supporting commercial and recreational fishing, nutrient cycling and protecting the shoreline. Due to the effects of increasing water temperatures and anthropogenic pressures, providing reliable cost-effective tools for managing coastal ecosystems is crucial. Establishing baselines for species richness across broad spatial scales provides information that managing bodies can use to make informed decisions. Developing predictive methods provides cost-effective information on fish diversity over large spatial scales, resulting in quantitative and spatially explicit maps (Stamoulis and Delevaux, 2015). Spatial modelling over such a broad area gives both managers and ecologists tools to assess fish-habitat relationships and distributions. This data will help inform management strategies that focus on high ecological, commercial and/or recreational significance for fish species (Shucksmith and Kelly, 2014). Our study provides a cost-effective method of mapping Victoria's nearshore environment over a broad spatial scale in a way that is effective for informing management decisions. With an increasing need to assess and manage our marine ecosystems, cost-effective quantitative techniques for managing current MPAs and investigating new hotspots will be key for maintaining biodiversity and local fisheries into the future (Ferrari et al., 2018; Leathwick et al., 2008).

## Part 4 – Summary of MPA impacts and effectiveness

#### 13. Introduction

Marine ecosystems support substantial biodiversity that is under threat from many human activities, including increasing populations along the coast, fishing, other forms of resource extraction, destructive fishing activities, run-off from poor land use practices and pollution (Agardy, 2000; Lubchenco et al., 2003; Sloan, 2002). MPAs are a necessary tool to preserve the biodiversity and integrity of marine ecosystems by buffering them from these damaging activities (Sloan, 2002). The effectiveness of MPAs depends on their shape, size, number, location and connectedness (Carr et al., 2017), but the scale and openness of the ocean make it difficult to define appropriate boundaries (Sloan, 2002).

Due to the historical practice of protecting those areas that do not have the potential for economic development, many protected areas were designated without regard to the ecology of the species requiring protection (Fuller et al., 2010; Polasky et al., 2005), and there are few direct measures to determine the performance of protected areas (Craigie et al., 2010; Nagendra, 2008). Therefore, there is a need to evaluate the current protected areas to determine whether they are capable of achieving management goals, including long-term biodiversity targets (Craigie et al., 2010). Very few large-scale quantitative studies to date have evaluated the effectiveness of protected areas, either terrestrial or marine, across the world (Nagendra, 2008). Although the goal of the International Union for Conservation of Nature (IUCN) to protect 10 of the world's surface has been surpassed, simple land surface percentages are not a good proxy for the amount of biodiversity under protection (Rodrigues et al., 2004; Soutullo et al., 2007). Rodrigues et al. (2004) looked at the international distribution of protected areas to determine the extent to which protected are coverage was adequate. They found that simply measuring the percentages of area covered was inadequate and produces gaps in biodiversity protection. Similar analyses focusing on marine protected areas have more recently been completed, but the science still lags behind that of terrestrial protected areas.

In a review of global 87 global MPAs, Edgar et al. (2014) found that 5 key features help determine the efficacy of marine protected areas. These include whether the MPA is notake, how well enforced regulations on activities in the MPAs are, the age of the MPA, the size of the MPA and how isolated the MPA is. Their findings showed that no-take MPAs, MPAs whose regulations are well enforced, older MPAs (>10 years), larger MPAs (>100 km²), and more isolated MPAs are seeing larger conservation gains within their boundaries. Other studies have also found that characteristics such as the connectiveness of MPAs across networks are also important for their success (Carr et al., 2017).

Size of MPAs is one of the basic parameters to be considered when designing a protected area; it is predicted to have an effect on how well the MPA works at preserving or increasing biodiversity (Botsford et al., 2003; Hastings and Botsford, 2003; Roberts et al., 2003). Although some studies have found that larger MPAs are not always more effective (Côté et al., 2001; Halpern, 2003), more extensive studies across a greater number of MPAs has shown that larger sizes result in greater effectiveness at increasing diversity within their MPA boundaries (Claudet et al., 2008; Edgar et al., 2014).

