

# Patterns of interaction between habitat and oceanographic variables affecting the connectivity and productivity of invertebrate fisheries

Ierodiaconou D<sup>1a</sup>, Young M<sup>1a</sup>, Miller AD<sup>1a</sup>, Treml E<sup>1b</sup>, Swearer S<sup>2</sup>, Sherman C<sup>1b</sup>, Murphy NP<sup>3</sup>, Strugnell J<sup>4</sup>, Gorfine, HG<sup>5</sup>

<sup>1</sup> School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Warrnambool<sup>a</sup> and Waurn Ponds<sup>b</sup> Campuses, Victoria, Australia

<sup>2</sup> School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia

<sup>3</sup> Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, Victoria, Australia

<sup>4</sup> Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Townsville, Queensland, Australia

<sup>5</sup> Victorian Fisheries Authority, Queenscliff, Victoria, Australia

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Researcher Contact Details	FRDC Contact Details	
Name: Daniel lerodiaconou	Address:	25 Geils Court
Address: 423 Princes Hwy,		Deakin ACT 2600
/arrnambool, Victoria, 3280	Phone:	02 6285 0400
Phone: 03 556333224	Fax:	02 6285 0499
Email: iero@deakin.edu.au	Email: Web:	frdc@frdc.com.au
		www.frdc.com.au

In submitting this report, the researcher has agreed to FRDC publishing this material in its edited form.

# 1 Foreword

A better understanding of the links between benthic habitat, oceanography, and fisheries productivity is a major priority of the abalone and rock lobster industries in order to improve the management of these important natural resources that sustain their fisheries. Identifying the drivers of fisheries productivity depends on knowledge of the factors influencing dispersal, settlement, survivorship and growth in early life, in particular the biophysical interactions between benthic habitats, animal behaviour, and oceanography.

Recruitment and persistence of stocks, and the potential impacts of fishing are often species-specific and dependent on spatial context, yet our understanding of the biotic and abiotic factors influencing recruitment processes is limited for many fisheries and largely based on generic models. This study improves our understanding of the importance of relationships between benthic habitat, oceanography, and biology and their independent and interactive impacts on larval dispersal, settlement and productivity in the Victorian Blacklip Abalone, *Haliotis rubra*, and Southern Rock Lobster (SRL), *Jasus edwardsii*, fisheries.

By using recent advances in geospatial, oceanographic and ecological modelling, and habitat and genomic population assessments, we have incorporated local variation into models of recruitment and persistence in Victoria for abalone and rock lobster fisheries. In so doing, we have improved the resolution and temporal availability of modelled hydrodynamic data for the Victorian coast. This in turn has informed biophysical models capable of modelling patterns of larval dispersal and stock connectivity that have a significant relationship with measures of biomass. Combined with high resolution seafloor structure data, oceanographic variables and fishery independent biomass data, we have for the first time provided spatially explicit models of abalone biomass along the Victorian coast allowing the assessment of spatial trends over a 21-year period and the identification of the relative importance of variables driving patterns in biomass observations. These data coupled with high-resolution bathymetry maps have also allowed us to contrast the genomic profiles of abalone from a range of habitat types to test for signatures of genomic adaptation, and to determine the spatial scales at which selection processes are likely to be influencing recruitment patterns. Results from these analyses have implications for understanding additional drivers of stock productivity, and for general stock management including future enhancement activities.

Population dynamics, habitat availability, complexity, and physiography determining dispersal, settlement, survivorship and growth need to be considered in order to understand the primary drivers of productivity on local geographical scales, the resilience of fishing stocks to fishing pressure, and threats associated with environmental change. Importantly, and pertinent to species such as SRL with prolonged planktonic larval phases, understanding these dynamics on broad spatial and temporal scales has assisted in determining the dependency of Victorian fisheries on interstate sources of recruitment and how Victorian populations contribute to the overall structure across the species range.

A new harvest strategy is currently being devised for the Victorian abalone fishery with Industry associations in the Central and Western Zones of the fishery pursuing biomass based approaches dependent on acquisition of spatially resolved catch, effort, area swept, and catch structure data. Although both groups have invested in electronic equipment for this purpose, the Western Zone is more advanced in terms of years of data and, with only five divers, has been able to implement a consistent approach covering much of the contemporary fishing grounds. The resulting biomass estimates have been used as a basis for determining abalone quota allocations in the Western Zone, although divers' qualitative observations also play a major role in decisions about catch quotas. This study shows spatial and temporal variability in modelled abalone biomass across Victoria's reef to extents previously not possible. In the absence of spatially explicit catch data across the Victorian fishery we used the fishery independent abalone survey sites to model biomass and gain an understanding of environmental drivers to the patterns observed. It was assumed that patterns observed at the fishery independent survey sites over time reflected the distribution of biomass across the fishery. FRDC 2011-033 (Jerodiaconou et al. 2011a) identified the benefits of having spatially explicit catch information to inform patterns in fishing over time. Whilst this was limited to a subregion of the fishery and structured fishing, expanding spatially explicit data capture would provide new opportunities in understanding patterns of change in spatial allocation of fishing effort and the productivity of the resource. We have shown the benefits of spatially explicit commercial fishing effort data (i.e., AbTrack, (Mundy 2012)) in the Western Zone of the fishery for evaluating patterns in fishing effort (Jalali et al. 2015a). The availability of these data across the resource would be beneficial for understanding harvesting behaviour and accurate assessment of whether serial depletion is occurring in the fishery. However, the greatest gains would be made if the total catch and fishing effort were provided in a spatially explicit way. Vessel VMS technologies fitted to the

abalone fleet would likely provide this type of information. Similarly, understanding patterns of change in spatial allocation of fishing effort for the SRL fishery would assist in resource management. Similar approaches to abalone biomass modelling combining high resolution seafloor structure data, oceanographic variables and SRL fishery independent survey data has the potential to provide spatially explicit models of SRL biomass along the Victorian coast.

This study provides a better understanding of the importance and relationship between benthic habitat, oceanography, and biology and their independent and interactive effects on larval dispersal, settlement and productivity in the Victorian Blacklip Abalone and SRL fisheries. This research has made several important findings that will improve the current management of the Blacklip Abalone and SRL fishery.

- This study provides industry with substantial benefits relating to the assessments of stock viability and implementation of management strategies that optimise sustainable yield primarily through the identification of biomass distribution, important source reefs, dominant dispersal pathways, and the role of genomic selection on recruitment processes.
- 2. This study improves our understanding of how abalone and SRL relate to their environment (e.g., influence of oceanographic, seabed structure, and biological factors), and the biotic and abiotic factors in Victorian coastal waters influencing fisheries productivity for abalone and SRL.

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## **3 Executive Summary**

A better understanding of the links between benthic habitat, oceanography, and fisheries productivity is a major priority of the Blacklip Abalone, *Haliotis rubra*, and Southern Rock Lobster, *Jasus edwardsii*, industries to improve sustainable management of these important natural resources. The persistence of fished stocks depends on factors influencing dispersal, settlement, survivorship and growth in early life. It is important that the geography and scales of these processes are identified to optimise management strategies.

This study brings together scientists from Australian Universities (Deakin University, The University of Melbourne, La Trobe University and James Cook University) across a range of disciplines (habitat mapping, landscape ecology, biophysical modelling and marine genomics) combined with industry experts in hydrodynamic modelling (Water Technology), fisheries managers (Victorian Fisheries Authority) and industry partners (Eastern Zone Abalone Industry Association (EZAIA), Abalone Victoria Central Zone (AVCZ), Western Zone Abalone Industry Association (WADA)) to improve our understanding of these dynamic fisheries. In particular, we quantify and map the influence of benthic habitat characteristics, oceanography, and biology on larval dispersal, settlement and productivity of Blacklip Abalone and Southern Rock Lobster for Victorian fisheries.

We have improved the spatial and temporal resolution of modelled coastal oceanography for the Victorian coast, and make available hindcast data to 1990. This in turn has informed biophysical models capable of modelling patterns of larval dispersal that have a significant relationship with measures of biomass observed. Combined with high resolution seafloor structure data, oceanographic variables and fishery independent biomass data for abalone, we have for the first time provided spatially explicit estimates of abalone biomass along the Victorian coast allowing the assessment of geographic trends over a 21–year period and identification of the important drivers. These data have also allowed us to test for genomic adaptation by contrasting the genomic profiles of abalone from different habitat types and across distinct environmental gradients. This enabled us to characterise the spatial scales that selection processes are influencing recruitment processes. Findings from this population genomic analysis provides further insights into the potential drivers of stock productivity, and have immediate implications for stock management and enhancement activities.

In addition, for Southern Rock Lobster, we also investigated local SRL populations in two Victorian marine parks and comparisons with fished adjacent waters with the goal of identifying the relative impact of marine parks on neighbouring fished stocks. Understanding the difference and variability in the demographics (e.g., size class structure, density, abundance) of these subpopulations and identifying the potential environmental drivers could have significant implications for improved management. Understanding these patterns relies on the continued compilation of geographic data on lobster populations in and around the marine parks of Victoria.

**Background:** Identifying the drivers of fisheries productivity depends on developing a better understanding of the factors determining dispersal, settlement, survivorship and growth in early life, in particular the biophysical interactions between benthic habitats, animal behaviour, and oceanography. Our understanding of most of these interactions is largely based on a generic understanding. However, the recruitment and persistence of stocks, and the potential impacts of fishing are often species-specific and dependent on spatial context. By using recent advances in geospatial, oceanographic and ecological modelling, and habitat and genomic assessment, we incorporate local variation into models of recruitment and persistence in Victorian abalone and rock lobster fisheries.

**Aims:** The management of Victorian invertebrate fisheries has been enhanced in recent years with the adoption of reef-scale assessment and management systems to achieve fisheries sustainability objectives. Although management efforts are geared towards sustainable harvesting through maintaining or rebuilding of stocks, effective management will be improved by an understanding of population connectivity and identifying the key environmental drivers influencing productivity. This will enable fisheries management strategies to be tailored, as far as practicable, to cater for spatial variation in population biology and associated fisheries productivity. In this study, we draw upon geospatial, biophysical modelling, and population genomic techniques to characterise key relationships between benthic habitat, oceanography, and biology and their effects on population connectivity and productivity in Victorian Blacklip Abalone (*Haliotis rubra*) and Southern Rock Lobster (SRL; *Jasus edwardsii*) fisheries.

**Methodology:** Local oceanography can drive distribution and productivity; however, these data are often unavailable at an appropriate spatial resolution. This study has developed a 500 m resolution coastal hydrodynamic model for Victorian waters with coverage for the past 25 years, which has allowed us to

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evaluate changes in oceanographic conditions. These temporally dynamic oceanographic conditions were then combined with high resolution seafloor structure data, sea surface temperature variability, and fishery independent biomass data to understand the spatially explicit and temporally dynamic relationships between biomass and associated environmental conditions. These models were then used to create temporally varying annual biomass prediction maps across the Victorian coast, allowing for the assessment of spatial trends over a 21-year period and identification of the relative importance of variables driving observed patterns in biomass. We used a similar approach at the local scale to investigate the influence of habitat on SRL populations including sampling within two Marine Protected Areas. These data also allow us to integrate seascape (habitat), oceanographic (waves, currents, temperature) and species-specific traits (e.g., larval behaviour, fecundity, adult abundance) into a study of larval dispersal, and capture decadal to intra-annual variability in larval dispersal for abalone and late-stage settlement of SRL puerulus larvae. We used dispersal simulations to quantify the level of larval connectivity and settlement through time across Victoria and surrounding seascapes for SRL and abalone.

Using our unique geospatial and oceanographic datasets we developed a replicated hierarchical sampling design for abalone reefs, sampling 30 reefs and 750 individual abalone, enabling us to contrast the genomic profiles of abalone stocks distributed across different habitat types and defined environmental gradients.

Specifically, the outputs of the project are:

- The first state-wide high-resolution assessment of the extent of abalone grounds derived from integrating fishery independent data with seafloor mapping, oceanographic parameters and measures of population connectivity to inform estimates of abalone biomass and trends through time;
- The characterisation of population connectivity among reef patches across the entire Victorian coastline with maps of the dispersal pathways, important stepping-stones, and source populations for abalone and SRL;
- An improved understanding of the relationships between seafloor structure information and fisheries productivity across all Victorian abalone fisheries and pilot locations for SRL in two Marine Park sites and adjacent waters;
- The development of the highest resolution hydrodynamic models available for Victorian coastal waters for biophysical modelling of abalone and SRL larval dispersal and settlement;

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- 5) Knowledge of spatial scales at which genomic selection processes operate and influence recruitment processes across Victorian abalone fisheries;
- Knowledge about the recruitment potential of specific reefs and potential drivers of abalone and SRL larval mortality and establishment and identification of coastal priority reefs; and
- A seascape genomic framework for guiding abalone translocation activities in virus and urchin affected fisheries for abalone.

This study provides industry with substantial long-term benefits relating to assessments of stock viability and implementation of management strategies that optimise sustainable yield primarily through the identification of important larval source reefs, dominant dispersal pathways and the role of genomic selection on population recruitment processes. Improved understanding of relationships between stock productivity and environment is supported by a repository of high-resolution maps of coastal habitat overlaid with oceanographic and biological factors that influence population structure and fisheries productivity for abalone and SRL. All data and results from this study will be widely disseminated, made freely and publicly available, and promoted through technical and peer-reviewed publications.

Keywords: Fisheries productivity, stock connectivity, habitat characterisation, biophysical modelling, population genomics, Blacklip Abalone, Southern Rock Lobster

## **4** Introduction

Identifying key drivers of fisheries connectivity and productivity depends on available knowledge of factors determining dispersal, settlement, survivorship and growth. This requires an understanding of the biophysical interactions between habitats, animal behaviour, and oceanography, yet knowledge of these interactions is often limited and based on a generic understanding. Biophysical interactions that underpin the integrity of our fisheries are often species-specific and dependent on spatial context (Hinrichsen et al. 2011), meaning that empirical evidence is often needed for individual fisheries. This information is critical for spatial management in determining the shared responsibility between Government as the regulator and Industry as the leading stakeholder for the implementation of appropriately scaled management strategies. However, characterizing these biophysical interactions has been historically challenging due to logistical difficulties associated with working in marine environments, and a lack of comprehensive and appropriately scaled habitat and oceanographic datasets for the majority of coastal waters around the world. When this data is available there is often a spatio-temporal disconnect between the resolution of physical (oceanography/habitat) and biological data. For example we often have fine-scale biological data but this is often limited by sample size and not well resolved temporally. Whereas we often have temporally resolved physical data but not at spatial scales relevant to the biology.

Recent advances in geospatial science now provide new opportunities for assessing benthic habitat structure on local and regional scales, such as LiDAR and SONAR technologies that are being used increasingly for imaging seabeds around the world (Brown et al. 2011, Ierodiaconou et al. 2011b, Lecours et al. 2015, Young et al. 2016b). The resulting high-resolution geo-physical datasets from these technologies are being used to describe the heterogeneity of benthic habitats (spatial arrangement, structural characteristics and connectedness), to explore ecosystem dynamics at both fine and broad geographical scales (Jalali et al. 2015b), to guide spatial sampling for genetic studies and help identify habitat features that may influence patterns of genetic structure (Miller et al. 2016), and to identify physical habitat features associated with fishery productivity (Young et al. 2015a). Biophysical models of larval dispersal developed with these spatial and high-resolution hydrodynamic data have the capacity to predict local to regional-scale patterns in dispersal (Treml et al. 2012), provide opportunities to inform gene flow (Davies et al. 2015, Matz et al. 2018) and conservation strategies (Kahui and Alexander 2008).

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The purpose of this study is to make use of these unique datasets and expertise to improve our understanding of the importance and scale of relationships between benthic habitat, oceanography, and biology and their independent and interactive impacts on stock connectivity and productivity in Victorian Blacklip Abalone (*Haliotis rubra*) and Southern Rock Lobster (*Jasus edwardsii*) fisheries. Australia's Black Abalone fishery is the world's largest wild abalone fishery, extending from Western Australia to southern New South Wales and Tasmania, with a net value of US\$79 million (Mundy et al. 2014). The Victorian Black Abalone fishery is divided into three commercial fishing Zones (Western, Central and Eastern), two of which have suffered major declines in recent years due to disease (Abalone Viral Ganglioneuritis; Mayfield et al. 2011), and the third from range expansion of an urchin species (*Centrostephanus rodgersii*; Ling et al. 2009) generating barrens and reducing suitable abalone habitat.

Whilst the abalone stock management approach is geared towards sustainable harvesting, there are key gaps in information about abalone recruitment dynamics and stock connectivity to guide management directed toward the recovery of depleted stocks (i.e. stock augmentation). Current management of the Australian Blacklip Abalone assumes limited connectivity among metapopulations with stock viability dictated by recruitment from local sources (Shepherd and Brown 1993). These assumptions are based on early ecological studies suggesting larval dispersal is likely to be extremely limited for many abalone species (Prince et al. 1987, McShane et al. 1988, Prince et al. 1988). However, genetic studies of various *Haliotis* species from coastlines around the world have produced conflicting estimates of stock connectivity, suggesting that larval movement may depend on species and/or geography (Brown 1991, Chambers et al. 2006, Li et al. 2006, Gruenthal et al. 2007, Gutierrez-Gonzalez et al. 2007, Gruenthal and Burton 2008, Piggott et al. 2008, Bester-van der Merwe et al. 2010, Coates et al. 2014, Miller et al. 2014).

In Australia, genetic studies on Blacklip Abalone from Tasmania and Victoria have also produced inconsistent findings, with evidence of local genetic structuring in Tasmanian fisheries (Temby et al. 2007, Miller et al. 2009), and panmixia across Victorian fisheries (Miller et al. 2016). These studies indicate that larval movement and stock connectivity may vary between regions of the fishery. Abalone larvae undergo two metamorphic stages, and during this period have the potential to remain planktonic for between 7 and 15 days, depending on temperature and availability of suitable habitat (Hahn 1988, McShane 1992, Grubert and Ritar 2005), although the maximum period is uncertain. Settlement rates will depend on the availability of suitable benthic substrate, with a strong link between settlement and encrusting coralline algae that typifies abalone habitat, either beneath the kelp overstorey or in crevices (McShane and Smith 1991, McShane 1995, Gorfine 2002, Huggett et al. 2005). The hydrodynamics (including current intensity and direction, wave exposure), as well as the physical and biological benthic structure of the Southern Australian coastal waters is variable (Ierodiaconou et al. 2007, Sandery and Kaempf 2007, Ierodiaconou et al. 2011b, Cameron et al. 2014). Therefore, it is possible that patterns of larval dispersal and recruitment success will be spatially variable across Blacklip Abalone fisheries, as has been observed for other marine species, including molluscs (Morgan et al. 2000, Gilg and Hilbish 2003, Cowen et al. 2006).

There is a clear need to characterise the potential for larval exchange between, and thus the connectivity among, individual fishing stocks across different regions of the fishery. Understanding the extent by which individual stocks are dependent on larval supply from local and non-local sources will help explain patterns of variation in productivity, as well as stock resilience to fishing and environmental pressure. The ability for stocks to replenish naturally following local depletion events is also dependent upon patterns of connectivity. In Victoria, for instance, stocks are begging to show sign signs consistent with recovery via recruitment a decade after the disease in the western region of the fishery, whereas stocks further to the east are either depleting or have yet to recover from depletion (Mundy et al. 2015)). Development of new tools in biophysical modelling provides the means by which to estimate spatial and temporal patterns of larval movement on broad and local spatial scales, considering suitable habitat, especially relevant for species that have an affinity for certain seabed characteristics. A spatially-explicit biophysical modelling approach can be used to predict the dispersal potential between habitat patches distributed across a seascape, thereby revealing the location, strength, and structure of a species' potential population connectivity (Treml et al. 2008, Treml et al. 2012). In a marine context, biophysical models rely on geographic data describing the seascape environment and biological parameters capturing species-specific qualities.

While biophysical modelling provides valuable insights into the potential for larval movement and traditional population genetics can examine gene exchange across, within, and between stocks, these methods do now allow for potential influences of genetic adaptation and selection on recruitment dynamics. Adaptation and selection can "unlink" the contribution of larval dispersal to population recruitment, as not

all potential recruits will survive upon settlement. Although estimates of neutral genetic diversity in the study by Miller *et al.* (2016) indicate a lack of genetic structure at various hierarchical spatial scales across Victorian coastal waters, adaptive genetic diversity could be playing a significant role in abalone recruitment processes. Recent genomic studies of marine fish and molluscs, including Haliotids, have demonstrated that under strong selection pressures, adaptive variation can be maintained in marine environments despite high levels of gene flow (Galindo et al. 2009, Martinez-Fernandez et al. 2010, Hess et al. 2013, Solas et al. 2013, Milano et al. 2014, Sandoval-Castillo et al. 2015, Sandoval-Castillo et al. 2018). Consequently, patterns of abalone larval settlement and establishment, and stock productivity, could be influenced by underlying adaptive genetic variation, where recruitment at the reef scale is dependent on the settlement of environmentally compatible genotypes. Scanning genomes for Victorian abalone stocks across environmental gradients will determine whether adaptive variation contributes to the process of stock structure and success of larval recruitment.

Another recreationally, commercially, and traditionally important species throughout its range in Southern Australia and New Zealand is the Southern Rock Lobster (SRL), Jasus edwardsii (Booth 1997, Gardner et al. 2003). The rock lobster fishery is Victoria's most valuable, and makes up 42% of wild-caught marine fishery value (Mobsby and Koduah 2017). This fishery is managed mostly through effort controls by limiting numbers of licenses and pots and also through total allowable commercial catch, which has recently declined due to poor stock status (Punt et al. 2013). Although exploitation has been linked to declining stocks of J. edwardsii, environmental change, such as changes in ocean temperatures or currents, can affect larval size, growth rates (Bermudes and Ritar 2008), and recruitment (Ridgway 2007). With declining stocks of J. edwardsii, MPAs have the ability to maintain a residual biomass while biomass is reduced through fishing outside the protected areas. Previous studies on the effect of MPAs on J. edwardsii have shown variable responses to spatial protection (Freeman et al. 2012). Some studies showed increased size and density inside MPAs (Edgar and Barrett 1997, Kelly et al. 2000, Barrett et al. 2009), but other studies showed that unmanaged fishing effort displaced by closed areas can have negative effects on populations in locations left open to fishing (Gardner et al. 2003). Additionally, foraging ranges may impact the ability of a small MPA to protect populations if foraging ranges cross MPA boundaries. Jasus edwardsii also have an extensive larval stage (~2 years) prior to settling on shallow, rocky reefs (Morgan et al. 2013), with broad scale dispersal and

stock connectivity. This in turn suggests that small MPAs will have minimal effect on broad-scale population resilience.

To effectively manage important fishery stocks, accurate information on species-habitat relationships is imperative, especially when applying spatially explicit management strategies. Landscape ecology approaches such as combining broad scale environmental data with observation data allows scientists to determine how the spatial and temporal patterns throughout seascapes affect those processes that drive distribution and abundance of organisms (Turner 1989, Wiens 2008). In addition, the incorporation of temporally dynamic variables (e.g., oceanographic processes) can help to account for both human impacts and natural disturbances in population fluctuations and to identify areas where stocks are increasing, decreasing or resilient. This knowledge can then be used to refine fishery management strategies and establish or monitor protected areas by providing more accurate and comprehensive maps of productivity.

In this study we will explore physical and biological drivers of population connectivity and productivity across Victorian Blacklip Abalone and Southern Rock Lobster fisheries. Using recent advances in geospatial, oceanographic, ecological modelling, habitat mapping, and genomic methods, we will quantify the influence local-scale environmental variability has on the recruitment and persistence of Victorian fisheries. This information regarding stock/population performance should enable a better overall assessment of the sustainability of these fisheries. Knowledge gained from this project will provide industry with a framework for guiding future spatially resolved management decisions; including guidance for assessing the resilience or vulnerabilities of specific fishing stocks to overharvesting or environmental disturbance, and the potential for natural replenishment in the event of stock depletion.

# **5** Objectives

- 1 Integrate commercial catch and survey data with LiDAR-derived seafloor structure information to identify the spatial structure and patch-level temporal productivity of reef systems, potential abalone fishable habitat extent and map important source reefs of abalone larvae.
- 2 Development of a high-resolution hydrodynamic model for Victorian coastal waters that allows the modelling of larval dispersal between individual reef complexes throughout state waters.
- 3 Development of a biophysical larval dispersal model to map the probable dispersal pathways for Blacklip Abalone and Southern Rock Lobster across Victorian reef complexes.
- 4 Determine if abalone recruitment across the respective fisheries is influenced by adaptive genetic factors.

### 6 Method

The study area for the abalone component of the project includes the entire ~2000 km coast of Victoria, Australia extending from the border with South Australia to the border with New South Wales. Along this region, there is a mix of cliffs, bluffs, sand dunes, and embayment's that correlate with variations in seafloor topography. Additionally, the orientation of the coast to dominant swell directions and temperature gradients from east to west cause a variety of oceanographic conditions affecting the distributions of marine communities. The study area was expanded to include all of southern Australia and New Zealand to quantify the broad-scale dispersal patterns in Southern Rock Lobster.

### 6.1 Spatial Data

### 6.1.1 Collation of seafloor mapping data

All seafloor information has been collated for the entire state of Victoria including both LiDAR and multibeam bathymetry data with a coverage of approximately 7000 square kilometres. Multibeam data were acquired as part of the ongoing Victorian Marine Habitat Mapping Project (Ierodiaconou et al. 2007). To provide information on the nearshore coastal zone, the Department of Environment and Primary Industries of the Victorian State Government commissioned the collection of high resolution LiDAR data across the entire state. The LiDAR dataset extends from elevations of +10 m to ocean depths around -25 m (Quadros and Frisina 2010). The multibeam datasets were transformed from Lowest Astronomical Tide (LAT) to the Australian Height Datum (AHD) using the Auscoast VDT transformation tool (Keysers et al. 2015) to match the vertical datum of the LiDAR data. Once all data were registered to the same vertical datum, we merged these datasets together to provide complete coverage of existing data across the state at 5 m resolution.

From the resulting seafloor bathymetry merged product, we derived a number of characteristics of the seafloor structure including depth, slope, vector ruggedness measure (VRM), bathymetric position index (BPI; relative elevation) at multiple spatial scales, substrate type, and reef areas. These variables were derived at the 5 m resolution scale and then the Focal Statistics tool within ArcGIS Spatial Analyst was used to take the mean value of each variable at 30 m resolution to match the sampling resolution of Blacklip Abalone.

### 6.1.2 Abalone Biomass Sampling

Blacklip Abalone abundance data from fishery independent diver surveys conducted by Fisheries Victoria were collated from 1995-2015. These data provide annual counts and size measurements of Blacklip Abalone at each monitoring site (n = 195) from 1995-2015. From these count data, we computed total biomass per site using the allometric relationship:

$$W = a \times (L_s)^b$$

where W is weight in kilograms;  $L_s$  is maximum abalone shell length in centimetres; and *a* and *b* are regression constants with specified values of 0.000412 and 2.76, respectively (McShane et al. 1988).

Previous work (FRDC 2011-033) with these data have looked at the distribution of productive reefs (Jalali et al. 2015a) and the distribution of abalone density and biomass for pre-recruits, recruits and adults for south-west Victoria (Jalali et al. 2015b). These efforts have been expanded for the entire state with the inclusion of a temporal component using annual oceanography, connectivity, and biomass information.

### 6.1.3 Abalone Catch Datasets

Information on abalone catch within each fishing subzone from 2003 to 2015 was provided by the Victorian Fisheries Authority. We used these datasets to develop spatially explicit maps of total biomass removed through fishing. We normalised total biomass removed through fishing by the percentage of suitable abalone habitat (reef area, derived from bathymetry information) within each fishing zone in order to weight them based on available habitat within each zone. For those years prior to 2003, we used total catch information from each of the broad-scale fishing zones (Western, Central, and Eastern) and weighted them by suitable habitat using the same process for the subzones which are defined as Spatial Management Units (SMU) which refers to groups of reef codes managed at the same size limit.

### 6.1.4 Southern Rock Lobster Sampling

Southern Rock Lobster (SRL) fishery independent catch datasets were acquired to assess spatially explicit habitat use by SRL. We used standardised fishery assessment trapping methods to provide fine-scale SRL population information in two Victorian marine protected areas (MPAs): Merri Marine Sanctuary (MMS) and Wilsons Promontory Marine Park (WP). Lobster pots were baited with 1 kg of locally available bait and escape gaps were wired shut (Woods and Edmunds 2013). We conducted sampling in and adjacent to the

MMS in February 2013. A total of 40 spatially referenced pots were placed within the MMS over three nights (n=15, 15, 10) and 100 pots over two nights in areas adjacent to the MMS (n=50, 50; Figure 1). Sampling in WP occurred in February 2016 over three nights with 150 pots sampled within the bounds of the MPA and 75 pots sampled outside the MPA. The sampling design for WP resulted in 150 pots allowing for inside/outside MPA comparisons over three distinct areas with 25 pots inside the MPA and 25 pots outside the MPA: East (shallow), West (deep), and West (shallow) (Figure 2). The remaining data only provided information from inside the MPA with no comparable areas sampled outside and were not used in the inside/outside analyses. Across both areas, all SRL captured in the pots were counted and sexed, females were assessed for reproductive condition, and all lobsters were measured for carapace length (CL). To calculate SRL biomass, we used the length-weight relationship provided in Punt (2003) and used by Woods and Edmunds (2013):  $W = aCL^b$ , where W is the weight in kilograms, *CL* is carapace length and *a* and *b* are coefficients related to sex and size class (Females: a = 0.000271, b = 3.135; Males: a = 0.000285, b = 3.114).



Figure 1 Study site for the Merri Marine Sanctuary Southern Rock Lobster study off Warrnambool, Victoria in south eastern Australia. The light grey circles represent sample locations inside and outside the Merri Marine Sanctuary (outlined in black).



Figure 2 Study site for the Wilsons Promontory Southern Rock Lobster study in south eastern Australia. The light grey circles represent sample locations inside and outside the Wilsons Promontory MPA (outlined in black).

### 6.1.5 Oceanographic datasets SST

Processed sea surface temperature (SST) datasets were downloaded from the Integrated Marine Observing System (IMOS) as NetCDF format at monthly intervals and converted into individual ArcGIS rasters. Annual and seasonal (winter and summer) means in SST were computed from 1992 to 2015 for use in the geospatial models. Wave and current information (mean/max current speed, mean/max wave orbital velocities, mean/max significant wave height, mean/max wave power, current direction, wave direction) were delivered from the coupled hydrodynamic and wave model with details provided below and were converted into ArcGIS rasters for use in the geospatial models along with the SST (for details see hydrodynamic section below).

### 6.2 Hydrodynamic modelling

Oceanographic parameters are potential drivers of stock distribution and productivity; however, these data are not available at an appropriate resolution for fine (reef) scale studies. We have improved upon our existing hydrodynamic model of coastal Victoria by hindcasting the wave exposure and ocean current dynamics over the past 25 years allowing for the complex coastal flows to be accurately depicted. Downscaling of regional hydrodynamic models using high performance computing and model parametrisation.

Hydrodynamic data quantifying the nearshore and far-field ocean currents around Victoria and the regional seascape were obtained from two sources: 1) Water Technology for local-scale depth-averaged and high spatial-temporal resolution products, and 2) global HYCOM providing regional scale 3-dimensional and moderate resolution products for the Australia-New Zealand seascape. Water Technology coupled a hydrodynamic (HD) and spectral wave (SW) model using the industry standard hydrodynamic software package MIKE by DHI (Danish Hydraulics Institute) with input from the research team. The approach uses a variable resolution depth-averaged approach to quantify currents along the Victorian coastline, including tides, winds, bottom rugosity, and regional forcing. Water level boundaries were applied to simulate tides. No wave boundaries were applied to the model as the domain extends past the extents of the Victorian coast and south to a latitude of -45 degrees, thus allowing swell to develop far offshore as well as local sea near the coast. Wind and pressure data were provided through the NCEP-DOE Reanalysis 2 model run by the Earth System Research Laboratory (ESRL) at the National Oceanic and Atmospheric Administration (NOAA) in the USA. Astronomical tidal conditions were applied to the model boundaries from a global model developed by DHI. The source data for these tidal predictions are based on tidal constituents quantifying the diurnal, semidiurnal, and shallow-water tidal behaviours at a grid resolution of 7.5 minutes. The tidal boundaries applied to the model have a spatial variation step of 13 km and a time step of 1 hour. The model domain consists of a flexible mesh incorporating triangular and quadrilateral elements of various sizes (Figure 3, Figure 4). This approach allows for detail in land boundaries and increased resolution in areas of particular interest or important variations in bathymetry, while also reducing the resolution and number of elements in the open ocean. The elements range in size from around 700 km<sup>2</sup> offshore to less than 1 km<sup>2</sup>

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near the coast. The model extends from 45.00 to 37.50 degrees south, and 138.75 to 125.25 degrees east. This includes the whole Victorian and Tasmanian coasts and into South Australia and New South Wales. Extending the model domain allows swell wave development within the model negating the need for wave boundaries for our study area of interest.

Spectral wave conditions were developed from the input wind conditions. The spectrum was divided into 25 frequencies logarithmically distributed with a factor of 1.1 from 0.05 Hz. The directional spectra was divided into 16 bins. The time step for spectral wave calculations was limited to between 0.01 and 720 seconds. Temperature and salinity were not included in the model as independent variables, rather they are set at constant 10°C and 32 PSU. A constant Manning's bed resistance of 0.02 m<sup>1/3</sup>s<sup>-1</sup> was applied across the model domain. Coriolis forcing was varied across the domain as it extends over 2.50 degrees in latitude. A Smagorinsky formulation was used for the horizontal eddy viscosity with a constant of 0.28.

Downscaled coupled wave and hydrodynamic models were provided in DHI-MIKE format for 1990 to 2015 in annual files describing ocean currents at a 5 minute time-step with a spatial resolution of ~500m at the shoreline to ~10km in Bass Strait, and to ~30km in the open ocean. Each simulation was started from still conditions with water levels and wave conditions then developed from the boundary conditions applied. Model results were output for the whole computational domain with a temporal resolution of 1 hr. Results were divided into hydrodynamic and spectral wave outputs resulting in two result files for each year of simulation. The raw results have data for each computational element across the domain, these outputs have been further processed prior to delivery.

The output parameters included were:

- Surface elevation
- Total water depth
- Depth averaged current vectors
- Significant wave height
- Wave period T02
- Mean wave direction
- Wave power

Monthly wave statistics have been calculated for the modelled period and interpolated to a regular grid along the Victorian coast. Parameters derived include:

• Current speed (max, avg)

- Significant wave height (max, avg)
- Wave period for max significant wave height.
- Orbital velocity (max, avg)
- Wave power (max, avg)



Figure 3 DHI Model Domain



Figure 4 Mesh elements in the zoomed-in section from Figure 3 for DHI model

### 6.2.1 Emerging Hot Spot Analysis of Oceanographic Variables

To assess the spatial and temporal variation in oceanographic conditions across the coastal waters of Victoria, we conducted an Emerging Hot Spot Analysis (EHSA) on the resultant products from the Water Technology downscaled hydrodynamic models and IMOS processed sea surface temperature data. To conduct the Emerging Hot Spot Analysis, we first had to convert the oceanographic rasters to point datasets. Therefore, we converted the 500 m resolution hydrodynamic datasets for each year to points using the raster to point tool in ArcGIS 10.5 and merged them into a single point shapefile across all years for each variable. For SST, we first resampled the downscaled SST data from 30 m to 500 m resolution and used the same process as the hydrodynamic datasets to convert SST to points. These point datasets were then used to create space time cubes for use in the Emerging Hot Spot Analysis tool. Emerging hot spot analysis (EHSA) incorporates both space and time into a clustering analysis of point densities using the Getis-Ord Gi\* statistic based on chosen bin sizes (Getis and Ord 1992). The Getis-Ord Gi\* statistic evaluates each feature in the context of its neighbouring features. Hot spots are defined as those features that have high values and are surrounded by features with high values. Hot spots are calculated proportionally based on all features in the dataset. Statistically significant hot spots occur when the sum of a feature and all of its neighbours is too large to have occurred by random chance (Ord and Getis 1995). For the oceanographic variables, we used a neighbourhood size of 5000 metres and five prior time-step interval (5 years) to determine the trends in the dataset. Within each of these bins, the tool evaluates trends in the data using the Mann-Kendall trend test, which is a rank-correlation analysis that compares neighbouring values in a time series by determining the direction of the trend and whether or not that trend is statistically significant (Hamed 2009). Once the evaluation is carried out across all years in the time series, each bin location within the study area is assigned a trend z-score and a *p*-value and is categorised into one of the categories outlined in Table 1. The EHSA run on the hydrodynamic dataset included the full time period of the hydrodynamic modelling (26 years; 1990 to 2015). The hydrodynamic variables we evaluated included maximum winter significant wave height, maximum winter wave power, and maximum winter wave orbital velocities. Winter variables were used to capture patterns associated with the more extreme wave events. The EHSA run on the SST dataset included the time period from 1995 to 2015 (21 years) and we used the summer SST values to capture variability at the warmest extremes.

Pattern Name	Definition
No Pattern Detected	Does not fall into any of the hot or cold spot patterns defined below
New Hot Spot	A location that is a statistically significant hot spot for the final time step and has never been a statistically significant hot spot before.
Consecutive Hot Spot	A location with a single uninterrupted run of statistically significant hot spot bins in the final time-step intervals. The location has never been a statistically significant hot spot prior to the final hot spot run and less than ninety percent of all bins are statistically significant hot spots.
Intensifying Hot Spot	A location that has been a statistically significant hot spot for ninety percent of the time- step intervals, including the final time step. In addition, the intensity of clustering of high counts in each time step is increasing overall and that increase is statistically significant.
Persistent Hot Spot	A location that has been a statistically significant hot spot for ninety percent of the time- step intervals with no discernible trend indicating an increase or decrease in the intensity of clustering over time.
Diminishing Hot Spot	A location that has been a statistically significant hot spot for ninety percent of the time- step intervals, including the final time step. In addition, the intensity of clustering in each time step is decreasing overall and that decrease is statistically significant.
Sporadic Hot Spot	A location that is an on-again then off-again hot spot. Less than ninety percent of the time-step intervals have been statistically significant hot spots and none of the time-step intervals have been statistically significant cold spots.
Oscillating Hot Spot	A statistically significant hot spot for the final time-step interval that has a history of also being a statistically significant cold spot during a prior time step. Less than ninety percent of the time-step intervals have been statistically significant hot spots.
Historical Hot Spot	The most recent time period is not hot, but at least ninety percent of the time-step intervals have been statistically significant hot spots.
New Cold Spot	A location that is a statistically significant cold spot for the final time step and has never been a statistically significant cold spot before.
Consecutive Cold Spot	A location with a single uninterrupted run of statistically significant cold spot bins in the final time-step intervals. The location has never been a statistically significant cold spot prior to the final cold spot run and less than ninety percent of all bins are statistically significant cold spots.
Intensifying Cold Spot	A location that has been a statistically significant cold spot for ninety percent of the time- step intervals, including the final time step. In addition, the intensity of clustering of low counts in each time step is increasing overall and that increase is statistically significant.
Persistent Cold Spot	A location that has been a statistically significant cold spot for ninety percent of the time- step intervals with no discernible trend, indicating an increase or decrease in the intensity of clustering of counts over time.
Diminishing Cold Spot	A location that has been a statistically significant cold spot for ninety percent of the time- step intervals, including the final time step. In addition, the intensity of clustering of low counts in each time step is decreasing overall and that decrease is statistically significant.
Sporadic Cold Spot	A location that is an on-again then off-again cold spot. Less than ninety percent of the time-step intervals have been statistically significant cold spots and none of the time-step intervals have been statistically significant hot spots.
Oscillating Cold Spot	A statistically significant cold spot for the final time-step interval that has a history of also being a statistically significant hot spot during a prior time step. Less than ninety

Historical Cold Spot

The most recent time period is not cold, but at least ninety percent of the time-step intervals have been statistically significant cold spots.

### 6.3 Biophysical modelling

We developed a new parametrisation of our biophysical dispersal model (Treml et al. 2012, Treml et al. 2015) to quantify the population connectivity patterns for Blacklip Abalone and the Southern Rock Lobster (SRL) fisheries occurring across Victoria's seascape. This modelling approach incorporates species-specific habitat, oceanographic, and biological data to effectively estimate the probability for larvae to 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 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 with the habitat patch is recorded at that time-step. Dispersal simulation data were saved in the form of a 3-D 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 pair-wise 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 the abalone and SRL (Table 2). All connectivity analyses were derived from these two matrices, as outlined below.

Table 2 Species-specific parameters used in the biophysical modelling of larval dispersal for abalone and Southern Rock Lobster.