The placement of MPAs within the surrounding landscape can have a significant difference on the effect they have on the populations under their protection. Many species have affinities for certain habitat types, and their willingness or ability to leave that habitat patch depends on the surrounding habitat and the behaviour of the organism under study (Stamps et al., 1987). The permeability of the edge of a habitat patch can either be 'hard', where species tend to not disperse across that edge, or 'soft', where there are no barriers to dispersal (Stamps et al., 1987). Reserve boundaries introduce a new 'edge' to the landscape where the species on one side of that boundary are protected from exploitation while those on the other side are not. If the reserve boundary lines up with the natural habitat edges, the reserve is more likely to retain species; however, if the reserve boundary intersects contiguous habitat, it is believed that species will spill over to areas outside the reserve (Bartholomew et al., 2008). Depending on the goals of the reserve, one of these situations may be more desirable. For example, if the goal of the reserve is to increase the population within its boundaries and serve as a sanctuary for those species, a reserve with boundaries that encompass the 'hard' edges of the habitat may help with reaching that goal better. On the other hand, if the main goal of the reserve is to increase the population both inside and outside the reserve, implementing a boundary through the middle of a habitat patch may help to enhance spill over. Bartholomew et al. (2008) found that, for a given area of reef habitat in a reserve (HA), the rate of density change reduced as the proportion of reserve boundary that intersects reef habitat (HI) increased. That study supported the idea that reserves whose boundaries follow natural habitat boundaries may have higher recovery rates than reserves whose boundaries intersect contiguous coral reef habitat. In this study, we used the HI/HA ratio as a measure of the isolation of an MPA in the landscape; a lower HI/HA ratio signified a more isolated MPA.

In this study, we look at different characteristics of the Victorian MPAs and how species diversity is changing through time in relation to those characteristics. The characteristics we measure include distance from human impacts, MPA area, reef habitat area within each MPA, isolation of MPAs and connectedness of MPAs. We will then analyse changes in species richness inside and outside the MPAs while accounting for the varying characteristics. These analyses will give us an overview of which characteristics are correlated with positive trends in biodiversity.

### 14. Methods

### 14.1 MPA size

To determine the size of the Victorian MPAs, we calculated the area of each MPA by using the 'Calculate Geometry' tool within the attribute table for the MPA shapefile. This provided the total area in kilometres squared for each MPA.

#### 14.2 Reef area

All sampling programs that had been done to assess biology along the Victorian coast had focused on species found on rocky reefs. Therefore, we wanted to determine how the total area of reef within each MPA affected the fish and invertebrate species richness. To calculate total area of reef within each MPA, we tabulated the area from the substrate classification in ArcGIS (ESRI, 2011).

## 14.3 Human impacts

Two variables were used to measure human impacts on MPAs: population of coast adjacent to the marine protected area and the distance of the marine protected area from a boat access point, including harbours and boat launch. The population data were obtained from the Australian Bureau of Statistics dataset, and we calculated total population within each catchment zone. A harbour and boat launch shapefile was obtained from the data.vic.gov.au website and used to calculate Euclidean distance rasters. These 2 datasets were then summarised within each MPA to provide the population in the catchment adjacent to the MPA and the average distance from a boat access point across the MPA.

## 14.4 Connectivity

To determine the relative connectivity of each MPA across Victoria, we calculated the average number of connections coming into each MPA (in-degree – see methods in Part 1). Higher in-degree values indicate more-connected MPAs than MPAs with lower values of indegree.

# 14.5 MPA isolation/boundary permeability

We used the methods of Bartholomew et al. (2008) to calculate the ratio between the proportion of the reserve boundary that intersects reef habitat (HI) and the total area of reef habitat within the reserve (HA). The ratio (HI/HA) provides a measure of the isolation of an MPA in the landscape; lower HI/HA ratios signify more isolated MPAs. Reef habitat was used in this measure due to the higher diversity of species associated with reef habitats.