Parameter	Abalone	SRL	
	Victorian coastline, including Bass	Southern Australia (WA to NSW and Tasmania)	
Model extent	Strait. (Figure 5)	and New Zealand. (Figure 6)	
Model resolution	1 km	7 km	
	1. DHI-Mike coastal model		
Hydrodynamic data used	(Water Technology)	HYCOM global model	
	2. HYCOM global model	C	
	Hard substrate within 10-meter	Adult and spawning habitat 0-200 m depth,	
Habitat requirements	depth	suitable habitat for larvae to settle 0-50m depth.	
Adult density	Relative to at	(Bradiord 2005, Bradiord 2014).	
Daily larval mortality	5% per day	1% per day	
	570 per dag	$220 \text{ days} \pm 15 \text{ days for phyllosoma stage X to}$	
Time to reach competency and/or	4.5  days + / - 2  days	XI larvae (Bruce et al 2002 FRDC; Kittaka et al.	
mobility for settlement	5 5	2005)	
Buoyance or fall velocity of eggs	Neutrolly buoyant and distributed in yeter column		
and/or young larvae			
Vertical migration	None. Distributed throughout water	None. Distributed in top 30 m	
	column or to 10 m		
Larval 'sensing' capacity	Yes, to 1km during competency phase	Yes, to 7km during competency phase	
Maximum larval duration (days)	12 days (+/- 30% to 8 and 16 days)	365 days	
Snawning seasonality	Annually, October to February	Annually, September through	
Spanning seasonancy		December	
Number of source/destination IDs	95 reef patches, each acting as	184 source patches (< 200 m)	
	potential source and destination	80 destination patches ( $< 50 \text{ m}$ )	
Precision of connectivity estimates	1/100,000,000 larvae	1/100,000 Jarvae	
Release frequency	Fortnightly	Monthly	
Total number of larval releases per reef per spawning season	10	4	
Wall-time for individual simulations	~7 hrs per simulation	$\sim$ 50 hrs per simulation	
and complete ensembles	124 days (wall-time) to complete two ensembles	158 days (wall-time) to complete ensemble	

Figure 5 Abalone connectivity model domain. The abalone model includes all rocky reef habitat of Victoria and Bass Strait, at a resolution of 1 km. All unique habitat patches (95 in total) are represented by red nodes, where the size of each node is shown relative to the area it represents. UTM projection.



Figure 6 Southern Rock Lobster model domain. The SRL model incorporates the entire species range, extending from Western Australia to New Zealand, at a resolution of 7 km. All unique habitat patches (rock hardbottom habitat less than 200 m deep) are represented by 184 red nodes, with the size of the node shown relative to habitat area. Mercator projection (145° CM).



#### 6.3.1 Biophysical models

The seascape model for abalone was developed based on the best-available reef habitat data derived from substrate classifications of the merged LiDAR and multibeam datasets. To reduce the number of individual reefs, the substrate raster was resampled to 500 m and converted to polygons representing rocky reef locations at a 500 m resolution. These habitat data were rescaled and projected onto our modelled seascape (Figure 5). For SRL, we modelled spawning habitat based on bathymetry data between 0 and 200 m deep, believed to be suitable spawning habitat (Bradford et al. 2005). SRL larvae were only allowed to settle to those habitat patches less than 50 m deep. This model resulted in 184 potential source patches (0-200 m) and 80 of these patches were also potential settlement sites (0-50 m deep). The SRL habitat patches were developed at a higher resolution for Victoria with lower resolution as one moves out from this focal region (Figure 6).

Hydrodynamic data quantifying the nearshore and far-field ocean currents around Victoria and the regional seascape were obtained from two sources: 1) DHI-MIKE data from Water Technology for local-scale depthaveraged and high spatial-temporal resolution products, and 2) global HYCOM + NCODA Global  $1/12^{\circ}$ Reanalysis hydrodynamic data product providing regional scale 3-dimensional and moderate resolution data 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 between 500-800 m within  $\sim$ 7km of the shoreline, to  $\sim$ 10 km resolution through Bass Strait, and up to 25-35 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 (0-10 m depth) and interpolated to 1 km (abalone) and from 0-30m depth at 7 km (SRL) biophysical model grids. The HYCOM product is assimilative and the primitive equation model results integrate satellitederived data (winds, sea surface height), heat fluxes, etc. Both data products have pros and cons and therefore we modelled abalone dispersal across two hydrodynamic scenarios: 1) 1-hourly currents at 1km resolution derived from Water Technology coastal model, and 2) 3-hourly currents at 1km resolution interpolated from the global HYCOM model for 0 to 10 metres depth. The dispersal model for the SRL was modelled using the global HYCOM model at the 7 km resolution for all of southern Australia to New Zealand.

This resulted in three model ensembles to be created and completed on the high performance computing system, Spartan (University of Melbourne). The abalone dispersal simulations were modelled for up to a 20-day larval duration period (potential settlement from 2.5 days) to explore the impact of uncertainty in the maximum larval duration parameter. Two abalone ensembles were completed, one each for the two hydrodynamic models (MIKE & HYCOM). Computational time for the abalone simulations were ~7 hr/release date resulting in approximately 124 days of computational time. The SRL dispersal simulations were completed for a larval duration of up to 365 days (settlement behaviour from 205 days) as an optimal compromise between computational requirements and the settlement likelihood of the late-stage (X to XI stage) puerulus larvae (Kittaka et al. 2005, Bruce et al. 2007). SRL dispersal simulations required ~ 50 hrs per simulation resulting in approximately 158 days of computations to complete 76 dispersal simulations.

### 6.3.2 Connectivity analysis

We had four broad goals of the connectivity analysis:

- to develop maps of the regional structure of population connectivity (or likely dispersal pathways) throughout the seascape,
- to quantify the role each reef (or population) plays in regional replenishment and identify the reefs acting as strong and persistent larval sources,
- to identify those reefs or populations acting as key stepping-stones in maintaining regional flow among populations, and
- to develop connectivity-based metrics which might help explain the spatial and temporal patterns in the empirically-based abalone biomass data.

To develop maps showing the spatial structure of potential population connectivity via larval dispersal, we summarised the three model ensembles as a probability matrix to show the likelihood of movement through the seascape and as a migration matrix to show the relative influence on downstream populations. The geographic location of each reef patch and the strength of connectivity from these matrices were used to develop network maps where connections between habitat patches are shown as arcs connecting sources to destinations (directionality implied by following the arcs in a clockwise direction), with the thickness of each arc drawn relative to the strength of connectivity. We used network algorithms to uncover the emergent structure within these networks, revealing natural clusters of tightly linked populations. Boundaries between
these network 'communities' show regions where larval flow may be lower indicating sub-population boundaries.

To identify those reefs or populations that may serve as strong and persistent larval sources, we used four complementary measures of replenishment: i) Outflow quantifies each source's contribution to other sites, ii) Local retention is the proportion of larvae released from each source that settles in that focal patch (derived from the probability matrix), iii) Inflow measures the total relative amount of larvae settling to each patch (including those larvae that are locally produced), and iv) the sourcesness metric quantifies the relative source-strength of each patch as Outflow/Inflow (Pulliam 1988, Cronin 2007). Across all these measures, we also quantify the variability through years (i.e., standard deviation) to show the temporal stability or persistence.

Stepping-stone habitat patches or populations are those sites that may fall along dispersal pathways connecting a high proportion of sites within the seascape. Important stepping-stone sites were identified using the betweenness centrality measure from graph theory. This algorithm counts the number of shortest dispersal pathways that are forced through each reef patch, thereby estimating the 'importance' of each reef site to maintaining network-wide connectivity. Here, we transformed the migration matrix to be the same rank-order as geographic distance (log[M]<sup>-1</sup>) and used the betweenness centrality to quantify the relative strength of centrality of each population. Those sites with a high value reflect populations which are consistently important in maintaining flow among a large proportion of sites. Mapping these sites with respect to the community structure (above) and dispersal networks reveals the geographic structure of stepping-stones.

The spatial structure of biomass, abundance, and genetic variation may be driven, in part, by the dispersal dynamics of the species of interest. The dispersal structure, as well as the environmental setting, local demographics and population history, may play a significant role in persistence, health, and sustainable fishing level of individual populations. To aid in the analysis of the biomass and genetic data, we provided several additional dispersal-based metrics capturing connectivity patterns: i) self-recruitment quantifies the relative proportion of settlers at each destination site that originated from that focal site (diagonal of the migration matrix), ii) in-degree is the total number of 'significant' connections coming into a destination site (ignoring the strength of individual connections) derived from the migration matrix, and iii) out-degree

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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 significant connection was counted if it contributed to more than 0.1% of settlers to a destination site in the migration matrix.

## 6.4 Spatial modelling

### 6.4.1 Spatio-Temporal Modelling of Abalone Biomass

To understand those factors that best explain the distribution of productive abalone reefs along the coast of Victoria, we combined assessments of annual, fishery independent abalone biomass with environmental variables (wave environment, current patterns, reef connectivity, seafloor habitat, reef patch characteristics, sea surface temperature (SST), spatial area of abalone viral ganglioneuritis (AVG) infection, and fishery information (catch data) using boosted regression trees (BRT). BRT is an ensemble method for modelling associations between response and explanatory variables (Leathwick et al. 2006, Elith et al. 2008). Rather than providing a single 'best' model, such as in traditional regression methods, the BRT method utilises a large number of relatively simple tree models to develop associations between response and explanatory variables and allows for more robust predictions (Elith et al. 2006, Leathwick et al. 2006, Elith et al. 2008). Explanatory variables used in BRTs can be numeric, binary, or categorical, don't require scaling, are not affected by outliers, can deal with missing data through the use of surrogates, and rarely incorporate irrelevant variables (Elith et al. 2008), making them good for developing ecological relationships.

Prior to running the BRTs, we applied multi-panel scatterplots, Spearman's rank correlation coefficients, and variance inflation factors (VIFs) to test for collinearity between explanatory variables. Those paired variables that had a correlation coefficient greater than 0.50 or a VIF value greater than five were not included in the same model. We also compared patterns in biomass with each of the explanatory variables to determine the type of relationship between the response and explanatory variables. Most of the relationships were complex and non-linear, making BRT models the ideal choice for analysing those relationships.

Once data were explored, we ran a series of BRTs using varying combinations of explanatory variables. The biomass data were rounded to the nearest integer to meet the assumptions of a Poisson distribution; therefore, BRTs with a Poisson distribution and log-link function were used. For fitting the BRT models, a learning rate of 0.001 was used, the interaction depth was specified at 5, and 17,700 trees were used. To assess model performance, we used a k-fold cross validation method (Leathwick et al. 2006) within R statistical software

(R Core Team 2008) using the *gbm* package (Ridgeway 2017). Performance was also assessed through calculation of  $R^2$  from the total mean deviance and residual mean deviance. The BRT was trained using 70% (n = 2143) of the biomass observations while the remaining 30% (n = 919) were held in reserve for evaluating the predictive ability of the resulting best model. The final BRT model was used to predict the biomass from the evaluation dataset and those predictive values were compared to the observed biomass values using a Pearson correlation analysis.

The environmental variables used within the BRT models included two categorical variables associated with year, one categorical variable associated with the outbreak of Abalone Viral Ganglioneuritis (AVG), 30 temporally dynamic oceanographic variables describing currents and the wave environment, 10 variables associated with connectivity, two variables associated with annual commercial catch, and nine static variables characterising the structure of the seafloor habitat. Table 3 Summaries of the explanatory variables investigated for use in the Boosted Regression Tree models. As stated above, no correlated variables were incorporated into the same BRT and models with different combinations of variables were run and tested until a model with a high  $R^2$  and good predictive ability was developed. Once we had a suitable model, that model was used to predict and extrapolate biomass across the coastal zone within the Victorian state waters by creating a raster stack using the *raster* package in R (Hijmans 2012) and then predicting biomass from that raster stack using the *gbm* package (Ridgeway 2017). A separate 30 m resolution predictive raster was created for each year we assessed using the BRT for a total 21 predictions from 1995 to 2015.

Variable Type	Variable	Variable Code	Description	Variable Source	Used in Final BRT (Y/N)?
Time	Quota Year	QuotaYear	The quota year associated with each biomass value was used as a factor in the model.	Fisheries Victoria abalone abundance surveys	Ν
	Grouped Quota Year	QuotaYearG	Clustered groups of years with similar biomass values Clusters were derived using the TSclust package in R (Montero and Vilar, 2014) and 7 time frames were defined.	Fisheries Victoria abalone abundance surveys	Ν

Table 3 Summaries of the explanatory variables investigated for use in the Boosted Regression Tree models.

AVG	Spatial and temporal location of AVG outbreak	AVG_Inf	For each year, the biomass data were categorised into four classes associated with the AVG outbreak: "0" for years pre-outbreak and those areas not affected by the virus, "3" for the spatial extent of the AVG outbreak from 2006-2008 (during outbreak), "2" for the spatial extent of the AVG outbreak in the 2 years following the outbreak, and "1" for the spatial extent of the AVG outbreak 3-5 years after the outbreak.	Spatial categorical maps were developed from virus outbreak observations (Gorfine et al. 2008).	Υ
Hydro- Dynamics	Average Current Speed	ACS_an ACS_s ACS_w	Annual, summer, and winter average current speeds were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	N
	Average Significant Wave Height	ASWH_an ASWH_s ASWH_w	Annual, summer, and winter average significant wave heights were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Ν
	Average Wave Orbital Velocity	AWOV_an AWOV_s AWOV_w	Annual, summer, and winter average wave orbital velocities were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Ν
	Average Wave Power	AWP_an AWP_s AWP_w	Annual, summer, and winter average wave powers were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Ν
	Current Direction	CD_an CD_s CD_w	Annual, summer, and winter average current directions were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Ν
	Maximum Current Speed	MCS_an MCS_s MCS_w MCS_an	Annual, summer, and winter maximum current speeds were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Υ
	Maximum Significant Wave	MSWH_an MSWH_s MSWH_w	Annual, summer, and winter maximum significant wave heights were calculated for each year from	Water Technology hydrodynamic	Ν

	Height		1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	models	
	Maximum Wave Orbital Velocity	MWOV_an MWOV_s MWOV_w	Annual, summer, and winter maximum wave orbital velocities were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Υ
	Maximum Wave Power	MWP_an MWP_s MWP_w	Annual, summer, and winter maximum wave powers were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Ν
	Wave Period	WP_an WP_s WP_w	Annual, summer, and winter wave periods were calculated for each year from 1990 to 2015. The original dataset was provided at 500 m resolution and were then downscaled to 30 m using Empirical Bayesian Kriging.	Water Technology hydrodynamic models	Ν
Seafloor Structure	Depth	depth	Water depth for each cell in the gridded data derived from the LiDAR/multibeam bathymetry data. Depth values were resampled to 30 m resolution.	Merged LiDAR/ multibeam dataset	Y
	Slope	slope	Maximum change in depth from each cell in its three-by-three neighbourhood. Calculated using the "Slope" tool in ArcGIS Spatial Analyst at 5 m resolution. Slope values were then resampled to 30 m resolution.	Merged LiDAR/ multibeam dataset	Ν
	Vector Ruggedness Measure (VRM)	vrm	A measure of surface roughness taking into account the aspect and slope in a three-by-three neighbourhood. VRM was calculated using the "VRM" tool in the Benthic Terrain Modeler (BTM; Wright et al. 2012) at 5 m resolution. VRM values were then resampled to 30 m resolution.	Merged LiDAR/ multibeam dataset	Υ
	Bathymetric Position Index (BPI)	BPI50 BPI100 BPI50 BPI250 BPI500	A measure of a cell's depth relative to its surrounding cells at a defined scale (50 m, 100 m, 250 m, and 500 m scales were computed). VRM was calculated using the "Broad Scale BPI" tool in the Benthic Terrain	Merged LiDAR/ multibeam dataset	Y

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			Modeler (BTM; Wright et al. 2012) at 5 m resolution. BPI values were then resampled to 30 m resolution.		
	Substrate	substrate	Seafloor substrate type ("reef", "mixed", "sediment") derived from bathymetry and backscatter and then manually edited to remove artefacts.We used a decision tree classification (outlined in Ierodiaconou et al. 2011 and Zavalas et al. 2014) to distinguish between rock and sediment. Then, manually edited the resulting classification to remove any areas of misclassification based on thresholds of VRM.	Merged LiDAR/ multibeam dataset	Ν
	Reef Area	reef_area	Area of each reef from the "reef" class in the substrate raster.	Merged LiDAR/ multibeam dataset	Y
Connec- Tivity	In Degree	d_indeg_an h_indeg_an	Incoming connections to a reef. The connectivity variables derived from HYCOM are denoted with a "h" and those derived from DHI-MIKE are denoted with a "d."	Output from biophysical modelling	Y
	Local Retention	d_lr_an h_lr_an	Proportion of larvae released that settle back to the source site. The connectivity variables derived from HYCOM are denoted with a "h" and those derived from DHI-MIKE are denoted with a "d."	Output from biophysical modelling	Ν
	Self Recruitment	d_sr_an h_sr_an d_sr_an	Proportion of settlers that originated from that site. The connectivity variables derived from HYCOM are denoted with a "h" and those derived from DHI-MIKE are denoted with a "d."	Output from biophysical modelling	Υ
	Total Inflow	d_totin_an h_totin_an	Total relative inflow from all sites including local retention. The connectivity variables derived from HYCOM are denoted with a "h" and those derived from DHI-MIKE are denoted with a "d."	Output from biophysical modelling	Ν
Catch Data	Zone Catch Data	WCE_catch WCE_CPUE	The total catch and CPUE from each of the commercial abalone fishing zones (Western, Central, Eastern) from 1995 to 2015 were weighted by the availability of reef habitat in each zone.	Victorian Fisheries Authority Catch Data	N
	Sub-Zone Catch Data	SZ_catch SZ_CPUE	The total catch and CPUE from each of the commercial abalone fishing	Victorian Fisheries	Ν

### 6.4.2 Emerging Hot Spot Analysis of Predicted Abalone Biomass

The predictive maps resulting from the BRT analysis were used to determine which areas along the coast are experiencing positive, negative, or neutral changes in biomass of Blacklip Abalone. Once the predictive biomass rasters from 1995 to 2015 were created in R, we imported these rasters into ArcGIS for further analysis. First, all rasters were resampled to 100 m and converted to point datasets with a point replacing each cell in the 100 m resolution rasters (100 m was chosen to reduce file size for data management purposes). These points were then combined into a single point shapefile to analyse using the 'Emerging Hotspot Analysis' tool in ArcGIS 10.5 (ESRI 2011). This analysis was similar to the analyses used to look at spatial and temporal variability in the oceanographic variables. For full methods on the Emerging Hotspot Analysis, see the section titled "Emerging Hotspot Analysis of Oceanographic Variables." To assign the spatio-temporal bins for the biomass analysis, we chose a neighbourhood size of 2500 m and five prior time-step intervals (5 years) to account for temporal correlation associated with abalone size classes.

## 6.4.3 Inside/Outside MPA Comparison for Southern Rock Lobster

The purpose of the SRL case studies was to compare populations inside and outside the MPAs and determine the role of environmental drivers on the spatially-explicit catch observed. In the dataset from the MMS, we first used t-tests to compare male and female size (average weight), female reproductive condition, number of individuals and total catch (biomass) per unit effort (CPUE, average catch per pot lift). Separate t-tests were run to compare male size, female size, female reproductive condition, count and CPUE inside and outside the MMS. To offset the problem of multiple comparisons, a Bonferroni correction was applied to the alpha level of 0.05 to reduce the occurrence of a Type *I* error. Due to sample size limitations from the Wilsons Promontory (WP) dataset, we were unable to run the analysis on all the different groups. Therefore, we only compared the length and biomass of SRL captured within each of the regions (West (deep), West (shallow), East (shallow)) using t-tests (Table 18).

To determine whether seafloor structure and biogenic habitat contributes to SRL distribution, and to remove any potential effects of habitat from the inside/outside comparisons, we first acquired benthic habitat data over the areas surrounding each pot location. These data were acquired using a Kongsberg Maritime EM2040C multibeam sonar system. After post-processing, the resulting 0.5 m digital elevation models were used to derive a number of structure variables with the Benthic Terrain Modeller 3.0 (Wright et al. 2012) and are summarised in Table 4.

Bathymetry derivative	Description	Tool used to calculate variable*
Depth	Water depth for each cell in the gridded data derived from the multibeam bathymetry data.	n/a
Slope	Maximum change in depth from each cell in its three-by-three neighbourhood.	<i>Slope</i> tool in BTM
Rugosity	Ratio between the three-dimensional surface area and the planar area of a surface in a three-by-three neighbourhood.	<i>Surface Area to Planar Area</i> tool in BTM
Bathymetric Position	A measure of a cell's depth relative to its surrounding cells at a defined scale (10 m, 15 m, 20 m, and 25 m scales were computed).	<i>Broad Scale BPI</i> and <i>Fine Scale BPI</i> tools in BTM
Curvature	Describes how much a cell in a three-by-three neighbourhood deviates from a straight line.	<i>Curvature</i> tool in BTM
Variation in Depth	Differences in depth within a three-by-three neighbourhood measured as the standard deviation of depth.	<i>Depth Statistics</i> tool in BTM
Cosine of Aspect (northing)	Identifies downslope direction (northing) of the maximum rate of change in value from a cell to its neighbour.	Aspect (Statistical) tool in BTM
Sine of Aspect (easting)	Identifies downslope direction (easting) of the maximum rate of change in value from a cell to its neighbour.	Aspect (Statistical) tool in BTM

Table 4 Description of multibeam bathymetry data data	derivatives used for physical habitat characterisation.
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\* BTM denotes Benthic Terrain Modeller 3.0 (Wright et al. 2012)

In addition to the physical structure of the seafloor, benthic algal communities can also be used as an index of environment and habitat conditions that may affect the distribution of SRL. To assess biogenic habitat in the MMS, we used a delta vision HD underwater video camera at a 45 degree angle to survey the benthic habitat around each trap position. The video footage was classified into one or more biotopes in accordance with a modified JNCC scheme (Connor et al. 2004), established for classifying subtidal reef communities across the state of Victoria. The scheme is based on the floristic (seaweed) composition of the reef

community and is hierarchical. Following the modified JNCC classification scheme: biotope complexes were determined according to major structural features; biotopes were identified according to suites of conspicuous species; and sub-biotopes were defined by less obvious differences in species composition but typically reflect more subtle geographic variations. There were 40 distinct biotopes and sub-biotopes recognised from the video ground truthing. The hierarchical scheme was used to pool these into 11 biotope complex classes for quantitative analysis (Table 5).

Biotope Complex Letter	Biotope Class No.	Biotope Complex and Biotope Description
А		High energy sublittoral rock Phyllospora communities
	1	Phyllospora comosa forest with coralline crusts and thallose red algae
	2	Complex of <i>Phyllospora comosa</i> stands with open sandy hollows or sandy veneer reef
В		High energy sublittoral rock Ecklonia-Phyllospora communities
	3	Ecklonia radiata and Phyllospora on exposed subtidal rock
	4	Complex of Ecklonia radiata and Phyllospora with sandy veneer patches
С		High energy sublittoral rock Ecklonia dominated communities
	5	<i>Ecklonia radiata</i> with crustose coralline algae and sparse foliose red seaweeds on exposed subtidal rock
	6	<i>Ecklonia radiata</i> with abundant foliose red seaweeds on exposed subtidal rock
D		High energy sublittoral rock Cystophora and other fucoid communities
	7	Acrocarpia, Cystophora and erect corallines on exposed subtidal rock
	8	Carpoglossum and Cystophora on exposed rock
	9	Mixed <i>Cystophora</i> , <i>Perithalia</i> and <i>Caulerpa</i> assemblages on moderately exposed rock.
	10	Mixed Cystophora sandy veneer complex with Rhodymenia
Е		Foliose red seaweeds on exposed upper infralittoral rock
	11	Foliose red seaweeds on exposed upper subtidal rock

# Table 5 Biotope complexes and classes for this study with classes in approximate order of highest to lowest wave exposure.

We developed GLMs using the *glm* function in R *statistical software* (R Core Team, 2017). GLMs are flexible and appropriate for analysing ecological relationships (Austin 1987) because they do not force data into unnatural scales and allow for non-linearity and non-constant variance structures in the data (Hastie and Tibshirani 1990, Guisan et al. 2002). Prior to running the GLMs, we tested for variable distribution using Cleveland dotplots and correlation between variables using Pearson's correlation and variance inflation factors (VIFs). We tested for assumptions of the GLMs, including independence of observations (spatial autocorrelation). No variables required transformation, and only those variables with Pearson's correlation coefficients less than 0.50 and VIF values less than five were included in the same model. Best fit GLMs were developed for each species response variable (male size, female size, total biomass, count, and female reproductive condition). Best fit models were developed based on the deviance explained, variable significance, and AIC. In the WP dataset, there were a large number of pot lifts that did not result in the capture of any lobsters. Therefore, to develop models that accounted for these zeroes, we used zero-inflated GLMs to associate SRL size and biomass with habitat inside and outside WP.

# 6.5 Population genomics

### 6.5.1 Sample collection and experimental design

To determine if adaptive genetic structure exists across the Victorian Blacklip Abalone fishery we contrasted the genomic profiles of abalone stocks spanning different habitat types and environmental gradients across the Victorian coastline and performed genotype by environment association analyses to identify signatures of selection, and the scales at which selection processes are operating and potentially influencing recruitment dynamics.

Using a combination of LIDAR derived seafloor structure and modelled oceanographic data, we developed a hierarchical and spatially replicated sampling design comprising 30 reef locations representing different habitat types and spanning the entire Victorian coastline, encompassing the Western, Central and Eastern Zone abalone fisheries. The selection of reef locations was optimised to provide a replication of habitat types varying in seasonal sea surface temperature (SST), local geology (substrate type and vector ruggedness measure), and exposure to wave energy and ocean currents (Table 7). Temperature was a key environmental parameter as the Victorian coastline is characterised by a strong longitudinal thermal gradient driven by

upwelling systems and converging ocean currents (Sandery and Kämpf 2007, Colton and Swearer 2012). Mean winter and summer SST, and annual temperature range for the years 1995-2015 were evaluated, after which mean winter SST was omitted due to correlation with summer estimates. The geology of benthic reef habitats is variable within and across regions of the Victorian coastline, and consist of basalt, calcareous and granite reef complexes. Information on substrate type for each location was inferred from existing terrestrial geology maps and inferences from bathymetric LiDAR intensity data and expert knowledge. Due to the 500 m resolution of oceanographic data along the coast, we applied a fetch correction (15 degrees either side of the mean directionality) to local estimates of wave power and orbital velocity to account for the local variability in swell protection from headlands and exposed offshore reefs not captured in our model.

Field sampling was conducted in 2016 with the assistance of commercial survey divers contracted by the Victorian Fisheries Authority. A total of 900 abalone tissue biopsies were collected from 30 localities (30 samples per location) spanning the Victorian Western, Central and Eastern Zone fisheries and provided for genomic analysis (Table 6 and



Figure 7). At each location, individual abalone were collected within a 25 m radius of an anchored vessel and were considered a random sample of the population. Multiple size classes were intentionally sampled to avoid sampling single cohorts (potentially related individuals) that might drive ambiguous estimates of

genetic structure. Animals were brought to the surface where 50 mg tissue biopsies were taken from each individual before returning them to the water. Dissection tools were sterilized between samples to avoid cross-contamination. The biopsied material was transferred to 2-mL microcentrifuge tubes containing either 100% ethanol or RNAlater (QIAGEN) and transported to the laboratory. A total of 25 samples per location were used for genetic analysis.

		GPS Loca	tion
Zone and Location	Code	Latitude	Longitude
Western Zone			
Whites Beach	WHI	-38.349	141.384
Bully Cove	BUL	-38.397	141.411
Inside Murrels	INM	-38.404	141.526
Inside Nelson	INE	-38.404	141.560
Lawrence Rocks	LRO	-38.404	141.667
Lady Julia Percy Island	LJP	-38.421	141.995
The Craggs	OSC	-38.390	142.135
Warrnambool	WAR	-38.397	142.459
Central Zone			
Cat Reef	CAT	-38.741	143.188
Moonlight Head	MLH	-38.767	143.266
White Cliffs	WCF	-38.758	143.330
Blanket Bay	BLK	-38.827	143.586
Point Cook, Port Phillip Bay	PCO	-37.946	144.756
Freds Farm, Port Phillip Bay	FFM	-37.870	144.888
Seal Rocks	SRO	-38.528	145.100
The Nobbies	NOB	-38.518	145.110
Cape Woolami	WOO	-38.564	145.346
Arch Rock	ARK	-38.847	145.894
Cape Liptrap	LIP	-38.889	145.906
Cape Liptrap site 2	CCC	-38.901	145.913
Grinder Bay	GRB	-38.902	145.956
Tongue Point	TON	-38.994	146.258
Norman Point	NRM	-39.025	146.242
Great Glennie Island	GGI	-39.087	146.231
Norman Island	NMP	-39.053	146.320
Eastern Zone			
Marlo Frenches Narrows	MFN	-37.809	148.596
Point Ricardo	PRC	-37.813	148.619
Cape Conron	CCO	-37.814	148.731

#### Table 6 Sites included in genomic analysis



Figure 7 Sampling locations for genomic analysis.

Table 7 Summary of environmental statistics Where: WP, wave power; OV, orbital velocity; WH, wave height; WT, average winter sea surface temperature; ST, average summer sea surface temperature; VRM, vector ruggedness measure

	Geolog	y Wave Power		<b>Orbital Velocity</b>		Sea Surface Temperature		
Code	Substrate	VRM	Winter	Summer	Winter	Summer	Summer	Seasonal Range
Western Zone								
WHI	Basalt	1.68	8196.82	4415.89	173.13	126.85	17.14	3.08
BUL	Basalt	2.79	17635.10	10540.54	177.84	135.03	17.93	3.07
INM	Calcareous	0.67	6513.34	4961.00	189.12	160.40	17.96	3.55
INE	Calcareous	0.74	5868.78	3894.07	84.83	63.09	17.96	3.55
LRO	Calcareous	2.83	4280.06	1810.54	36.42	17.77	18.30	3.74
LJP	Basalt	0.03	28757.18	15941.97	97.71	60.13	18.14	3.67
OSC	Basalt	1.35	20964.05	12041.08	171.03	121.20	18.21	3.83
WAR	Calcareous	3.69	3310.76	2242.23	56.00	44.62	18.07	3.97
Central Zone								
CAT	Calcareous	4.94	20655.47	12860.78	206.55	159.15	17.69	3.41
MLH	Calcareous	2.16	3.24	2.19	0.03	0.02	17.69	3.45
WCF	Calcareous	1.53	14520.39	8955.13	168.51	123.96	17.65	3.47
BLK	Calcareous	1.07	2364.61	1805.34	39.58	32.55	17.88	3.96
PCO	Basalt	0.04	4.15	5.04	0.78	0.72	21.12	9.39

FFM	Basalt	0.12	5.30	7.06	0.66	0.70	21.34	9.61
SRO	Basalt	1.01	1.31	0.85	0.01	0.01	19.04	6.11
NOB	Basalt	1.21	7067.74	4770.08	79.35	62.28	19.04	6.11
WOO	Granite	3.41	8819.50	5624.23	22.65	13.86	19.05	5.52
ARK	Calcareous	0.86	9166.47	5422.33	110.09	85.43	18.78	5.13
LIP	Calcareous	1.84	9583.72	5286.04	107.92	77.24	18.78	5.13
CCC	Calcareous	2.92	11335.62	6270.07	89.30	61.95	18.68	4.92
GRB	Granite	1.91	4462.76	3115.95	107.46	87.20	18.68	4.92
TON	Granite	0.78	7010.70	3774.63	42.15	29.24	18.58	4.99
NRM	Granite	0.15	8864.68	3544.49	5.76	2.48	18.43	4.76
GGI	Granite	0.46	9847.41	4929.26	4.46	2.08	18.15	4.49
NMP	Granite	3.45	3902.73	2473.83	41.60	35.35	18.58	4.99
Eastern Zone								
MFN	Calcareous	0.29	3265.20	1772.07	26.99	14.92	18.62	5.20
PRC	Calcareous	0.34	3149.57	1745.89	25.07	14.19	18.62	5.20
CCO	Calcareous	0.52	3628.69	1997.11	21.93	12.16	18.59	4.87
ECD	Calcareous	0.50	3654.31	2004.29	33.98	20.03	18.59	4.87

#### 6.5.2 DNA extraction and GBS library construction

Total genomic DNA was extracted from 10 mg of muscle tissue using the Qiagen DNeasy 96 Blood and Tissue Kit (Venlo, Limburg, NL), and reduced representation genome libraries were prepared with a modified genotyping by sequencing (GBS) protocol of Elshire et al. (2011). Three hundred nanograms of genomic DNA from each individual was digested in 20 μL reaction containing four units of restriction enzymes Msel and Sbfl for 2 h at 37 °C. Digestion products were then ligated to modified P1 and P2 adapters with unique barcode combinations to allow for subsequent multiplexing of all individuals. Fifty μL ligations were performed containing the enzyme digested DNA, 1.125 ng of P1 and P2 adapters, 400 units of T4 ligase and T4 buffer (New England Biolabs, Beverly MA, USA). Ligations were incubated at 16 °C for 90 min followed by a 30 min of denaturation at 80 °C. Adapter ligated DNA fragments were purified using a Qiagen MinElute PCR purification kit (Redwood City, CA, USA), eluted in 20 μL of ddH20 and subsequently used for PCR amplification. Fifty μL PCRs were performed using 29 MyTaqTM HS Mix (Bioline, Taunton, MA, USA), and containing 0.2 μL each of Illumina Dual Index Sequencing Primers 1 & 2 (Illumina Inc., San Diego, CA, USA) and 10 μL of above purified DNA. PCR conditions were as follows: 95 °C for 1 min, 24 cycles of 95 °C for 30 s, 65 °C for 30 s, 72 °C for 30 s and a final extension step of 72 °C for 5 min. DNA quantitation and qualitative analysis of individual PCR products were performed on a MCE\_-202 MultiNA with a DNA-1000 kit (Shimadzu, Kyoto). Samples were then pooled equimolar into groups of 71 samples (11 pooled libraries in total), with each pooled library being sequenced on a single Illumina HiSeq 4000 (Illumina, San Diego) lane by Macrogen (Seoul, Korea).

## 6.5.3 Bioinformatics processing and genotyping

Illumina HiSeq 4000 runs yielded an average of 380 million assigned 100 base pair (bp) paired-end reads per lane, providing an average of 5.2 million paired-end reads per sample for genomic analysis. Raw sequences were first processed using the FASTX-Toolkit program (http://hannonlab.cshl.edu/fastx\_toolkit/) by trimming the raw reads to 80 bp length and discarding all reads that had a Phred score below 20. We used the *de novo* program from *Stacks* 1.19 (Catchen et al. 2013) to create a catalogue of SNPs and genotypes for all individuals. Because we expected a high level of intra-population genetic diversity based on microsatellite data from this and previous studies (Miller et al. 2016), we tested several combinations of parameters that allowed *de novo* assembly of GBS loci from orthologous sequences while rejecting paralogous sequences. The final parameter settings included: the maximum distance allowed between stacks (M = 3), the distance between loci in the catalogue (n = 3), while the minimum depth of coverage to form a stack was kept constant (m = 3). SNPs and genotypes at each locus were called using a maximum likelihood framework with default *Stacks* 1.19 parameters at the significance level of 5%. A subset of polymorphic GBS loci were found in at least 70% of individuals at each sampling location (Boehm et al. 2015, Dierickx et al. 2015) and having SNPs with a global minor allele frequency of  $\geq 0.01$  were used for downstream genomic analyses.

## 6.5.4 Detecting signatures of genomic selection

To detect genomic signatures of selection we conducted genotype by environment association analyses (GEAs) using two complementary models; Latent Factor Mixed Models (LFMM; Frichot, Schoville, Bouchard, & Francois, 2013) and the Bayesian method available in BayPass V1.01 (Gautier 2015). LFMM

and BayPass account for potentially confounding allele frequency differences due to population structure in a mixed linear model framework, but in different ways: LFMM models the effects of population structure on individual allele frequencies as latent factors, while BayPass uses a neutral covariance matrix constructed from population allele frequencies.

We first used LFMMs (lfmm 1.3; Frichot, Schoville, Bouchard, & Francois, 2013) to detect genotype–environment correlations with the continuous variables described above. Each analysis consisted of 10 repetitions of the Gibbs Sampling algorithm with 10,000 iterations each, which were performed after discarding the initial 5,000 steps as burn-in. The number of latent factors was set from one to three, and only those loci systematically recovered across analyses with different latent factors were kept. p-values were readjusted in *R* using the Stouffer method on the combined z-scores from all runs, as recommended in the lfmm manual. Significance was assessed after correcting with a FDR threshold of 0.1 and a median z-score larger than 3 and q -value < 0.001, as advised for these kinds of analyses (de Villemereuil et al. 2014).

Second, we explored GEAs with the Bayesian method available in BayPass V1.01 (Gautier 2015) under the AUX covariate mode (-covmcmc and -auxmode flags), after scaling the variables with the - scalecov flag. The underlying models explicitly accounts for the covariance structure among the population allele frequencies that originates from the shared history of the populations under study, through the estimation of the population covariance matrix  $\Omega$ , which renders the identification of SNPs subjected to selection less sensitive to the confounding effect of demography (Bonhomme et al. 2010, Gunther and Coop 2013). The auxiliary covariate model specifically involves the introduction of a binary auxiliary variable to classify each locus as associated or not. This allows the computation of posterior inclusion probabilities (and Bayes Factors) for each locus while explicitly accounting for multiple testing issues. For each SNP, the Bayes factor was expressed in deciban units (dB) via the transformation 10 log10 (BF). Significance was assessed based on the Bayes Factor (BF) between models and according to Jeffrey's rule (1961); that is, markers with moderate (3 < BF < 10), strong (10 < BF < 20) to decisive evidence (BF > 20) were retained as potential candidates under positive selection.

Discriminant analysis of principal components (DAPC) were implemented in the adegenet package for R (Jombart 2008, Jombart and Ahmed 2011), to obtain a graphical depiction of patterns of genetic structure based on datasets consisting of only candidate SNPs with BFs > 3 for each environmental variable.

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The number of genetic clusters was then defined using k-means, a clustering algorithm that looks for the value of K that maximizes the variation between groups. The Bayesian Information Criterion (BIC) was calculated for K = 1-28 and the K value with the lowest BIC was selected as the optimal number of clusters. A discriminant analysis was then performed using the function DAPC, implemented in R, to efficiently describe the genetic clusters.

#### 6.5.5 Determination of neutral population structure

Neutral population genetic structure among our samples was assessed using a putatively neutral subset of the main SNP data set (described above). This was generated by removing SNPs potentially under selection identified by LFMM and BayPass analyses. Neutral patterns of genetic structure were used to assess patterns of connectivity and gene flow across Victorian abalone stocks. Estimates of genetic diversity, observed (H<sub>o</sub>) and expected (H<sub>E</sub>) heterozygosity across loci, marker independence, as well as global and pair-wise measures of  $F_{ST}$  (Weir and Cockerham 1984), were calculated using Genepop. Population genetic differentiation was also assessed using the Discriminant Analysis of Principal Components (DAPC) implemented in the adegenet package for R (Jombart 2008, Jombart and Ahmed 2011).

# 7 RESULTS

# 7.1 Oceanographic Variables

The downscaled hydrodynamic models show the spatially explicit variability of oceanographic variables across Victorian waters driven by swell direction, coastal orientation, seabed bathymetry and shadowing of landmasses. The wave climate characterised for the Victorian coast is similar to much of the continental margin of southern Australia, being largely dominated by swell waves propagating from low pressure systems moving in an easterly direction in the Southern Ocean (Hemer et al. 2008). Figure 8 Examples of oceanographic patterns from 2015 for three of the variables used in this study: maximum mean annual current speed (A), max mean winter significant wave height calculated from June to August (B), and mean summer sea surface temperatures calculated from December to February (C). The majority of Australia's southern shelf is subject to persistent high energy swells of above 3.5 m occurring 30-50% of the time (Porter-Smith et al. 2004) and annual significant wave heights of up to 8.7 m (Harris and Hughes 2012). The west coast of Victoria is the region of the state most exposed to the prevailing swells originating from the southwest quadrant. The orientation of Cape Otway causes a gradient of wave energy across this Cape from highly exposed on its western side to moderately exposed in the east. During the winter, winds are predominantly from the southwest, driving a south-westerly swell. South-westerly swell dissipates as it rounds Wilsons Promontory towards the east coast (maximum ~5 m). The east coast of the promontory is exposed to easterly and south-easterly swells driven by south-easterly wind patterns in summer months. Using those areas of greater maximum significant winter wave heights in the western and central abalone fishing regions (Figure 8), we looked at temporal trends across the duration of the hydrodynamic dataset. Although there is a lot of variability across each of these regions, overall there is an increasing trend in significant wave height (Figure 9).







Figure 8 Examples of oceanographic patterns from 2015 for three of the variables used in this study: maximum mean annual current speed (A), max mean winter significant wave height calculated from June to August (B), and mean summer sea surface temperatures calculated from December to February (C).







Bass Strait marks the confluence of the warm waters of the Eastern Australian Current (EAC) that flow further south seasonally along the east coast and the colder waters of western Bass Strait from the South Australian Current. In winter, sub-Antarctic waters are forced eastward into Bass Strait, resulting in cool water temperatures and a well-mixed water column. In summer, intrusions of the EAC above cool sub-Antarctic waters result in a stratified water column with a warmer and more saline surface layer (James and Bone 2011). Prevailing westerlies drive the west to east water currents observed in Bass Strait (James and Bone 2011). Geostrophic currents are primarily driven by tides, wind, coastally trapped waves and density driven flows (Sandery and Kaempf 2007). Based on the IMOS processed SST dataset, there are clear areas of warmer waters along the Victorian coast. To determine if there was a warming trend in those regions (central zone and eastern zone) we looked at summer SST through time in those areas associated with warmer waters. Through this analysis we found that both regions have a general increasing trend in SST, with a much clearer, and less variable trend in the eastern zone (Figure 10).



Figure 10 Annual average summer SST from those areas in the Central (a) and Eastern (b) abalone fishing zones along the coast of Victoria experiencing trends of increasing temperatures. The variance around the means are shown as error bars. The Western abalone fishing zone is not shown because it is experiencing cooling or non-significant trends.