## 14.6 Statistical analyses

To determine which MPA characteristics were correlated with changes in fish and invertebrate species richness, we ran generalised additive models (GAMs). The fish and

invertebrate richness data are the same data used in Part 2 and includes a combination of diver survey data. GAMs were selected for use in this study because of their ability to allow for nonlinear relationships (Austin, 1998; Yee and Mitchell, 1991), as well as their being a conventional and well-developed method for modelling fish-habitat relationships (Galaiduk et al., 2017b; Valavanis et al., 2008). Before running GAMs, spatial dependence (spatial autocorrelation) of the response variables was tested using a spline correlogram generated in the R package 'ncf' (Bjørnstad, 2009). Cleveland dotplots were used to test for outliers resulting in the square root transformation of both MPA area and reef area inside the MPAs. The R package 'mgcv' (Wood, 2015) was then used to run GAMs, using species richness for fish and invertebrates (in separate models). All MPA characteristics were included as explanatory variables in the models for fish species richness and invertebrate species richness. Model selection was conducted using the 'MuMIn' package in R (Barton, 2018), in which all models were ranked based on a number of model parameters including loglikelihood, AICc, ΔIC and Akaike weights. We randomly selected 75 of richness records (n = 154 (fish), n = 154 (inverts)) and deployed them for training the models, reserving the remaining 25 (n = 52 (fish), n = 52 (inverts)) for testing the accuracy of predictions. Pearson's correlations were used to assess the accuracy of the predicted data compared with observed data.

### 15. Results

#### 15.1 MPA size

Marine national parks are much larger than marine sanctuaries across the state. Overall, MPA size varies greatly: the smallest MPA (the Marengo Reefs MS) only occupies 0.13 km<sup>2</sup> of the coastal zone, and the largest, Wilsons Promontory MNP, extends over 154.03 km<sup>2</sup> (Figure 15.1, Table 15.1).

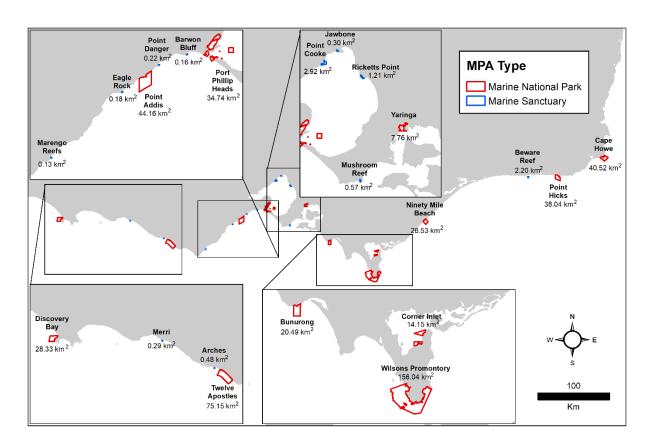


Figure 15.1: Location and size of Victorian marine protected areas. Marine national parks are outlined in red and marine sanctuaries outlined in blue

Table 15.1: Marine protected areas and their respective sizes, from smallest to largest

Marine protected area	Size (km²)
Marengo Reefs MS	0.13
Barwon Bluff MS	0.16
Eagle Rock MS	0.18
Point Danger MS	0.22
Merri MS	0.29
Jawbone MS	0.30
Arches MS	0.48
Mushroom Reef MS	0.57
Ricketts Point MS	1.21
Beware Reef MS	2.20
Point Cooke MS	2.92
Yaringa MNP	7.76
Corner Inlet MNP	14.15
Bunurong MNP	20.49
Ninety Mile Beach MNP	26.53
Discovery Bay MNP	28.33
Port Phillip Heads MNP	34.74
Point Hicks MNP	38.04
Cape Howe MNP	40.52
Point Addis MNP	44.16
Twelve Apostles MNP	75.15
Wilsons Promontory MNP	156.04

## 15.2 Reef area

MPAs varied from those with no reef (Corner Inlet MNP and Ninety Mile Beach MNP) to those with over 20 km<sup>2</sup> of reef (Twelve Apostles MNP and Point Addis MNP) (Table 15.2).