## 7.1.1 Emerging Hotspot Analysis of Oceanographic Variables

The results from the Emerging Hot Spot Analysis (EHSA) applied to the oceanographic variables across Victoria showed strong spatio-temporal patterns that varied depending on the characteristic being examined. The first hydrodynamic variable we analysed was annual max current speed. The EHSA found that the eastern half of the Victorian coastal waters are generally experiencing increasing current speeds while the western half contains more areas with decreasing trends (Figure 11). Overall, 31.6% of Victorian coastal waters had no detectable pattern in current speed while 38.8% are associated with cold spots and 29.5% with hot spots (Table 8). In the Western Zone, 5.8% of the region had no detectable patterns, no hot spot patterns were found, and the remaining 94.2% of the region was classified as cold spots. The Eastern Zone had an opposite pattern to the Western Zone with no cold spots and 71.1% of the region classified as hot spots. In the Central Zone, 37.2% of the region was unclassified, 27.4% were classified as hot spots, and 35.4% were classified as cold spots (Table 8).

Table 8 Results from the Emerging Hot Spot Analysis completed on annual max current speed. Each of the patterns detected during the analysis is shown along with the percentage of that pattern from each Victorian abalone fishing zone. The final column shows the percentage of each pattern across the entire state.

	Percentage of Region within Pattern						
Emerging Hot Spot	Victorian Western	Victorian Central	Victorian Eastern				
Analysis Pattern	Abalone Zone	Abalone Zone	Abalone Zone	All Victoria			
No Pattern Detected	5.8%	37.2%	28.9%	31.6%			
Intensifying Hot Spot	0.0%	12.9%	68.7%	18.7%			
Persistent Hot Spot	0.0%	9.0%	1.2%	6.6%			
<b>Consecutive Hot Spot</b>	0.0%	5.5%	0.0%	4.0%			
Historical Hot Spot	0.0%	0.0%	1.2%	0.2%			
Sporadic Cold Spot	1.2%	1.8%	0.0%	1.5%			
Persistent Cold Spot	0.0%	0.5%	0.0%	0.3%			
Consecutive Cold Spot	26.7%	6.4%	0.0%	8.4%			
Intensifying Cold Spot	65.1%	23.0%	0.0%	25.8%			
New Cold Spot	1.2%	3.7%	0.0%	2.8%			

#### **EMERGING HOT SPOT RESULTS – ANNUAL MAX CURRENT SPEED**

Patterns from the wave variables analysed using the EHSA showed similar spatial trends with the southwest facing coastlines experiencing the largest increases in significant wave heights, wave orbital velocities, and wave power (Figure 11). The south and southeast oriented coastlines and embayments either had no significant patterns or were classified as cold spots (Figure 11 B, C, D). Max significant wave height

(MSWH) had the largest percentage of hot spots across Victoria with 34.8% while max wave power (MWP) and max wave orbital velocities (MWOV) had similar percentages (30.2% and 30.1%, respectively). Comparing all three zones, the Western Zone is experiencing the largest increase in wave energy (MSWH = 82.6% hot spots, MWP = 81.5% hot spots, MWOV = 82.6% hot spots). The Central Zone is experiencing differing trends across all three wave environment variables with the mix in coastal orientations and presence of embayments (Table 9,Table 10,Table 11). The Eastern Zone is not experiencing dramatic changes to its wave environment based on this analysis. The majority of the Eastern Zone across all three variables has no detectable patterns (MSWH = 89.2% no pattern detected, MWOV = 65.1% no pattern detected, and MWP = 94.0% no pattern detected). However, there are some intensifying and sporadic hot spots for MSWH and MWOV on the furthest east section in this zone (Figure 11 B, C).

Table 9 Results from the Emerging Hot Spot Analysis completed on winter max significant wave height. Each of the patterns detected during the analysis is shown along with the percentage of that pattern from each Victorian abalone fishing zone. The final column shows the percentage of each pattern across the entire state.

# **EMERGING HOT SPOT RESULTS - WINTER MAX SIGNIFICANT WAVE HEIGHT**

	Percentage of Region within Pattern						
Emerging Hot Spot	Victorian Western	Victorian Central	Victorian Eastern				
Analysis Pattern	Abalone Zone	Abalone Zone	Abalone Zone	All Victoria			
No Pattern Detected	11.6%	28.5%	89.2%	34.4%			
New Hot Spot	1.2%	0.0%	0.0%	0.2%			
Intensifying Hot Spot	75.6%	20.7%	2.4%	26.0%			
Consecutive Hot Spot	2.3%	0.2%	0.0%	0.5%			
Sporadic Hot Spot	3.5%	9.9%	4.8%	8.3%			
Sporadic Cold Spot	0.0%	19.3%	3.6%	14.4%			
Consecutive Cold Spot	1.2%	0.7%	0.0%	0.7%			
Persistent Cold Spot	4.7%	13.1%	0.0%	10.1%			
Intensifying Cold Spot	0.0%	7.6%	0.0%	5.5%			

Table 10 Results from the Emerging Hot Spot Analysis completed on winter max wave power. Each of the patterns detected during the analysis is shown along with the percentage of that pattern from each Victorian abalone fishing zone. The final column shows the percentage of each pattern across the entire state.

## **EMERGING HOT SPOT RESULTS - WINTER MAX WAVE POWER**

	Percentage of Region within Pattern			
Emerging Hot Spot	Victorian Western	Victorian Central	Victorian Eastern	
Analysis Pattern	Abalone Zone	Abalone Zone	Abalone Zone	All Victoria
No Pattern Detected	12.8%	29.4%	94.0%	35.6%
New Hot Spot	1.2%	0.2%	0.0%	0.3%
Intensifying Hot Spot	73.3%	11.5%	0.0%	18.6%
Persistent Hot Spot	2.3%	0.7%	0.0%	0.8%
Consecutive Hot Spot	0.0%	1.8%	0.0%	1.3%
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Sporadic Hot Spot	4.7%	12.0%	0.0%	9.2%
Sporadic Cold Spot	0.0%	13.1%	6.0%	11.0%
Diminishing Cold Spot	0.0%	0.5%	0.0%	0.3%
Consecutive Cold Spot	0.0%	0.5%	0.0%	0.3%
Persistent Cold Spot	5.8%	24.4%	0.0%	18.2%
Intensifying Cold Spot	0.0%	6.0%	0.0%	4.3%

Table 11 Results from the Emerging Hot Spot Analysis completed on winter max wave orbital velocities. Each of the patterns detected during the analysis is shown along with the percentage of that pattern from each Victorian abalone fishing zone. The final column shows the percentage of each pattern across the entire state.

# **EMERGING HOT SPOT RESULTS - WINTER MAX WAVE ORBITAL VELOCITIES**

	Percentage of Region within Pattern			
Emerging Hot Spot	Victorian Western	Victorian Central	Victorian Eastern	
Analysis Pattern	Abalone Zone	Abalone Zone	Abalone Zone	All Victoria
No Pattern Detected	17.4%	38.6%	65.1%	39.2%
New Hot Spot	1.2%	0.2%	0.0%	0.3%
Intensifying Hot Spot	66.3%	16.1%	8.4%	22.1%
Persistent Hot Spot	9.3%	0.2%	0.0%	1.5%
Consecutive Hot Spot	5.8%	0.5%	2.4%	0.7%
Sporadic Hot Spot	0.0%	5.3%	6.0%	5.5%
Sporadic Cold Spot	0.0%	4.4%	8.4%	4.3%
Consecutive Cold Spot	0.0%	1.1%	1.2%	1.0%
Persistent Cold Spot	0.0%	27.1%	8.4%	20.7%
Intensifying Cold Spot	0.0%	6.4%	0.0%	4.8%

The emerging hot spot analysis for summer SST showed that a large portion of the Victorian coast is experiencing an overall warming trend (43.2%, Figure 11, Table 12). Only 12.9% of the coast has decreasing temperatures resulting in cold spots and the remaining 44.1% had no significant patterns. The eastern portion of the state waters and the embayments are where the majority of the hot spots are located. The western side of the state has the majority of the cold spots but most of those cold spots are classified as "Diminishing Cold Spots," signifying that the cooling trend is becoming less prominent. The Western Abalone Zone is mostly made up of areas with no significant patterns (70.3%) and the remaining area is classified as diminishing cold spots (24.3%) or persistent cold spots (5.4%). Over half of the Central Zone (53.1) is warming and classified as hot spot patterns. Only 12.0% of the Central Zone has a cold spot pattern and the remaining 34.9% had no significant patterns. No significant patterns were detected across 61.6% of the Eastern Zone and the remaining 28.4% is split between new hot spots and intensifying hot spots (Table 12).

Table 12 Results from the Emerging Hot Spot Analysis completed on summer sea surface temperature (SST). Each of the patterns detected during the analysis is shown along with the percentage of that pattern from each Victorian abalone fishing zone. The final column shows the percentage of each pattern across the entire state.

# **EMERGING HOT SPOT RESULTS – SUMMER SEA SURFACE TEMPERATURE**

	Percentage of Region Within Pattern			
Emerging Hot Spot	Victorian Western	Victorian Central	Victorian Eastern	
Analysis Pattern	Abalone Zone	Abalone Zone	Abalone Zone	All Victoria
No Pattern Detected	70.3%	34.9%	61.6%	44.1%
New Hot Spot	0.0%	0.3%	13.7%	2.2%
Intensifying Hot Spot	0.0%	17.7%	0.0%	12.5%
Consecutive Hot Spot	0.0%	13.7%	0.0%	9.7%
Oscillating Hot Spot	0.0%	9.4%	24.7%	10.3%
Sporadic Hot Spot	0.0%	12.0%	0.0%	8.5%
Diminishing Cold Spot	24.3%	12.0%	0.0%	12.1%
Persistent Cold Spot	5.4%	0.0%	0.0%	0.8%

# Percentage of Region within Pattern



Figure 11 Results from the Emerging Hot Spot Analysis for oceanographic variables. The 5000 m spatial zones from the analysis are classified into one of the emerging hot spot patterns and coloured based on those patterns. The results for all of Victoria are shown for Max Annual Current Speed (A), Max Winter Significant Wave Height (B), Max Winter Orbital Velocities (C), Max Winter Wave Power (D), and Summer Sea Surface Temperature (E). Background basemap imagery provided by ESRI.

# 7.2 Biophysical modelling

The DHI-driven dispersal model for abalone resulted in an average dispersal network (averaged across 217 simulations over 25 years) revealing general west-to-east connectivity of larvae (Figure 12). Some connectivity appears to exist between the reefs of Tasmania and into eastern Victoria across Bass Strait. Using the HYCOM ocean current data, the time-averaged dispersal pathways for the abalone ensembles (205 simulations over 20 years) show clear west-to-east structure along the Victorian coastal zone, with some potential connectivity with Tasmania through a northerly route in eastern Bass Strait (Figure 13). Although general structure of connectivity is similar between the HYCOM and DHI current models, the DHI-driven connectivity patterns are weaker as a result of larvae being lost at sea and not reaching downstream habitat. At a much broader scale, the SRL dispersal networks show primarily weak linkages (probability matrix), with dense connectivity around Australia and low-probability pathways to New Zealand (Figure 14).

Strong larval sources which are key to regional replenishment were identified primarily using the Outflow metric quantifying the total relative contribution each population provides to downstream habitat patches. Identifying and mapping these key populations clearly shows the distribution of source patches (Figure 15). The primary sources of abalone larvae are from those large populations in the west half of the state, with a few strong sources in the east and along northern Tasmania. Strong source populations for SRL are more continuously distributed across the seascape without strong clustering (Figure 15, bottom). All other population-level metrics related to larval replenishment are provided in the supplemental data files.

Betweenness and community structure network algorithms help reveal the critical population stepping-stones and emergent clustering within the dispersal networks. Significant stepping-stones (with high betweenness centrality values) are responsible for maintaining flow across the population networks (Figure 16). The majority of these sites are located in central Victoria and along the dispersal corridor leading up from Tasmania. The emergent clustering in the dispersal networks are shown in Figure 17. Although there is general consistence among the abalone ensembles (DHI vs HYCOM), the clusters derived from the DHI data reveal a greater level of partitioning (Figure 17, top). Figure 12 Abalone dispersal network from DHI local-scale ocean currents. The dispersal network for abalone derived from the migration matrix (top) and the probability matrix (bottom) where the strength and direction of connectivity are illustrated by the weight and bend of the links (direction following clockwise).





Figure 13 Abalone dispersal network from HYCOM ocean currents. The dispersal network for abalone derived from the migration matrix (top) and the probability matrix (bottom) where the strength and direction of connectivity are illustrated by the weight and bend of the links (direction following clockwise).





Figure 14 Southern Rock Lobster dispersal network from HYCOM ocean currents. The dispersal network for SRL derived from the migration matrix (top) and the probability matrix (bottom) where the strength and direction of connectivity are illustrated by the weight and bend of the links (direction following clockwise).





Figure 15 Strong larval sources. Sourceness based on the OutFlow metric for abalone with DHI currents (top), abalone with HYCOM currents (middle), and SRL with HYCOM currents (bottom). The strongest average sources are those shown in dark blue (top quantile) for each ensemble. Size of the nodes represent the strength of replenishment to neighbouring populations.







Figure 16 Stepping-stone habitat patches. Those patches with high betweenness centrality, symbolised with larger nodes, represent those habitat patches that may act as key stepping-stones, maintaining population cohesion throughout the seascape. Stepping-stones are illustrated for abalone using DHI currents (top), HYCOM currents (middle), and for the SRL (bottom).





Figure 17 Community structure. The emergent community structure derived from the migration matrices illustrate the natural clustering among populations. Unique and closely linked communities in these networks are illustrated with different colours (specific colours were chosen randomly to show adequate contrast). Community structure is illustrated for abalone using DHI currents (top) and HYCOM currents (middle), and Southern Rock Lobster (bottom).







# 7.3 Spatial Data Modelling

## 7.3.1 Spatio-Temporal Modelling of Abalone Biomass

The parameters for the final BRT model along with results from the cross-validation are shown in Table 13. The final BRT model used 16,700 trees across 10 explanatory variables. The performance statistics outlined in Table 13 show that the model performed relatively well at explaining variation in biomass of Blacklip Abalone across the study area and time period. The *R*-squared of the fitted model shows that the BRT explains 62% of the spatial and temporal variation in biomass. Additionally, when we used the BRT model to predict the biomass from the evaluation dataset and compared those predictions to the observed biomass, we found that the BRT model was fairly accurate in predicting biomass across both space and time. However, the model consistently underestimated biomass where high biomass values were observed. The Pearson correlation from this comparison was 0.66 and statistically significant (*P*-value < 0.001; Figure 18).

BRT Model Parameters	Abalone Biomass Model
Error distribution	Poisson
Learning rate	0.001
Interaction depth	5
Number of trees	16,700
Mean residual deviance	5.18
Training data correlation	0.782
R-squared (fitted model)	0.620
Pearson correlation with evaluation data (P-value)	0.66 ( <i>P</i> < 0.001)

Table 13 Model parameters and performance statistics from the final boosted regression tree (BRT) model used to associate abalone biomass with spatial and temporal explanatory variables.


Figure 18 Pearson correlation between observed biomass and biomass predicted from the boosted regression tree (BRT) model in the evaluation dataset, which was reserved for testing the prediction accuracy of the BRT model. The Pearson correlation (r) is shown on the figure with its associated *P*-value.

The nature and relative magnitude of influence from each explanatory variable used in the final BRT is shown in Figure 19 and the relative influence of each variable is summarised in Figure 20. Summer SST has the strongest correlation with biomass of Blacklip Abalone with an influence of 25%. The relationship with summer SST is also negative, with higher biomass being associated with areas of lower SST. Self-recruitment from the connectivity modelling was the second most influential variable in the BRT at 13.1%. The relationship with self-recruitment is complex but there is an overall negative relationship with higher biomass values associated with lower values of self-recruitment. Current speed has an asymptotic relationship with biomass and is the third most influential variable in the model. Blacklip Abalone biomass increases dramatically with increasing current speeds up to about 0.5 m/s with only a slight positive relationship after that threshold. The relative number of reefs providing larval supply to a particular location is the fourth most important variable in the BRT at 11.8%. As the number of reefs upstream increases, biomass increases. There is a slight levelling off between 12 and 16 but an overall positive correlation with

biomass. Maximum winter wave orbital velocity is the fifth most influential variable. The highest values of biomass are found in areas where wave orbital velocity is the lowest and then a slight but steady decrease as wave orbital velocity increases. Depth, as the sixth most influential variable, has an asymptotic relationship with biomass. Biomass fluctuates, but is relatively consistent, from 5 to 20 metres depth with a steep decline in biomass as we reach depths shallower than 5 metres. Reef area has a 6.3% influence on the overall model but there is only a slight increase in biomass with increasing reef area. Bathymetric position index (BPI) at the 50 m scale was also found to be influential (6%). Higher Black Abalone biomass is correlated regions of lower bathymetric position (e.g. valleys in the terrain). As BPI increases, we see a decline in biomass. Complexity of the seafloor, calculated using the vector ruggedness measure (VRM), showed that abalone biomass increases with increased complexity up to a value of around 0.010 (moderate complexity) and then decreased from that point as complexity continued to decrease. VRM is the ninth most influential variable with an influence of 4.9%. Finally, the categorical variable for AVG infection had a 2.2% influence on the final BRT. Highest Blacklip Abalone biomass was observed in areas unaffected by the virus (AVG Inf = 0). The lowest biomass was observed during the 1-2 years following the virus outbreak ( $AVG_Inf = 2$ ). The years during the outbreak (AVG Inf = 3) and 3-5 years after the outbreak (AVG Inf = 1) had moderate biomass values relative to the other categories with the time during the outbreak showing a pattern of decline in biomass.



Figure 19 The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for *H. rubra* biomass. The variables are ordered based on their decreasing influence on the fitted relationship with the percentage influence in parentheses following the variable name on the x-axis of each graph. All relationships are shown for median values of the other variables in the model.\*Variable Codes: summer\_sst = annual summer average SST values in degrees Kelvin; d\_sr\_an = annual proportion of settlers that originated from that reef; MCS\_an = annual average max current speed; d\_indeg\_an" = annual incoming connections to a reef; MWOV\_w = annual winter average wave orbital velocities; depth = water depth; reef\_area = area of each contiguous reef; BPI50 = bathymetric position index at 50 m scale; vrm = vector ruggedness measure; AVG\_Inf = categorical variable associated with spatial and temporal effect of the AVG virus outbreak: "0"=no affect, "1"= affected area 3-5 years after outbreak, "2"=affected area 1-2 years after outbreak, "3"=affected area during outbreak



Figure 20 Relative influence (%) of each of the explanatory variables used in the boosted regression tree model developed for abalone biomass spatio-temporal distribution (summer\_sst = annual summer average; SST values; d\_sr\_an = annual proportion of settlers that originated from that reef; MCS\_an = annual average max current speed; d\_indeg\_an" = annual incoming connections to a reef; MWOV\_w = annual winter average wave orbital velocities; depth = water depth; reef\_area = area of each contiguous reef; BPI50 = bathymetric position index at 50 m scale; vrm = vector ruggedness measure; AVG\_Inf = categorical variable associated with spatial and temporal effect of the AVG virus outbreak: "0"=no affect, "1"= affected area 3-5 years after outbreak, "2"=affected area 1-2 years after outbreak, "3"=affected area during outbreak)

The relationships between Blacklip Abalone biomass and each of the explanatory variables used in the final model, allowed us to develop predictive maps of abalone biomass over all the reefs in the study area, including those with no survey data. These maps were produced at 30 m resolution and can be used to evaluate spatio-temporal patterns in predicted abalone biomass (2015 example in Figure 21).

#### 7.3.2 Emerging Hotspot Analysis of Predicted Abalone Biomass

The results from the emerging hot spot analysis showed that predicted abalone biomass is experiencing an overall negative trend across Victoria (Figure 22). From the 2500 m analysis cells, 37.9% had no detectable pattern, 12.1% were classified with hot spot patterns, and 50.1% were classified as cold spot patterns (Table 14). In the Western Zone, the largest percentage of area was defined as "Consecutive Cold Spots" followed by "Oscillating Cold Spots". Only 7.7% of the region was made up of hot spots and those are "Historical Hot Spots." In the Central Zone, 38.9% of the region had no detectable patterns. The remaining area of the region

was split between 2.9% hot spots and 58.2% cold spots, with 36.0% of the cold spots "Consecutive Cold Spots." In the Eastern Zone, the majority of the zone is classified with hot spot patterns with 1.0% "Persistent Hot Spots," 62.2% "Diminishing Hot Spots," and 15.3% "Historical Hot Spots." The remaining 21.4% in this zone had no detectable patterns.



Figure 21 Predicted biomass raster for the year 2015 calculated from the biomass-environment relationships derived using the BRT model. The top map shows the predicted biomass across the Victorian coastal waters with the warmer colours representing high predicted biomass, the cooler colours representing low predicted biomass, and dark blue signifying those areas where abalone are absent. Extent indicators a-d correspond to the zoomed in areas along the coast shown across the bottom of the figure. We clip predictions to the 20 metre contour as fishery independent data to drive the model was <20 metres.



Figure 22 Results from the Emerging Hot Spot Analysis for the predicted biomass of *H. rubra*. The 2500 m spatial zones from the analysis are classified into one of the emerging hot spot patterns and coloured based on those patterns. The results for all of Victoria are shown (A) along with those for the Western Abalone Zone (B), the Eastern Abalone Zone (C), and the Central Abalone Zone (D). Background basemap imagery provided by ESRI.

100

Kilometres

 Table 14
 Results from the Emerging Hot Spot Analysis completed on the predicted Blacklip Abaone biomass.

 Each of the patterns detected during the analysis is shown along with the percentage of that pattern from each

 Victorian abalone fishing zone. The final column shows the percentage of each pattern across the entire state.

	Percentage of Region within Pattern						
Emerging Hot Spot Analysis Pattern	Victorian Western Abalone Zone	Victorian Central Abalone Zone	Victorian Eastern Abalone Zone	All Victoria			
No Pattern Detected	46.2%	38.9%	21.4%	37.9%			
Persistent Hot Spot	0.0%	0.0%	1.0%	0.1%			
Diminishing Hot Spot	0.0%	1.2%	62.2%	7.9%			
Sporadic Hot Spot	0.0%	0.6%	0.0%	0.5%			
Historical Hot Spot	7.7%	1.1%	15.3%	3.6%			
Oscillating Cold Spot	1.7%	11.6%	0.0%	9.0%			
Sporadic Cold Spot	32.5%	36.0%	0.0%	31.5%			
Consecutive Cold Spot	0.0%	3.8%	0.0%	2.9%			
Intensifying Cold Spot	0.9%	4.6%	0.0%	3.6%			
New Cold Spot	11.1%	2.3%	0.0%	3.2%			

#### 7.3.3 Inside/Outside MPA Comparison for Southern Rock Lobster

We used spatially explicit, standardised fishery sampling methods to compare Southern Rock Lobster (SRL) populations inside and outside of two Victorian MPAs. Detailed results from the study done in and around Merri Marine Sanctuary (MMS) can be found in Young et al. (2016) and are briefly summarised here. A total of 715 SRL individuals were captured during this study (328 inside the MMS over 40 pot lifts and 387 outside the MMS over 100 pot lifts; Figure 23,Table 15 T). Based on the results from the t-tests, we found that the small MPA (MMS) supports a large population of SRL with increased size and number of individuals within its boundary. The GLM analysis showed that depth, distance to MMS boundary, biotope complex and some measure of complexity (variation in depth, slope), were important in explaining SRL distribution. The GLMs for most response variables (all but Male size when biotope was included) retained an MPA effect (distance from MPA) as a significant predictor in the model (Table 16).



Figure 23 Southern Rock Lobster (*J. edwardsii*) male and female size distributions (carapace length) inside and outside the Merri Marine Sanctuary (MMS) with the length of legal size for males and females displayed as a dashed black line in each distribution plot: (a) males inside the MMS, (b) females inside the MMS, (c) males outside the MMS and (d) females outside the MMS.

Table 15 Comparison of Southern Rock Lobster statistics inside (*n* = 40) and outside (*n* = 100) the Merri Marine Sanctuary (MMS).

Location	Sex	No. of Individuals	No. of Legal Size Individuals	Average Carapace Length (mm)	SD of Average Carapace Length	Biomass (g)	Average Biomass per Pot Lift (g)	Average Weight (g)	SD of Average Weight	No. of Reproductive Females
Inside MMS	Male	131	87	115	17	3031	761	870	364	
	Female	197	71	100	7	3393	482	551	84	177
	Total	328	158	107		5766	1243	712		
Outside MMS	Male	159	43	104	15	1388	432	617	364	
	Female	228	9	96	6	2222	349	521	75	166
	Total	387	52	99		1978	781	579		

Table 16 Results from the generalised linear models (GLMs) used to associate Southern Rock Lobster population characteristics with habitat and protection status in and around the Merri Marine Sanctuary (MMS).

Population Characteristic	Biotope Complex Included	Variables	Relationship	<i>P</i> -value	Total Deviance Explained (pseudo R <sup>2</sup> )
Male Size	no	Depth	negative	<0.001	19.4%

(average weight)					
		Distance to MMS	negative	0.035	
	yes	Depth	negative	< 0.001	23.2%
		Biotope Complex	n/a	0.004	
Female Size	no	Distance to MMS	negative	0.001	7.6%
(average weight)					
	yes	Distance to MMS	negative	0.001	7.6%
# of Reproductive Females	no	Distance to MMS	negative	<0.001	21.5%
	yes	Biotope Complex	n/a	< 0.001	25.0%
		Distance to MMS	negative	<0.001	
# of Individuals per pot lift	no	Distance to MMS	negative	<0.001	24.7%
		Depth	negative	0.001	
		Variation in Depth	negative	0.013	
	yes	Biotope Complex	n/a	< 0.001	30.2%
		Distance to MMS	negative	< 0.001	
		Slope	negative	< 0.001	
		Depth	negative	< 0.001	
Average Biomass per pot lift	no	Distance to MMS	negative	<0.001	39.2%
		Depth	negative	<0.001	
		Slope	negative	0.017	
	yes	Biotope Complex	n/a	< 0.001	42.6%
		Distance to MMS	negative	0.001	
		Depth	negative	0.002	
		Slope	negative	0.014	

Compared to the population associated with the MMS, sampling of the SRL population around WP showed that, although fewer lobsters were captured despite more pots being deployed, the individuals in this region were much larger (Figure 24). All but one individual caught over the duration of this study were of legal size and the overall average weight was just over 2 kg per individual. Results from the t-tests comparing population characteristics inside and outside the WP MPA showed that there were no significant differences in length or biomass in any of the sampling regions with a *P*-value of 0.01 following the Bonferroni correction (Table 17). In the West (deep) region, larger individuals were captured outside the MPA while the

biomass was almost the same inside and outside (Length: mean = 57.5 (inside), mean = 80.7 (outside), *P*-value = 0.27; Biomass: mean = 0.9 (inside), mean = 0.9 (outside), *P*-value = 0.98; Table 18). Although not significant, the West (shallow) region experienced the greatest differences in size of SRL individuals with larger and heavier averages inside the MPA compared to outside (Length: mean = 121.7 (inside), mean = 81.6 (outside), *P*-value = 0.04; Biomass: mean = 1.7 (inside), mean = 1.0 (outside), *P*-value = 0.02). The East (shallow) region experienced a similar pattern as the West (shallow), although differences were slightly less (Length: mean = 113.1 (inside), mean = 93.4 (outside), *P*-value = 0.27; Biomass: mean = 1.7 (inside), mean = 1.0 (outside), *P*-value = 0.03).



Figure 24 Southern Rock Lobster (*Jasus edwardsii*) male and female size distributions (carapace length) inside and outside the Wilsons Promontory Marine Park (WP) with the length of legal size for males and females displayed as a dashed black line in each distribution plot: (a) males inside the WP, (b) females inside the WP, (c) males outside the WP and (d) females outside the WP.

The zero-inflated GLMs used to associate SRL length and weight with habitat characteristics were unsuccessful in understanding habitat associations. The habitat variables used in the models were non-significant and less than 5% of the deviance was explained. Therefore, we decided to remove this analysis from the study.

Table 17 Comparison of Southern Rock Lobster (*Jasus edwardsii*) statistics inside (n = 125) and outside (n = 75) the Wilsons Promontory Marine Park.

Location	Sex	No. of Individuals	No. of Legal Size Individuals	Average Carapace Length (mm)	SD of Average Carapace Length	Biomass (g)	Average Biomass per Pot Lift (g)	Average Weight (g)	SD of Average Weight
Inside WP	Male	65	64	182	25	197123	1049	3033	1112
	Female	39	39	146	19	61102	361	1567	761
	Total	104	103	164		258225	1410	2300	
Outside WP	Male	21	21	165	27	48488	674	2309	996
	Female	37	37	135	18	46980	686	1270	438
	Total	58	58	150		95468	1360	1790	

Table 18 Comparison of Southern Rock Lobster (*Jasus edwardsii*) statistics between each of the comparable zones from the sampling design inside and outside Wilsons Promontory Marine Park.

Comparison Zone	Inside/Outside Marine Park?	No. of Individuals	No. of Legal Size Individuals	Average Carapace Length (mm)	SD of Average Carapace Length	Average Biomass (g)	SD of Average Biomass
West Deep	Inside	9	9	172	38	2734	1661
	Outside	18	17	148	23	1740	818
West Shallow	Inside	29	29	128	59	2267	1878
	Outside	16	16	153	21	1041	773
East Shallow	Inside	28	28	124	61	2556	1181
	Outside	24	24	121	61	1517	971

## 7.4 Population Genomics

#### Genotyping and neutral population structure

Genome scans of 725 Blacklip Abalone specimens from 29 locations distributed across the Victorian western, central and eastern zone abalone fisheries were performed by reduced genome representation sequencing. Illumina sequencing yielded a total of 3,794, 534, 348 base paired reads, providing an average of 5,221,020 base-paired reads per sample. *De novo* assembly using the STACKS bioinformatics pipeline yielded a total of 4,665,377 polymorphic GBS tags, and 1,108,067 tags containing 5,239 SNPs. Levels of diversity were consistent across sites with percentage of polymorphic loci ranging 59.3% to 96.8% (mean %P = 85.956%) (Table 19), and expected heterozygosities ranging from 0.13 to 0.23 (mean  $H_{\rm E} = 0.21$ ).

	Na	HE	НО	%P
WHI	1.958	0.244	0.233	59.3
BUL	1.972	0.271	0.208	90.6
INM	1.97	0.27	0.214	79.7
INE	1.98	0.278	0.221	94.9
LRO	1.969	0.271	0.214	79.2
LJP	1.971	0.275	0.217	83.5
OSC	1.882	0.274	0.218	80.6
WAR	1.956	0.27	0.199	66.5
CAT	1.97	0.272	0.209	90.2
MLH	1.972	0.274	0.211	92.7
WCF	1.977	0.276	0.215	80.6
BLK	1.962	0.279	0.216	79.2
PCO	1.952	0.271	0.215	84.6
FFM	1.939	0.265	0.204	74.8
SRO	1.977	0.275	0.215	93.5
NOB	1.98	0.277	0.22	95.0
WOO	1.973	0.279	0.227	83.4
ARK	1.977	0.273	0.212	94.9
LIP	1.975	0.277	0.216	89.4
CCC	1.975	0.276	0.218	94.3
GRB	1.973	0.275	0.214	94.5
TON	1.976	0.277	0.218	94.1
NRM	1.98	0.276	0.22	96.8
GGI	1.976	0.272	0.214	95.6
NMP	1.973	0.272	0.214	93.3
MFN	1.922	0.247	0.195	88.1
PRC	1.913	0.247	0.196	86.9
CCO	1.91	0.245	0.187	83.8

Table 19 Summary of statistics for populations including average number of alleles per locus (Na), observed and unbiased expected heterozygosity ( $H_E$  and  $H_O$ ) and percentage of polymorphic loci (%P)

ECD 1.897 0.239 0.181 72	2.7
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Global  $F_{ST}$  was weak but significantly different from zero ( $F_{ST} = 0.009$ ; 95% CIs = 0.008 – 0.009) indicating some genetic structuring and limitations to gene flow among sample locations. Significant genetic structuring appears to be associated with the Victorian eastern zone and Port Phillip Bay fishing stocks, as all pairwise  $F_{ST}$  comparisons were significantly different from zero (Table 20). In contrast all pairwise estimates of  $F_{ST}$  between western zone and central zone fishing stocks (except for Port Phillip Bay) did not differ significantly from zero. Excluding the eastern zone and Port Phillip Bay fishing stocks, global  $F_{ST}$  did not differ significantly from zero ( $F_{ST} = 0.002$ ; 95% CIs = 0.000 – 0.003) indicating a lack of genetic structuring between western and central zone fishing stocks. These patterns of population genetic differentiation are graphically depicted by DAPC analyses which retained 300 principal components, and the first two discriminant functions, capturing 75% of the total variance within the SNP dataset (

Figure 25). When plotted across the x- and y-axes individuals from the eastern zone and Port Phillip Bay sample locations cluster separately from each other and from the main population cluster consisting of admixed individuals from the western and central zone fisheries. Removing the eastern zone and Port Phillip Bay sample locations (retaining 250 principal components, and the first two discriminant functions, capturing 65% of the total variance) no genetic structuring between the western and central zone fisheries is apparent.

Table 20 Pairwise estimates of F<sub>ST</sub> between 29 Blacklip Abalone sample locations. Values shown in **bold** are non-significant (P > 0.001)

WHI BUL INM INE LRO LJP OSC WAR CAT MLH WCF BLK PCO FFM SRO NOB WOO ARK LIP CCC GRB TON NRM GGI NMP MFN PRC CCO WHI --BUL 0.00 --INM 0.01 0.00 ---INE 0.00 0.00 0.00 --LRO 0.00 0.00 0.00 0.00 ---LJP 0.01 0.00 0.00 0.00 0.00 ---OSC 0.01 0.01 0.00 0.00 0.00 0.00 WAR 0.00 0.00 0.01 0.01 0.01 0.01 0.01 CAT 0.00 0.00 0.00 0.00 0.00 0.00 0.01 0.00 MLH 0.00 0.00 0.00 0.00 0.00 0.00 0.01 0.00 0.00 ----------------------



Figure 25 Discriminant Analysis of Principle Components including; (A) individuals from all 29 sample location across the state of Victoria (colour coded by fishing zone); (B) all individuals excluding the eastern zone and Port Phillip Bay sample locations

Detection of candidate SNPs under positive selection

BayPass and Latent Factor Mixed Modelling each identified a number of candidate SNP loci exhibiting significant genotype-by-environment associations for each of the environmental covariables tested (Table 21). BayPass identified between 14 (0.26%) and 76 (1.45%) SNPs with significant correlations (log10(BF) > 3) for each of the environmental covariables (average = 49.28 SNPs; 0.94%), while a significantly larger number of SNP loci showed significant correlations with summer SST (658 SNPs; 12.60%). In contrast, LFMM identified between 0 (0%) and 147 SNPs showing significant correlations (q < 0.001) with each of the environmental covariables (average = 70.86 SNPs; 1.35%). LFMM analyses could not be performed on categorical data, therefore estimates for reef geology are not provided. For each of the environmental covariables between 0 and 5 SNPs were identified by both BayPass and LFMM as exhibiting significant correlations.

			LFMM		
	3 < BF < 10	10 < BF < 20	BF > 20	q <0.001	Total candidates
Geology	54	18	4	NA	79
VRM	48	23	3	95	164
Winter wave power	46	12	6	147	208
Summer wave power	39	11	5	126	179
Winter orbital velocity	13	0	1	64	78
Summer orbital velocity	13	7	0	64	84
Summer avaregae SST	268	270	120	0	658
Seasonal temp range	24	18	0	0	42

Table 21\_Numbers of candidate SNP loci identified as having significant correlations with environmental covariables by BayPass and LFMM.

Discriminant Analysis of Principle Components (DAPC) was performed on independent datasets consisting of SNP loci showing significant correlations with each environmental covariable (putatively neutral SNP loci were omitted from each analysis). Patterns of genetic differentiation between ecotypes are graphically depicted following the retention of principal components and discriminant functions that captured between 60 and capturing 85% of the total variance within each SNP dataset. To visualise patterns of genetic structuring populations were colour coded based on their respective ecotypes. For geology, which is a categorical variable, this involved colour coding populations sampled from the various substrate types (blue = basalt, black = calcareous, red = granite;



Figure 26). For the remainder of the continuous environmental variables, populations were colour coded based on ecotype scores (low, intermediate, high). When plotted across the x- and y-axes patterns of genetic structuring is observed separating populations from basalt, calcareous and granite reef systems. Likewise, genetic structuring between populations from reef complexes of low, intermediate and high VRM values is evident (



Figure 26). For summer wave power and orbital velocity, populations with low, intermediate and high environmental values separate across the axes, while patterns associated with winter are less clear (Figure 27,

Figure 28). Finally, DAPC plots indicate genetic structuring between populations of varying seasonal temperature ranges, while patterns associated with summer SST are not clear despite a disproportionately large number of SNP loci having significant correlations with this covariable (Figure 29). However, this could be due to a large number of loci are contributing to selection and may differ between populations.



Figure 26 DAPC plots based on candidate SNPs putatively under selection and associated with habitat geology (substrate and VRM)



Figure 27 DAPC plots based on candidate SNPs putatively under selection and associated with winter and summer wave power.



Figure 28 DAPC plots based on candidate SNPs putatively under selection and associated with winter and summer orbital velocity.



Figure 29 DAPC plots based on candidate SNPs putatively under selection and associated with summer sea surface temperature and seasonal temperature range.

# 8 Discussion

## 8.1 Oceanographic Variables

Much of the science concerning climate change impact on marine communities has focussed on changes in temperature, sea level rise (Harley et al. 2017), and acidification (Poloczanska et al. 2007, Kroeker et al. 2013). Less is known about the impacts of changing hydrodynamics despite the influence of wave climate on the distribution and productivity of coastal and marine communities (Wernberg and Thomsen 2005). Wave energy has been shown to be a primary variable influencing the morphology, community structure and spatial organization of taxa in the marine coastal zone (Rattray et al. 2015) and determines benthic habitat availability through a number of direct and indirect processes (Young et al. 2015b). In particular, sessile benthic taxa are reliant on water circulation for delivery of nutrients and oxygen, and removal of waste. 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. In addition, ocean currents 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.

Climate change is a reality for Victoria's fisheries with notable changes in sea surface temperature and modelled wave climate over the last 25 years evident. Downscaling these parameters by integrating high resolution bathymetry in a coupled hydrodynamic and wave model, our study shows modelled changes to be spatially variable across Victoria. We have identified emerging hotspots indicating that an increase in wave energy for Victoria's southward facing coasts has had the greatest ramification for the western and central zones of the state over this period. Our results are corroborated by an analysis of a 30-year historical global altimeter record showing globally increasing wave heights over this period with greatest increases observed in the Southern Ocean (of order 0.7cm/year) (Young et al. 2011). 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 30-50 cm over the 21st Century (Hemer et al. 2013). Changes in the position of storms may lead to

wave direction changes which has the potential to influence coastal stability and likely impacting sedimentation patterns in coastal reefs impacting habitat quality, dispersal of larval phases, habitat suitability, and food supply. As a result, these future storm-driven shifts in the coastal environment could alter the dispersal trajectories and recruitment patters in abalone and SRL. The effects this has on dispersion of larvae and propagules and their subsequent exposure to wave energy will influence benthic community composition thereby changing the distribution of suitable habitat for abalone and SRL and influencing their recruitment patterns in ways that may give rise to spatial shifts in fisheries productivity.

Considering the importance of oceanographic variables in explaining abalone biomass, and dispersal pathways for abalone and SRL, there is a likelihood that changes in oceanographic patterns will impact these species as well as the habitats that they are reliant on (i.e. macroalgae reefs) (Reed et al. 1988, Wernberg et al. 2005). In California, Young et al. (2016a) showed that there was a hyperbolic relationship between the persistence of *Macrocystis pyrifera*, a canopy forming macroalgae, and increasing wave orbital velocities. This relationship indicates that increases in wave action have a positive relationship with this habitat forming species up to a certain threshold and then that relationship becomes negative. With high wave energy capable of removing macroalgae (Wernberg et al. 2005), increases in these disturbance events could indirectly affect abalone and SRL populations by removing the habitat-forming species they rely on. Additionally, local wave and circulation climate has a significant impact on the retention and dispersal of larvae and propagules (Treml et al. 2015) and therefore determines, in large part, the local persistence of many demersal/sessile marine populations (e.g., abalone, SRL). The local hydrodynamic environment along the coastal zone determines the location and strength of propagule adventive and retention zones contributing to the selfreplenishment of local populations and the connectivity between protected/managed areas with these fished zones which is likely to change based on future projections. The increase in current velocities observed shows a spatial association with the lee of headland to the prevailing wave energy. In particular, topographically-induced changes in wind speed and wind stress curl are usually associated with flow variability, formation and growth of instabilities around capes and promontories. This suggests that as wave climate increases, so will the strength of counter currents that are likely to develop in the lee of these headlands, potentially changing dispersal pathways.

Bass Strait marks the confluence of the warm waters of the Eastern Australian Current (EAC) that flow further south seasonally along the east coast and the colder waters of western Bass Strait from the South Australian Current. Timeseries SST data shows the strengthening of the East Australian Current with some local and regional environmental changes impacting species ranges (Parmesan et al., 1999, Thuiller, 2004, Lough & Hobday, 2011). Oceanic waters in southeast Australia are experiencing rapid warming, three to four times the global average, making this region a hotspot for ocean temperature change (Ridgway, 2007). The distribution of urchins, especially *Centrostephanus rodgersii*, has historically been restricted to subtidal reefs along the coasts of New South Wales (NSW), eastern Victoria, and the Flinders Island Group in the Bass Strait (Andrew and O'Neill 2000). In recent years, the range of *C. rodgersii* has expanded southwards to the east coast of Tasmania and westward along the coastline of Victoria, specifically in the region identified as an emerging hotspot on the east coast (Ling et al. 2009). Emerging hotspots in SST are also observed in Western Port and Port Phillip Bay and may exacerbate the effects from changes in nutrient inputs from rivers, streams, water treatment discharges and runoff on key species such as abalone, urchins, and sand flathead, which over the past decade have undergone large changes in abundance.