Table 15.2: Area of reef within each marine protected area, from smallest to largest

Marine protected area	Reef area (km²)
Corner Inlet MNP	0.000
Ninety Mile Beach MNP	0.000
Marengo Reefs MS	0.053
Jawbone MS	0.068
Point Danger MS	0.069
The Arches MS	0.071
Barwon Bluff MS	0.076
Eagle Rock MS	0.086
Merri MS	0.179
Point Cooke MS	0.196
Beware Reef MS	0.299
Mushroom Reef MS	0.348
Ricketts Point MS	0.756
Point Hicks MNP	1.663
Port Phillip Heads MNP	4.212
Cape Howe MNP	5.615
Bunurong MNP	7.016
Discovery Bay MNP	16.120
Wilsons Promontory MNP	18.142
Twelve Apostles MNP	20.383
Point Addis MNP	20.981

## 15.3 Human impacts

Human impacts on Victorian MPAs were calculated using population and distance to nearest harbour or boat launch as proxies. The MPAs most impacted by humans are in Port Phillip Bay where there is the largest population (over 1 million in the catchment region) and close proximity to multiple harbours and boat launches within the Bay. On the other hand, MPAs with the least impact are those in the eastern portion of the state where populations within the catchments are lower and the distance to the nearest harbour is larger (Figure 15.2).

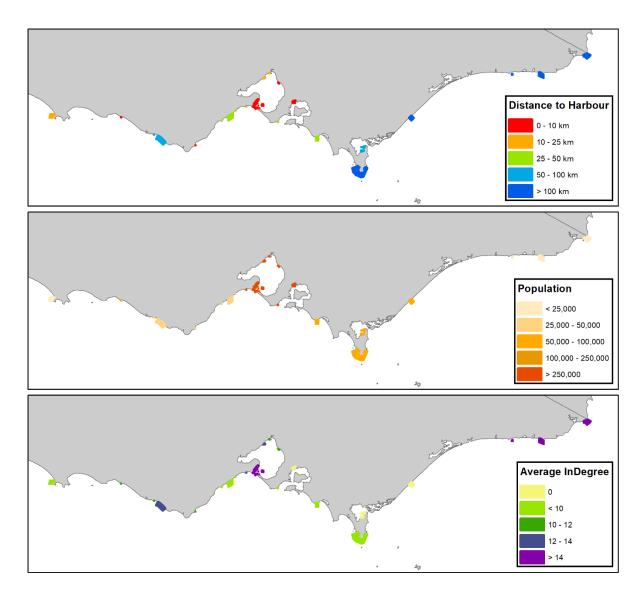


Figure 15.2: Marine protected area characteristics including distance to nearest harbour, population of adjacent catchment region, and average connectivity using a measure of in-degree, which is a measure of the total significant connections coming into an marine protected area

# 15.4 Connectivity

Using in-degree as a measure of connectivity, we calculated the average in-degree for each MPA. MPAs vary in the average number of connections coming into them (in-degree) but there is a general pattern of higher average in-degree as you move east along the coastline (Figure 15.2). The highest connectivity values are found in Port Phillip Heads and in the MPAs in the far east of the state (Point Hicks MNP, Cape Howe MNP and Beware Reef MS).

# 15.5 MPA boundary permeability

Using the ratio between boundary length intersecting reef habitat (HI) and reef area within each MPA (HA), we calculated the isolation of the Victorian MPAs. MPAs with no reef area

within them (Corner Inlet MNP and Ninety Mile Beach MNP) had ratios of 0.000. For the remaining MPAs that contained some amount of reef habitat, the ratio ranged from 0.576 in the Beware Reef MS to 26.667 in the Point Danger MS (Table 15.3). Figure 15.3 shows the variation in HI/HA ratio across 4 Victorian MPAs. The marine sanctuaries with large areas of rock intersecting their boundaries (Ricketts Point MS and Merri MS) have the highest ratios, while the larger marine national parks require a lot more reef intersection along their boundaries to increase the HI/HA ratios. Wilsons Promontory MNP has very little boundary overlap with reef while the Point Addis MNP boundary intersects reef but not enough to compensate for the large area of reef within its boundaries (Figure 15.3).