## 8.2 Biophysical models

The potential dispersal patterns quantified through the biophysical modelling show some strong geographic patterns which appear to be broadly consistent with contemprorary understanding. Although there remains some uncertainty in several of the biological and physical parameters (e.g., larval mortality, maximum competency, reproductive output, stratified current speeds), the larval connectivity distance of abalone appears to be on the order of less than 50 km (perhaps occasionally up to 100 km). This scale is consistent with the results of a drift tube study simulating the dispersal of abalone in California (Tegner and Butler 1985). Southern Rock Lobster (SRL), with larval stages over a year, has the capacity to consistently disperse up to several 100s of km (200-500 km) with longer distances possible for several locations. These dispersal distances are similar to those published for other marine invertebrates (e.g. Kinlan and Gaines 2003). The dominant direction of connectivity for abalone and rock lobster is from west to east through the seascape, with potential connectivity to New Zealand for the SRL. These results are mostly concordant with genetic studies of Southern Rock Lobster which demonstrate that although there are differences between Australian and New Zealand populations (Morgan et al. 2013), there is clear evidence of gene flow from Tasmania to

New Zealand (Villacorta-Rath et al. 2016). In addition, with the relatively short larval phase of abalone, there appears to be some evidence for a dispersal corridor from Tasmania, potentially influencing the recruitment dynamics of Victoria's central and eastern zones. In this respect, the scale of significant larval dispersal for abalone is quite local, with some longer-distance dispersal (to 100s km) possible for those sources in exposed sites.

Identifying those sites which may serve as persistent sources of larvae to the broader seascape may help identify candidate sites for management actions. For abalone, these key sites were 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 with potential recruits. Management strategies accommodating these potential strong source populations would help ensure a longer-term and persistent abalone fishery. Source sites for SRL, on the other hand, are more geographically distributed making strong management recommendations related to dispersal pathways more difficult, but does suggest multiple sources may contribute to recruitment on local and regional scales and enhance population resilience to fishing pressure and environmental disturbance (e.g. disease). A fishery of this broad geographic extent may therefore have to be dependent on multi-jurisdictional coordination at regional scales. In fact, a significant proportion of SRL recruits to Victoria are likely to have originated from outside of the state of Victoria (South Australia and Tasmania). In addition, managing for the uncertainty in these dispersal estimates is critical. With an exceptionally long larval dispersal period, the SRL simulations necessarily included fewer larval release periods (76 releases over 20 years), and translating these results into management actions requires caution.

In light of the emergent community structure or partitioning in the abalone dispersal networks, and the position of key stepping-stones, there appears to be clear divisions within Victoria's coastal zone. Regions separated by Cape Otway, Wilsons Promontory, and Bass Strait appear strongly delineated, with potential boundaries occurring around the Western Port entrance and Lake Tyers (or Gippsland Lakes) estuary in the east. In contrast, the clustered structure for SRL is less cohesive at a regional scale, with Victorian SRL populations clustering with Tasmania and perhaps acting as a source to populations in New Zealand. West of Victoria, the SRL habitat is well connected without strong barriers and largely acts as a source to the reefs of coastal Victoria and Tasmania. Genetic studies of SRL puerulus indicate that the source of recruitment at any

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one site can vary, suggesting that population connectivity fluctuates through both time and space (Villacorta-Rath et al. 2018), however the long term trend of this fluctuation ultimately results in a lack of differentiation of amongst south-east Australian populations (Villacorta-Rath et al. 2016) suggest strong geneflow and dispersal in the area.

## 8.3 Spatial Models

#### 8.3.1 Spatio-Temporal Modelling of Abalone Biomass

Understanding how species are distributed throughout their environment and those factors that drive that distribution are important for developing effective management strategies, especially with changing oceanographic conditions related to climate change. In this study, we looked at temporal and spatial variability in the distribution of Blacklip Abalone along the coast of Victoria, Australia. We associated a downscaled hydrodynamic dataset hindcasted over 25 years, a 20 year dataset on sea surface temperature patterns, annual connectivity information from biophysical modelling, seafloor structure information collated from existing LiDAR and multibeam bathymetry data, and spatial variability in a virus outbreak with Blacklip Abalone biomass derived from long-term, fishery independent diver surveys to understand long-term patterns in abalone productivity. Our results show that a variety of these factors can be combined to accurately determine distributions of Blacklip Abalone.

The BRT analysis showed that summer SST was the most important variable correlated with the biomass distribution of Blacklip Abalone across Victoria, accounting for 25% of the influence in the model. Based on this relationship, increasing summer SST will have a negative influence on biomass, with lower biomass values associated with higher temperatures. This result is consistent with Jalali et al. (2018), which found that increases in SST resulted in lower abundance of Blacklip Abalone. Based on the results of our hot spot analysis along this coast and future projections for increased SST in southeast Australia, temperature could have a major negative effect on future productivity throughout the abalone fishery in Victoria. With the strengthening of the East Australian Current causing an increase in warmer waters being transported to the southern coast, the rate of ocean warming in southeast Australia is faster than the global average (Butler et al. 2007).

After summer SST, annual self-recruitment was the second most influential variable in the model. The overall relationship between biomass and self-recruitment is negative, but the relationship is variable. At

lower levels of self-recruitment, there is a slightly positive increase in biomass up to about 0.30. Following that threshold, biomass tends to decrease with increasing self-recruitment, with the exception of a few intermittent increases. Earlier research suggested that local abalone populations are predominantly self-recruiting (Prince et al. 1987, McShane et al. 1988, Prince et al. 1988) but more recent genetics research has found a lack of genetic structuring at local spatial scales, indicating recruitment is not predominantly local in Victorian fisheries (Miller et al. 2016). These findings align with the positive association we found between productivity and the number of incoming connections (in degree) to each reef. In the model, in degree was the fourth most important variable with an influence of 11.8%.

The hydrodynamic variables which were identified as important in explaining the spatio-temporal distribution of Blacklip Abalone biomass were annual maximum current speed and maximum winter wave orbital velocities. Maximum current speed was slightly more influential (12.1%) and displayed an asymptotic relationship with biomass. This relationship shows a sigmoidal pattern in which current speeds between 0 and 0.25 m/s are associated with very low biomass and then biomass drastically increases prior to becoming relatively stable with further increases in current speed. Because of the sedentary nature of abalone and their reliance on opportunistic feeding on drift algae (Gorfine 2002), higher current speeds could be providing more food sources across the reefs. In addition, areas of increased current speed could be associated with increased delivery of larvae. The primary dispersal phase of Blacklip Abalone lasts up to 10 days (Hahn 1988) and, therefore, dispersal distance during that phase will vary based on current speed. The relationship between biomass and maximum winter wave orbital velocities was less clear but nevertheless influential in the model (10.6%). There appears to be an overall negative relationship with increasing orbital velocities associated with decreasing biomass. However, that relationship is not dramatic and there is variability across changes in orbital velocity. Because water movement is important for nutrient delivery to the system, some level of exposure is necessary but too much exposure can cause smothering or dislodgment of smaller abalone (McShane and Naylor 1996). Based on the BRT from this study, increases in wave orbital velocities above ~0.75 m/s results in decreased biomass signifying that more productive areas have some degree of protection from the wave environment.

Those variables associated with the structure of the seafloor were secondary to environmental conditions driven by oceanographic processes but were still important for explaining the finer, reef scale variations in

biomass across the state. Of these variables, depth had the strongest influence on the overall model (7.9%). Biomass had a relatively steady relationship with depth from 5-20 m with a sharp decrease in biomass shallower than that. As a relatively shallow dwelling species (McShane 1994), Blacklip Abalone don't inhabit an extensive depth range but there appears to be a decrease in biomass in very shallow depths (< 5m). These results could be explained by greater water movement causing smothering or dislodgement of recruits in shallow habitat as was found by McShane & Naylor (1995) during their study on Haliotis iris. Reef area was the second most important seafloor variable with increasing biomass correlated with increased area of the reef. Based on the theory of island biogeography (MacArthur and Wilson 1963), larger "islands" are more likely to support larger populations. Additionally, larger reef areas also provide bigger targets for larval settlement. Bathymetric position index (BPI) at the 50 m scale had a 6% influence on the overall BRT model and there was a negative relationship between increases in relative elevation and biomass. Based on these results, higher biomass tends to be found in lower elevations of the terrain (e.g. valleys and crevices). One potential reason for this pattern is likely accumulation of drift algae in these lower areas (Figurski 2010), which is an important food source for Blacklip Abalone. The gutters and surge channels likely associated with these lower regions in the terrain help to concentrate macro-algal drift, enabling opportunistic feeding by abalone (Gorfine 2002). The final seafloor structure variable incorporated in the model with an influence of 4.9%, was vector ruggedness measure (VRM), a measure of the complexity of the seafloor. Seafloor complexity has been previously associated with increases in diversity and abundance of invertebrates (Holmes et al. 2008, Galparsoro et al. 2009) and provides suitable habitat, feeding, and breeding grounds for benthic organisms (Kuffner et al. 2007, Alexander et al. 2014). The relationship between biomass and VRM in our model showed that biomass increases with increasing complexity up to areas of moderate complexity. Then, there is a slight decrease followed by a levelling off. This pattern shows that the highest biomass is found in moderate complexity terrain with lower biomass in areas of low and high complexity.

The categorical variable for infection of abalone viral ganglioneuritis (AVG) was the final variable used in the BRT and had an overall influence of 2.2%. This virus caused an epidemic resulting in catastrophic mortality across all size and age classes with mortality rates of >95-30% along a 280 km section of the western region of the fishery (Gorfine et al. 2009). Those areas and years outside the infection range of the virus were associated with the highest abalone biomass. During the AVG outbreak from 2006-2008 in the

Western Zone (and 2008 – 2010 in the Central Zone west from Cape Otway), there was a decrease in biomass, which is expected based on the quick mortality associated with the virus (Gorfine et al. 2009). Additional decreases in biomass were also seen in the two years following the outbreak period followed by moderate increases 3-5 years after the outbreak. These results show that the biomass continued to decrease following the active period of the outbreak but there are slight increases in biomass in recent years.

The combination of these environmental variables and their associations with abalone biomass across Victoria allowed us to accurately model the spatial and temporal distribution of Blacklip Abalone, including into areas where no observation data currently exist. Although the final BRT model does not explain all the variation in biomass, the model accounted for 62% of the variation. Additionally, the predictions from the BRT model had a 78% correlation within the training dataset and 66% when we compared the predictions to a reserved dataset not used in the model. Although not perfect, these models provide guidance on which habitats are most suitable for supporting highly productive abalone populations with reasonable accuracy. In addition, by extrapolating those predictions over the entire study area across multiple years, we can use those predictions to help understand how habitat and changing oceanographic conditions are affecting these populations.

## 8.3.2 Emerging Hotspot Analysis of Predicted Abalone Biomass

We used the BRT model and all of the spatially explicit environmental layers to create a time series of predictive grids from 1995 to 2015. The resulting predictive grids showed that there is both temporal and spatial variability in the biomass distribution of Blacklip Abalone within the coastal zone of Victoria. We then used the predictive grids in the emerging hot spot analysis tool to analyse spatial and temporal trends in predicted biomass. While ~40% of the predicted abalone habitat shows no notable trend in abalone biomass, the remaining habitat indicates a declining trend. The results should be interpreted with caution as the annual biomass model used for model input explains 62% of the variability in biomass observed, thus a large proportion of the variability is unexplained in model outputs used to drive the emerging hotpots analysis. However these data do provide a glimpse into probable spatial change in biomass across the fishery previously not possible over a 21 year period.

#### 8.3.3 Southern Rock Lobster Case Studies

We looked at two different sites to determine the impact of habitat and protected status on the distribution of Southern Rock Lobster (SRL) in Victorian coastal waters. From these two areas, we got very different results in how those factors are affecting the distribution across different life histories of SRL. The data collection and analysis from the Merri Marine Sanctuary (MMS) showed that this small MPA is potentially having a positive impact on populations of SRL within its boundaries and in locations adjacent to it. In accordance with other studies that have looked at the effect of MPAs on SRL populations (Kelly et al. 2000, Shears and Babcock 2003, Barrett et al. 2009, Freeman et al. 2012), we found that more and larger individuals were found inside the MMS boundaries compared to inside. These patterns were consistent even when we used GLMs to incorporate the potential impacts of habitat on distribution.

In contrast to the findings from the MMS, the SRL sampling in Wilsons Promontory (WP) provided different results. We found no significant differences between population characteristics inside and outside the boundaries of the MPA when accounting for habitat and the GLMs were unsuccessful at explaining variation in SRL populations across varying environmental conditions even when accounting for the increased zeroes in the dataset. Despite this lack of difference within the study area and failure to model distribution of the WP populations, there were large differences between this site and the MMS. The individuals captured in WP were much larger across the whole study area and there were much fewer individuals. There are some potential causes for the difference in size of individuals between these two study areas. First, the remoteness of WP and its distance from the nearest port is much greater than in MMS, potentially providing an opportunity for lobsters to reach larger sizes without strong fishing pressure both inside and outside the reserve. Additionally, there is known spatial variation in growth rates of SRL, which could be linked to density-dependent processes (McGarvey et al. 1999). McGarvey et al. (1999) completed a study in South Australia on SRL populations and found that, in areas where habitat is more fragmented and catch is lowest, the growth rate is fastest. These findings could potentially help explain the lower numbers and larger size of individuals in WP.

In the study done in the MMS (Young et al. 2016b), we found that biotope complex was the most consistent and important environmental variable associated with SRL distribution and abundance. The presence of macroalgae, which is classified in the biotope complex, helps to reduce predation risk, increase structural

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complexity, and provide habitat for prey species (Villegas et al. 2007, Kovalenko et al. 2011). These services provided by macroalgae are likely important to the distribution of SRL. Unfortunately, we did not have data available for biotope complexes at the sampling locations in WP at the time of this study. Future work, however, could look at the potential of extrapolating biotope complex characterisations from nearby regions where classified video data are available to improve the modelling of lobster-habitat relationships in WP.

The sampling conducted on SRL in these two, differing regions displays the variability in lobster populations across the coast of Victoria. There is a need for additional sampling locations along the coast to better understand the relationships between lobster populations, habitat, and protected status. Despite these limitations of the current dataset, the methods we used for both of these surveys are the first step towards determining which variables are correlated with SRL abundance and distribution. They not only allow us to gain information about the ecology of the species but also help to determine the benefit of protected areas on SRL populations. The MMS dataset, an area strongly targeted by fisheries, shows there is a possible benefit of the sanctuary to supplementing the fished population in the area. As more sites are added in this study, we can begin to determine if the MMS is an anomaly or if we are seeing similar patterns along the coast. Other studies have shown that small MPAs can help populations recover by protecting critical habitat (McLeod et al. 2009). Overall, these small case studies are the start to providing a baseline assessment of SRL populations inside and outside MPAs, which can be sampled through time to follow population trajectories.

## 8.4 Population genomics

### 8.4.1 Neutral genetic structure

Analyses based on putatively neutral genomic loci indicate a lack of genetic structuring among Victorian western and central zone Blacklip Abalone stocks spanning from the South Australian border to Wilsons Promontory, which is highly consistent with previous genetic studies (Brown 1991, Conod et al. 2002, Li et al. 2006, Miller et al. 2016), and the connective analysis presented here (Figure 12-17a). In contrast, abalone stocks from the Victorian eastern zone fishery (east of Wilsons Promontory) appear to be weakly genetically differentiated, possibly influenced by breaks in population connectivity (Figure 17). These findings are largely consistent with community structure analyses generated by our biophysical models (Figure 17), and biogeographic and genetic studies suggest that community assemblages either side of the Wilsons Promontory region differ genetically (York et al. 2008, Ayre et al. 2009, Colton and Swearer 2012, Miller et

al. 2013). This structuring has been attributed to historical (Lambeck and Chappell 2001) and contemporary physical factors, such as converging ocean currents (Figure 17), environmental gradients (temperature and salinity) and habitat discontinuities that persist in the region (Baines et al. 1983, Ridgway and Godfrey 1997, Ridgway and Condie 2004, Sandery and Kaempf 2007, Colton and Swearer 2012). Gene flow also appears to be somewhat limited between Port Phillip Bay and the remaining Central Zone sample locations. Again, this is consistent with the oceanography of the region, with the low flushing rates of Port Phillip Bay (~270 days; (Walker 1999) likely limiting gene flow to some extent between local stocks and those from outside coastal waters. The apparent mismatch between the connectivity model (Figures 15 17) showing stronger population connectivity between PPB and the open coastline may be due to the very northerly sampling locations for the genetic data (Figure 7c) and the inclusion of all potential habitat in PPB in the biophysical model. Earlier work shows the relative environmental and hydrodynamic isolation of northern PPB (Treml et al. 2015), possibly contributing to the limited gene flow shown here.

The genetic homogeneity between the Victorian Western and Central Zone Abalone Fisheries indicates that gene flow is occurring over large spatial scales. However, these data alone cannot be used to quantify the extent of gene flow and connectivity between fishing stocks, as panmixia (genetic homogeneity) can be theoretically achieved by low levels of effective migrants per generation (Waples et al. 2008, Lowe and Allendorf 2010, Meirmans and Hedrick 2011). Also, like most previous studies, our geographic sampling was biased towards commercially fished stocks with large effective sizes (Ne > 10000) and potentially not at migration-drift equilibrium (Slatkin 1993, Hauser and Carvalho 2008). However, Miller et al. (2016) previously addressed this issue by sampling within and across abalone habitats at a range of spatial scales, and targeting small local populations expected to be susceptible to drift processes; assuming local populations are predominantly self-recruiting (Prince et al. 1987, McShane et al. 1988, Prince et al. 1988). Such sampling approaches have been previously adopted to identify significant patterns of local genetic structure in various benthic marine species from southeastern Australia, including Haliotis species (Piggott et al. 2008, Miller et al. 2014, Teske et al. 2015). However, Miller et al. (2016) found no evidence of local genetic structuring among fishing stocks from multiple regions across the Victorian coastline, indicating that recruitment at local scales is influenced from larval supply from non-local sources. As these findings differ from those reported from Tasmanian Blacklip Abalone fisheries where local genetic structuring was evident, Miller et al. (2016) suggest that larval movement is likely to be variable within and between fisheries due to

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oceanographic factors. This notion of spatially and temporally variable larval movement has since been further supported by biophysical models undertaken in this study and supported by the variable importance analysis in the biomass modelling.

#### Evidence of locally adaptive genotypes influencing recruitment processes

The population genomic analysis undertaken in this study has taken advantage of unique high-resolution benthic habitat maps and oceanographic data to develop one of the most sophisticated experimental designs for testing for patterns of genetic selection in any marine species. Identifying signatures of selection using genomic tools is critically dependent on a well replicated sampling design capturing populations distributed across different habitat types and defined environmental gradients (Frichot et al. 2013). In terrestrial systems where habitat heterogeneity is relatively easy to measure, and is often well described, genomic studies of this nature are common, many of which have demonstrated evidence of selection operating on both local and regional scales (Buehler et al. 2013, Jordan et al. 2017, Termignoni-Garcia et al. 2017, Pfeifer et al. 2018). In contrast, the availability of information on the heterogeneity of marine habitats (particularly the connectivity and complexity of benthic habitats) is limited for most of the world's coastlines, inhibiting our ability to develop effective sampling regimes for testing patterns of genetic adaptation and the scales at which selection operates in marine environments. For this reason, the majority of population genomic studies which have described patterns of genetic adaptation in marine environments have been limited to sampling regimes structured over broad longitudinal and latitudinal environmental gradients (temperature, pH, salinity gradient) (Hess et al. 2013, Milano et al. 2014, Sandoval-Castillo et al. 2018), limiting their ability to test for patterns of selection on local spatial scales.

Strong signatures for adaptive genetic structure associated with temperature and salinity gradients spanning hundreds of kilometres have recently been reported in *Haliotis* species, including *Haliotis laevigata* and *Haliotis roei* populations from Western Australia (Sandoval-Castillo et al. 2015, Sandoval-Castillo et al. 2018), and *Haliotis rufescens* from California in the United States (De Wit and Palumbi 2013). The present study has revealed for the first time that selection processes in abalone fisheries are potentially responding to environmental heterogeneity at not just broad regional scales (10s to 100s of kilometres) but also local spatial scales (hundreds to thousands of meters). Two complementary analyses have identified numerous candidate genetic markers showing significant genotype-by-environment associations (GEAs) with respect to

several environmental factors that vary within and between Victorian abalone fishing zones. These include factors relating to local reef geology, exposure to wave power and ocean currents, and sea-surface temperature. Without further quantitative assessments it is not possible to determine if these factors are influencing selection directly or indirectly. For example, substrate type can influence benthic community composition, biological interactions and resource availability (Edmunds et al. 2000 ). Likewise, VRM is a physical measure of habitat structure where structure can also influence benthic community compositions and biological interactions, as well as exposure and oxygenation, and nutrient and resource availability. This is also true for reefs that vary with respect to exposure to wave power and ocean currents (Young et al. 2015b). As a result, the exact drivers of selection are not clear, but selection is responding to habitat heterogeneity at local and regional scales. Interestingly, GEAs indicate that variation in summer wave power and orbital velocity are likely to contribute strongly to local adaptation compared with winter months. This is consistent with our current understanding of the Blacklip Abalone life cycle, where spawning typically occurs during the warmer months of the year (between February and April and again between October and December (McShane and Smith 1991), and the literature which suggests selection can act strongly on early life stages (Fraser et al. 2008, Postma and Ågren 2016).

Our findings indicate that the recruitment potential (larval supply) and productivity of specific reef complexes is potentially influenced by genetic factors, in addition to the environmental and oceanographic factors highlighted above. Effectively, selection could be determining which habitat types a larva with a given genetic make-up can or cannot recruit to, despite arriving to a habitat patch during dispersal. Our biophysical models indicate that the integrity of many Victorian abalone fishing stocks is likely to be dependent on larval supply from non-local sources. In such cases recruitment potential of a given reef is determined by the supply of admixed larvae from different reef complexes following a spawning event. The distance which larvae move and the degree of admixture will be determined by abiotic factors such as current intensity and wave power, and biotic factors such as population sizes. However, the results from our genomic study indicate that natural selection is possibly influencing where individual larva can recruit, depending on the local habitat type and the compatibility of their genotype (suitable habitats being closely matched with natal habitats). For example, the progeny of abalone parents from low energy environments are less likely to have a genetic makeup allowing them persist in habitats exposed to high energy. Similarly, the progeny of abalone parents from basalt reef complexes are expected to have a genetic makeup best suited for habitats

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with basalt substrates. Further research is needed to determine the true influence of local genetic adaptation on the productivity of reef codes across the fishery. Hypothetically, high performing stocks might represent common habitat types meaning that they have the greatest recruitment potential (high density of larvae with compatible genotypes in the water column), while poor performing stocks might instead represent rare habitat types meaning that opportunities for the settlement of larvae with compatible genotypes is significantly lower.

Natural selection could potentially be occurring at pre- or post-settlement stages in Blacklip Abalone. In some marine species environmental cues influence the settlement of larvae from the water column (Rodriguez et al. 1993, Sneed et al. 2014). In regards to members of the *Haliotis* genus, larvae can settle in response to encrusting coralline algae (Morse et al. 1984), macroalgae (Huggett et al. 2005), and mucus trails (Takami et al. 1997). For Blacklip Abalone specifically, anecdotal evidence from commercial farm operations indicate that larvae can remain suspended in the water column for more than 30 days, with settlement triggered by the introduction of macroalgae to the water column (AAGA Pers. Comm.). It is possible that abalone larvae with different genotypes respond to specific cues, maximising the chance of establishing and surviving through to adult life stages by settling upon suitable habitats (Meyer et al. 2009). Conversely, selection may occur post-settlement, where settlement of mixed genotypes might be occurring, and only those with environmentally compatible genotypes are capable of establishing and surviving through to adult life stages (Plough et al. 2016). There are many examples in the literature demonstrating that individual fitness under local environmental conditions is dependent on genetic profiles (Hess et al. 2013, Manthey and Moyle 2015, Nayfa and Zenger 2016). This has been identified as a possible constraint on larvae settlement and subsequent survival following reproduction in highly dispersive marine species (Marshall et al. 2010, Moody et al. 2015). Post-settlement juvenile mortality is known to be extremely high in Haliotis (McShane and Smith 1991, Kiyomoto 2007). This study indicates that post-settlement selection could be a contributing factor to high juvenile mortality and warrants further investigation.

These findings add another level of complexity to our understanding of the recruitment processes shaping Victorian abalone fisheries. However, this information improves our knowledge of the factors influencing stock connectivity and potential drivers of productivity across the fishery. It is important to note that while the resolution of genetic patterns observed in this study has not been previously demonstrated for any other marine organism (as far as we are aware), these findings are not novel nor unexpected. Over the last decade numerous studies have reported that local and regional habitat heterogeneity (e.g. geological, ecological and climatic factors) contribute strongly to local adaptation and recruitment processes in terrestrial systems (Buehler et al. 2013, Jordan et al. 2017, Termignoni-Garcia et al. 2017, Pfeifer et al. 2018). Therefore, the results from our study are unsurprising, particularly given the heterogeneity of marine benthic habitats along south-eastern Australia (Ierodiaconou et al. 2011b). The power of our analyses was made possible by the availability of high definition marine benthic habitat maps and oceanographic data for developing a replicated hierarchical sampling design comprising abalone populations distributed across different habitat types and defined environmental gradients. This is a unique geospatial dataset, but as data acquistion on the complexity and connectivity of coastal habitats around the world expands so will opportunities for characterising patterns of genetic adaptation and the scales at which selection operates in other fisheries.
## 9 Implications

This study provides the first state-wide high-resolution assessment of the extent of abalone biomass derived from integrating fishery independent data with seafloor mapping, oceanographic parameters and measures of stock connectivity to inform models and how abalone biomass varies in space and time. Abalone are not distributed uniformly on temperate reefs and tend to be patchy at various spatial scales. The boosted regression tree approach adopted in this study was able to explain over 60% of the spatial and temporal variability in abalone biomass within Victorian coastal waters across the study period. This approach represents the first time that dynamic oceanographic parameters, variability in dispersal patterns, and localised seafloor structure were combined into a single model to understand how the combination of these factors are driving variation in the productivity of Blacklip Abalone, Haliotis rubra, populations. These models developed for biomass predictions were reliant on data collected from fishery independent survey locations, which is the only spatially-explicit datasets available that provide long-term biomass information (1995-2015) across the state to develop these environmental relationships and resulting predictions. Therefore, we assume that the relationships between biomass and the environmental covariates extend beyond the fishery independent sampling locations and provide insight into the biomass distribution through time across the state. These models could potentially be improved in the future by combining the fishery-independent data with spatially explicit biomass data from precise geo-referenced fisheries catch data, which would allow the addition of more sites in areas that are not currently sampled by the fishery-independent surveys.

In addition to abalone, we also collected and analysed data from two pilot studies on localised populations of Southern Rock Lobster (SRL; *Jasus edwardsii*) to assess variation inside and outside two MPAs. Through these studies, we found that there is a need for more spatially-explicit data on *J. edwardsii* to understand the link between oceanography, recruitment, habitat, and protection status. The study in Merri Marine Sanctuary (MMS) showed that there are strong relationships between *J. edwardsii* and benthic habitat factors. Additionally, there is the potential positive benefit of the MPA for preserving biomass, as we found significantly larger and more individuals within the boundaries of the MPA compared to outside. However, the results from Wilsons Promontory (WP) differed from those around the MMS with no

significant differences inside and outside the MPA and a lack of strong relationships with habitat. These differences could be due to a number of factors including lower recruitment to the area around WP. The individuals captured in and around WP were much larger and found in lower numbers, potentially representing a single recruitment event. To better understand these spatial differences in productivity across the *J. edwardsii* populations in Victoria and the potential benefit of MPAs for increasing productivity, there is a need for more spatially-explicit observation data, similar to the fishery-independent abalone dataset that allowed us to successfully model abalone productivity. Access to these types of datasets would allow us to better understand how the environment and protection by MPAs are affecting *J. edwardsii* productivity.

The development of the associations between these important fisheries species and the underlying seafloor structure was reliant on high-resolution information of seafloor habitat derived from a combination of LiDAR and multibeam bathymetry data. These data provide the first detailed information about seafloor structure across the Victorian coastal fisheries. Having access to bathymetry derived habitat information has direct benefits to users and managers of a fishery where the stock varies across extremely small spatial scales. For example, prior to commencing this study, only coarse scale information about the distribution of reef structure and abalone fishing grounds was available. McShane et al. (1986) delineated productive abalone reefs, which were identified through aerial photography and commercial abalone diver consultation. In the past, these findings have been used to stratify monitoring localities and avoid the inclusion of reef areas that do not produce commercial quantities of abalone. These previous approaches were limited, as light attenuation often results in poor visibility through the water column, making it difficult to define reef extents in deeper water using aerial imagery. It also provides limited information about fine scale localised variation in topographic complexity that may influence habitat availability within these reef systems.

The hydrodynamic datasets developed for this project and the temperature information compiled for the region provide important information on how the Victorian waters vary spatially and temporally over a long (25 year) time period. Whilst much of the science concerning climate change impact on marine communities has focussed on changes in temperature, which we show is changing notably throughout the

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region, less is known about the impacts of changing hydrodynamics on marine habitats and the fisheries they support. By downscaling hydrodynamic parameters through the integration of high resolution bathymetry in a coupled hydrodynamic and wave model, we show changes are modelled to be spatially variable across Victoria. We have identified emerging hotspots indicating an increase in wave energy for Victoria's south facing coasts with greatest ramification for the western and central zone of the state over this period. Our results are corroborated by an analysis of a 30-year historical global altimeter record showing globally increasing wave heights over this period with greatest increases observed in the Southern Ocean (of order 0.7cm/year) (Young et al. 2011). Future projections indicate 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). Our abalone biomass modelling suggests that changes in oceanographic variables (e.g. increase wave energy and ocean temperatures) are likely to have a negative impact on Victoria's abalone fishery.

The findings from our population genomic analyses and biophysical models, combined with those from previous ecological (Prince et al. 1987, 1988; McShane et al. 1988), and genetic (Temby et al. 2007; Miller et al. 2009; Miller et al. 2016) research, indicate that larval movement and recruitment patterns are likely to be spatially variable across the Blacklip Abalone fishery. The integrity of some fishing stocks is likely to be dependent on local larval retention, and while others are dependent on larvae supply from non-local sources. Population size structure, frequency and timing of spawning events, the persistence of favourable benthic habitat, and oceanographic conditions in combination may lead to fluctuating patterns of larval movement and recruitment success across space and time, as indicated by recent genetic analyses of pink abalone off the Californian coast (Coates et al. 2014). These findings have significant fisheries management implications.

Firstly, it is likely that factors other than larval supply are likely to be influencing the recovery potential of depleted fishing stocks. Until recently, the limited dispersal capacity of larvae has been attributed to the slow recovery of depleted fishing stocks (Prince et al. 1987, McShane et al. 1988, Prince et al. 1988), however our research has shown that larval supply is not likely to be the limiting factors in all cases. Several studies have found that the removal of Blacklip Abalone can result in overgrowth of reef substrate by a range of biota (including colonial invertebrates, filamentous and foliose algae, and sediment matrix) that can have a

negative influence on recruitment (Hamer et al. 2010, Strain and Johnson 2012). A reduction of suitable habitat may therefore contribute to a slow recovery of depleted local fishing stocks, despite opportunities for larval supply. Additionally, changing hydrodynamic conditions observed are likely to influence the distribution of suitable benthic habitat, as well as altering dispersal patterns of pelagic larvae.

A new understanding of stock connectivity and the potential for larval movement provide insights into the risks associated with disease spread, and the likely resistance of fished Blacklip Abalone stocks to environmental disturbance. High levels of stock connectivity driven by larval movement suggest that any heritable diseases will have the potential to spread quickly throughout fisheries in south-eastern Australia. Larval movement will also facilitate the rapid spread of disease resistant alleles, but the evolution of resistance may be slow given the large interconnected nature of the Victorian Blacklip Abalone population. High gene flow and large population sizes are likely to enhance the resilience of fishing stocks to environmental change generally, as larval supply will help replenish affected stocks and assist in the maintenance of genetic diversity that can then respond to natural selection (Miller et al. 2016).

For the first time we have demonstrated that local and regional habitat heterogeneity may be contributing to local adaptation and influencing recruitment patterns in abalone fisheries. It appears that abalone are genetically adapted to local environmental conditions, meaning that selection is likely to be dictating where larvae with specific genetic make-ups can successfully establish and develop to adult life stages. Our geospatial analyses suggest that the productivity of fisheries stocks is significantly associated with larval supply and recruitment potential, with stocks varying in their dependency on larval supply from local and non-local sources. For the latter, the potential for larval supply will be determined by oceanographic conditions that influence larval movement, and potentially selection, which determine where larvae can and cannot recruit to depending on local environmental conditions. Consequently, selection could be directly influencing patterns of productivity across Victoria's abalone fisheries. Further research is needed to validate our findings and to quantify the true influence that local genetic adaptations have on the recruitment potential and productivity of individual fishing stocks across the fishery.

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Understanding patterns of local genetic adaptation is important for guiding stock augmentation activities. Translocation activities are used to establish new fishing stocks and to catalyse the recovery of depleted stocks. These activities require significant investment of resources, and our results suggest that managers should pay careful attention to the selection of genetically suitable animals for translocation purposes to maximise the return on investment. Failure to consider the genetic profiles of fishing stocks could lead to the movement of animals that are maladapted to their new habitat and lead to stocking failure. Population genomic studies have been used recently to guide restocking programs in Western Australia, following mass stock depletion of Roe's abalone (Haliotis roe) and greenlip abalone (Haliotis laevigata) stocks as a result of abnormal heatwave event (Wernberg et al. 2013). Sandoval-Castillo et al. (2015) revealed significant adaptive genetic differences among stocks for each species along the Western Australia coastline, associated with broad temperature gradients. The Western Australian fishing industry is using this information to guide their selection of animals for translocation (through habitat and genetic matching) to ensure the successful replenishment of depleted fisheries. In Victoria, the western and eastern zone Blacklip Abalone fisheries have also been undertaking limited translocation activities to assist the recovery of specific virus and urchin affected fishing stocks. Given the outcomes of this study we advise that managers make use of local genomic and geospatial information to guide local activities. In cases where this information is not available managers are advised to match habitats where possible (Weeks et al. 2011), or look to a composite mix of animals from a range of habitat types assuming that some animals will persist and others may perish in their new environment.

Marine ecosystems around the world are experiencing rapid environmental transformations with climate change contributing to rising ocean temperatures and the build-up of anthropogenic CO<sub>2</sub>, posing a direct threat to global fisheries (Glantz 1990, Perry et al. 2005, Poloczanska et al. 2013). This is pertinent in south eastern Australia where SSTs are rising at a rate four times that of the global average (Ridgway 2007, Ling 2008, Wernberg et al. 2011). Research geared toward assessing standing genetic variation for adaptation to more acidic and higher temperature environments is therefore important for understanding the environmental resilience of marine species and ecosystem function (Sandoval-Castillo et al. 2018; De Wit and Palumbi 2013). Furthermore, having a general understanding of how adaptive a species has been to historical

environmental changes can assist in gauging how responsive the species will be in the future. Therkildsen et al. (2013) performed a series of genome scans on populations of Atlantic cod dating back 80 years and found temporal allele frequency shifts at certain loci that correlate with local temperature variation and potential fishery induced life history changes. They argue that this evidence of historical selection has important implications for predicting future adaptive potential of the commercially important species to environmental variation. Similar studies exploring historical selection have found ongoing adaptation over time in wild populations (Orsini et al. 2012), and suggest that some species are likely to adapt to future environmental pressures. The present study demonstrates signatures of historical selection in Blacklip Abalone to a range of environmental factors, suggesting that the species may have adequate standing genetic variation and the capacity to respond positively to future environmental pressure via natural selection.

### 10 Recommendations and future development

#### Recommendations

The project findings have implications for management and the fishing sector The Victorian Fisheries Authority and the Victorian abalone industry will be embarking on the progressive implementation of a new harvest strategy and engaging in reviews of abalone fisheries management arrangements and regulations during 2019. There are a number of findings from this study that can be explicitly considered to determine how to improve the biological compatibility of management of the Victorian abalone fishery. This will involve balancing the institutional and resourcing limitations imposed on VFA as a regulatory agency with the capacity of industry to undertake an increased level of self-determination supported by VFA within the existing or a revised regulatory framework. To some extent this is already occurring with size limits and catch targets being regulated at sub-zonal scales by VFA and industry actively collecting spatially resolved data about fishing events on a voluntary basis, but industry could take this further via regulated adoption of technology e.g. VMS which provides greater regulatory efficiency and surety upon which finer scale approaches can be based. The 2019 regulatory review will also affect SRL providing an opportunity for similar enhancements to the management of the fishery.

- The geographic structure of abalone connectivity and biomass patterns are variable and driven at a finer scale than the current management structure. Future assessments and management may consider a more fine-scale (reef level) strategy to optimise fishery regulations to ensure a long-term sustainable stocks.
- The abalone biomass hotspots and primary larval sources are in the western and west central management zones. An investment strategy whereby a proportion of productive reefs across these zones are actively managed would help safeguard the long-term persistence of Victoria's stocks.
- Abalone stocks in eastern Victoria appear to be more isolated and genetically differentiated from those to the west. This region also appears to be influenced by potential dispersal from Tasmania and the unique environmental setting and more sparse distribution of suitable habitat patches. Evidence suggests the eastern zone requires a more local-scale approach to management to ensure sustainable abalone fisheries.
- Southern Rock Lobster dynamics (abundance, size-class structure, etc.) appear to be determined more by local-scale influences and protection rather than planktonic larval supply. The environmental characteristics and protection status influences SRL biomass. Perhaps counterintuitively for a species with the capacity to disperse long-distances, strong local-scale management can have profound impacts.

#### Future development

As with any project of this nature there are often many new questions arising from the findings than those questions that the project was originally scoped to answer. A number of these are described in the list which follows with the intention of forming the basis for future collaborative bids to FRDC and other funding providers.

- Projection of future climate impacts, in particular the likely impact of changes in currents and waves in addition to temperature over shorter time periods relevant to fishery management (5-25 years).
  Preliminary future climate and oceanographic data are now becoming available.
- Improved access to spatially explicit catch and fleet movement across the SRL and abalone fishery to enhance analysis of spatial patterns of resource use and productivity. Whilst this project was restricted to analyses across fishery independent survey sites due to the consistency of data collection

over a 21 year time period, fishery collected biomass estimates would provide an additional source for future modelling. New approaches to streamline data acquisition should be explored. For example diver based and remote stereo camera surveys have the potential to collect quantitative data on abalone densities to inform training for developing spatially explicit biomass models.

- Infrastructure in Victorian coastal waters to fill a regional and national gap in wave and current modelling to improve parameterisation and validation of future hydrodynamic and biophysical outputs.
- Experiments on the early life history parameters of abalone, including early buoyancy, competency transitions, and the extent and plasticity in the settlement window.
- Range-wide studies of recruitment and dispersal in SRL to better understand the larval input into Victorian stocks, and the export of Victorian larvae.
- Extend focus to fisheries managed in South Australia as these populations are likely larval sources to those populations in Victoria. A coordinated and cross-jurisdictional approach to abalone management may be essential for ensuring supply from source populations.
- The genotype-by-environment associations described in this study provide convincing patterns of genomic selection acting at both local and regional scales. However, these results should be interpreted with caution until further validate tests have been performed (e.g. genome annotations, generalized dissimilarity modelling, common garden and laboratory stress experiments). Our team has value added to the current FRDC project by sequencing, assembly and annotation of the *H. rubra* genome. We expect this resource to be available in the coming months, and it is expected to assist in the validation of our findings and the identification of genes and genomic regions influenced by selection.
- Our geospatial analyses suggest that stock biomass is linked to larval supply and recruitment potential, while our population genetic analyses indicate that genomic selection is potentially dictating which habitats larvae can and cannot recruit to. Consequently, selection could be directly influencing patterns of productivity across Victoria's abalone fisheries. Further biophysical modelling integrating habitat heterogeneity and genomic data will help determine the true recruitment potential of individual fishing stocks, and quantify the impact that genomic selection could be having on the fishery productivity.

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- Understanding the role of habitat at finer spatial scales on different life stages. We know that juveniles have a preference for cryptic spaces on reefs, but the importance of surge channels with vertical surfaces and why some large abalone occupy sparsely populated exposed horizontal surfaces. New approaches in high resolution image capture (e.g. high resolution sonar data, 3-dimensional rendering and photomosaicing) provide new opportunities to contextualise site selection. Another aspect is the role of habitat (e.g. kelp over-storey) and structural complexity of reefs in in attenuating wave energy, and facilitating larval retention. Low cost wave sensors provide new opportunities to characterise local scale variability in wave energy that could be paired with collector plates to quantify larval retention.
- We observed contrasting patterns of biomass among SRL populations from two Victorian marine parks with fished adjacent waters for the first time in Victoria. For the Merri Marine Sanctuary, we found a large population of *J. edwardsii* with significantly larger and more individuals compared with fished adjacent waters. In Wilsons Promontory MNP we found comparatively smaller population of much larger individuals with no significant differences in numbers or sizes when comparing the populations inside and outside the Marine National Park. Understanding these patterns and drivers (e.g. environmental, habitat, recruitment patterns, fishing intensity) relies on the continued compilation of spatially-explicit data on lobster populations in and around the marine parks networks but these pilot studies highlight the existing variability.

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