Table 15.3: Marine protected area isolation based on the ratio between boundary length intersecting reef and reef area within marine protected area. The marine protected areas are ordered by their level of isolation with the most isolated at the top

	Boundary length intersecting			
Marine protected area	reef (km) - HI	Reef area (km²) - HA	HI/HA	
Beware Reef MS	0.172	0.299	0.576	
Point Addis MNP	12.597	20.981	0.600	
Wilsons Promontory MNP	11.208	18.142	0.618	
Point Hicks MNP	1.248	1.663	0.750	
Cape Howe MNP	5.049	5.615	0.899	
Discovery Bay MNP	16.607	16.120	1.030	
Bunurong MNP	7.605	7.016	1.084	
Twelve Apostles MNP	25.112	20.383	1.232	
Point Cooke MS	0.946	0.196	4.833	
Port Phillip Heads MNP	31.143	4.212	7.394	
Ricketts Point MS	6.117	0.756	8.088	
Mushroom Reef MS	3.133	0.348	8.999	
Marengo Reefs MS	0.758	0.053	14.271	
The Arches MS	1.065	0.071	14.948	
Eagle Rock MS	1.632	0.086	18.923	
Merri MS	3.595	0.179	20.044	
Jawbone MS	1.392	0.068	20.438	
Barwon Bluff MS	1.604	0.076	21.038	
Point Danger MS	1.850	0.069	26.667	

Note: Corner Inlet MNP and Ninety Mile Beach MNP were removed from this table due to their lack of reef

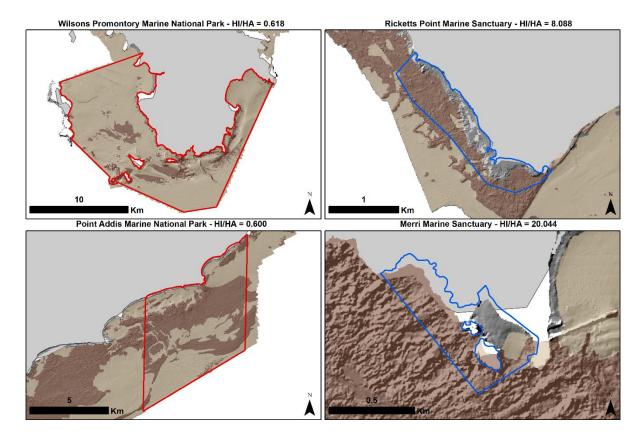


Figure 15.3: Examples of the ratio of boundary length intersecting reef (HI) and reef area (HA) for 4 marine protected areas. Wilsons Promontory MNP and Point Addis MNP have much lower boundary ratios than Ricketts Point MS and Merri MS, where large portions of reef intersect the boundaries

## 15.6 Statistical analyses

Results from the GAMs showed that multiple characteristics were correlated with fish richness, including year as a random effect, inside or outside an MPA, MPA area, reef area, average in-degree, population and distance to harbour. The comparison between inside and outside the MPAs showed that fish species richness is greater inside the MPAs (Figure 15.4). There was a negative relationship between fish species richness and the population level of the catchment: MPAs adjacent to larger populations had the lowest species richness (Figure 15.4). The relationship between fish species richness and the continuous variables in the model showed varying trends, but there was a general positive relationship between richness and reef area, connectivity (average in-degree) and area of the MPA. Higher richness was found in MPAs with more reef, higher connectivity and larger areas under protection (Figure 15.5). The relationship with distance to harbour is parabolic, showing increasing richness up to around 100 km from harbour followed by a continuous slight increase as distance to harbour became greater. Overall, the GAM performed well, explaining 73.1 of deviance and having a predictive accuracy of 72.9 (Table 15.4).

Table 15.4: Results from the GAMs comparing variations in fish and invertebrate species richness to marine protected area characteristics. 'Plus' signs indicate a significant correlation

	Year	MPA status	MPA area	Reef area	In- degree	Popul- ation	Distance to harbour	Deviance explained (%)	Test data correlation
Fish richness	+	+	+	+	+	+	+	73.1	0.729
Invert richness	+	+	+	+				26.8	0.540

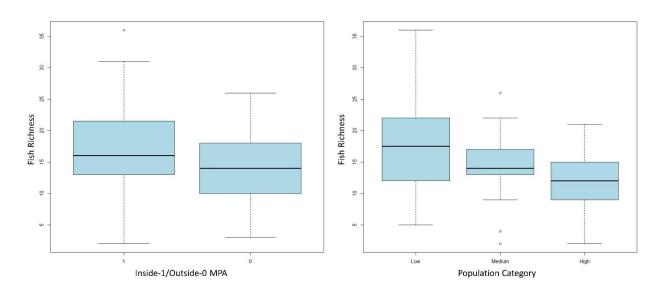


Figure 15.4: Fish species richness inside and outside marine protected areas and across adjacent population categories

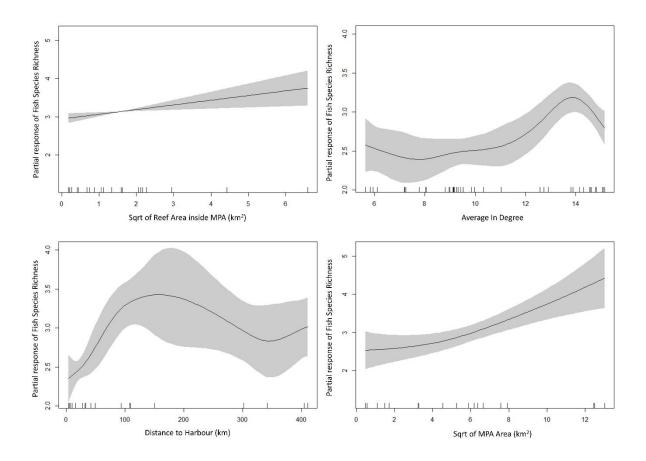


Figure 15.5: Partial effect plots from the GAMs (generalised additive models) showing the effects of reef area, average connectivity (in-degree), distance to harbour and marine protected area on fish species richness. Grey shading shows the standard errors (95 confidence interval)

The GAM associating invertebrate richness with MPA characteristics did not perform as well as the fish richness GAM. Only 4 variables, including year as a random effect, were significant, and the resultant model explained 27 of the deviance and had a predictive accuracy of 54 (Table 15.4). The model shows that there is slightly higher invertebrate species richness inside the MPAs than outside, but there is a lot of variability in richness across the MPAs (Figure 15.6). The 2 continuous variables found significant in the invertebrate richness GAM were reef area and MPA area. The relationship with reef area showed an initial increase in richness as reef area increased followed by a decrease with the opposite pattern with MPA size (Figure 15.7).

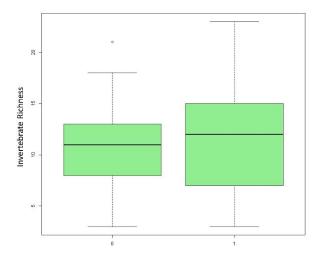


Figure 15.6: Invertebrate species richness outside (0) and inside (1) marine protected areas

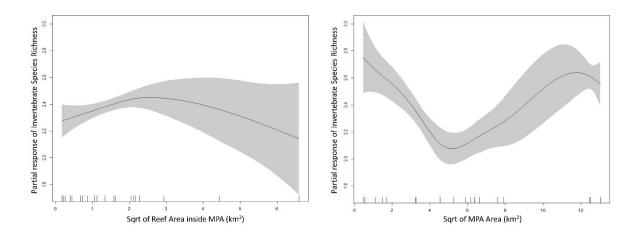


Figure 15.7: Partial effect plots from the generalised linear models showing the effects of reef and marine protected area on invertebrate species richness. Grey shading shows the standard errors (95 confidence interval)

### 16. Discussion

Several factors can influence the success of marine protected areas (MPAs), including the characteristics of the MPAs, habitat availability and anthropogenic influences. In this study, we looked at how the characteristics of the MPAs (size, reef area and human impacts) influence the biodiversity within them. We found that protection status, reef area and size of MPA all influence both fish and invertebrate species richness, and population and distance to harbour also affect fish species richness. Both fish and invertebrate diversity were greater within the MPAs than in the reference areas sampled outside them. This result is promising as it shows that the MPAs are affording protection that is allowing a greater

diversity of species to persist. The importance of reef area in both models, and the greater reef areas within MPAs compared to their adjacent biounits, potentially helps to explain this pattern as MPAs are providing more suitable habitat than is provided outside the MPAs. Also, the protection provided by the MPAs also allows more species to live undisturbed from extractive human activities, such as fishing. These results are consistent with other studies that have looked at the effect of protection on species richness and diversity (Claudet et al., 2008, 2006; Edgar and Barrett, 1999; Edgar et al., 2014; Rees et al., 2014; Young and Carr, 2015).

Size of MPA was one of the main contributing factors that positively influences the fish and invertebrate richness inside MPAs. This pattern is relatively linear; greater reserve size resulted in greater richness without reaching a peak for fish. Invertebrate richness has a more complicated relationship with size. High richness is found in both small and large areas of protection. This could be a result of the habitat protected in both marine sanctuaries and national parks. Even though they are smaller, marine sanctuaries tend to protect more reef habitat than sediment, possibly resulting in a higher richness of invertebrates. The pattern of higher diversity being found in larger MPAs is consistent with other studies that show larger reserves have a positive influence on recovery of biodiversity (Claudet et al., 2008; Edgar and Barrett, 1999; Edgar et al., 2014). The impact of reserve size could be an effect of greater surface area for species to inhabit and recruit to. Additionally, the larger reserves along the Victorian coast tend to expand across a greater depth range, resulting in greater variations in species' niches. Larger reserves have also been shown to increase fish diversity due to encompassing a greater area of fish home ranges (Chapman and Kramer, 2000; Claudet et al., 2008).

Reef area inside MPAs also had an effect on fish and invertebrate richness. Because the sampling used in this study all occurred over reef habitat, and thus focused on reefassociated species, it is not surprising that the area of reef within the MPAs had a strong, positive effect on the richness of both fish and invertebrates. More reef area provides more suitable habitat for species to occupy. However, the models did show that invertebrate richness decreases after a certain point of increasing reef area. Previous studies have found that larger areas of reef are often associated with greater biodiversity, as reef tends to provide a greater number of surface area for habitat and higher productivity (Rees et al., 2014).

Connectivity was also found to be important in the fish richness model: richness generally increased with a greater number of connections to local habitat sources (measured as indegree). More incoming connections to an MPA provide greater opportunities for recruitment events, resulting in higher species richness. This pattern is expected as it is well known that MPAs with high connectivity have greater resilience (Carr et al., 2017; Feist and Levin, 2016)

In this study, we used 2 measures of human influence to determine how variations in human impacts affect species richness: human population in the catchment adjacent to MPAs and distance of the MPA from harbours (to determine how accessible the MPA is). Although not important in the invertebrate richness GAM, fish richness does appear to be negatively affected by both. Human populations along the coastlines can have many negative influences on the marine environment, including inputs of pollution (Hwang et al., 2009; Van Dolah et al., 2008), increased sedimentation (Syvitski et al., 2009), increased eutrophication (Costanzo et al., 2001; Rabalais et al., 2010) and shoreline alteration (Morley et al., 2012).

Overall, these analyses show that it is important to take into account multiple factors when assessing biological change within MPAs. As shown by previous studies, the size and placement of an MPA within the seascape can have a large effect on its effectiveness (Edgar et al., 2014). The results from this study also affirm for Victoria what has been found in global studies, including that MPAs have higher richness within them than outside (they are affording species protection and thus increasing biodiversity) and that large, isolated MPAs with better connectivity contain higher species richness (also affording better protection of biodiversity). Therefore, the marine national parks are better at protecting more diverse assemblages than are the marine sanctuaries in Victoria. Although the Victorian MPAs show promise at effectively protecting biodiversity, ongoing monitoring is required to assess how assemblages may vary through time, including under future impacts of climate change.

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