

FINAL REPORT

Spatial patterns, landscape genetics and post virus recovery of blacklip abalone, *Haliotis rubra* (Leach), in the western commercial fishing zone of Victoria



Ierodiaconou D., Miller A.D., Rattray A., Weeks A.R., Gorfine H.K., Peeters H., Van Rooyen A., Jalali M.A., Bell J.D., Worthington D. April 2014 FRDC Project No. 2011/033



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1 NON-TECHNICAL SUMMARY

2011/033 Spatial patterns, landscape genetics and post virus recovery of blacklip abalone, *Haliotis rubra* (Leach), in the western commercial fishing zone of Victoria

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OBJECTIVES:

- 1. Investigate methodologies to integrate commercial catch data with LiDAR-derived seafloor structure information to identify the spatial connectivity of reef systems and potential abalone fishable habitat extent.
- 2. Conduct a population genetic assessment of *Haliotis rubra* in the Western Zone to determine stock population structure, and assess the impact of Abalone Viral Ganglioneuritis (AVG) on the genetic diversity and recruitment of the species.
- 3. Integrate population genetics, landscape ecology and spatial analyses to elucidate how genetic variation in *H. rubra* is affected by landscape and environmental variables at both broad (Western Zone) and fine (Port Fairy to Warrnambool) spatial scales.

NON-TECHNICAL SUMMARY:

OUTCOMES ACHIEVED TO DATE:

This research has made several important findings that will improve the current management of the Victorian Western Zone blacklip abalone fishery, including post- Abalone Viral Ganglioneuritis (AVG) recovery planning. Geospatial and genetic technologies were used effectively to provide new information about potential habitat availability and fisheries productivity as well as key genetic parameters that reflect patterns of stock connectivity, genetic diversity and recruitment. Specifically, the outcomes of this project are:

- 1. The first high-resolution assessment of the extent of suitable fishing grounds derived from integrating commercial catch data with light detection and ranging (LiDAR) in spatially explicit models of habitat suitability and fishery footprint.
- 2. Patterns of change in spatial allocation of fishing effort identified from GPS tracked abalone diver data.
- 3. Impacts of AVG on genetic diversity and population structure across the Western Zone fishery.
- 4. Spatial patterns of larval recruitment determined from genetic measures of relatedness within and across reef complexes at various distance classes.

Historically, collecting nearshore habitat information has been problematic. Existing methods, such as aerial and satellite image interpretation are limited due to the attenuation of light in the water column obscuring the seabed structure. The advent of airborne bathymetric LiDAR (Light Detection and Ranging) systems (laser scanning of the seabed) now provides high-resolution seabed 'images' in areas that were previously difficult to survey. LiDAR imagery is available for the entire coastline of Victoria, Australia to depths of around 25 m, after being initially collected for climate change modelling by the Future Coasts Program (http://www.climatechange.vic.gov.au/adapting-to-climate-change/future-coasts). This dataset has provided the opportunity to test its applicability to inform fisheries management. Detailed geophysical information combined with spatially explicit AbTrack GPS located fisheries records and targeted genetic sampling is used in this study to provide a better understanding of the extent of available fishing grounds, direction of fishing effort and stock population structure within the Victorian western zone abalone fishery.

The species distribution modelling technique MaxEnt was used to produce a potential habitat suitability map for abalone in an attempt to capture the effective footprint of the fishery. Also, by interrogating the spatially defined effort localities, we demonstrate an approach that may be used to identify areas where fishing effort is concentrated, and how this parameter changes temporally.

Despite barriers to adult dispersal (soft sediment barriers between reef patches), the genetic study indicates that larval movement is able to homogenize the gene pool over large geographic distances. The western, central and eastern zone abalone stocks in Victoria were found to be a single large panmictic unit. This indicates high levels of stock connectivity and no obvious impacts of Abalone Viral Ganglioneuritis (AVG) on the genetic health of western zone stocks. We used detailed seafloor structure information interpreted from LiDAR to inform a replicated hierarchical fine scale genetic sampling design. We demonstrated that there may be extensive migration among abalone stocks across the Victorian abalone fishery. This is contrary to previous studies that suggest recruitment is highly localised. In combination, these findings provide a valuable insight into the biology of *H. rubra* and immediate benefits for fisheries management. We discuss these results in the context of predicting resilience and adaptive potential of *H. rubra* stocks to environmental pressures and the spread of heritable diseases.

Adoption pathways are also provided to benefit future stock augmentation activities to catalyse the recovery of AVG affected reef codes. As larval dispersal is likely to be spatially and temporally variable, some AVG affected stocks are likely to recover through natural recruitment, while others will benefit from augmentation activities to 'kick-start' stock recovery. Evidence of neutral genetic homogeneity across Victorian reef codes suggests that the relocation of animals is unlikely to have significant genetic risks; however the potential for locally adaptive genetic differences may exist, and should be taken into consideration in future stock augmentation planning.

When combined, the spatial and genetic analyses provide valuable insights into stock productivity within the western zone fishery. Reefs appear to be expansive and support much

available habitat, and the movement of larvae among reef structures is likely to be extensive in this region. Consequently, we propose that colonisation success and productivity is likely to be driven by ecological factors such as resources and/or competition, or physical factors such as wave exposure.

KEYWORDS: *Haliotis rubra*, microsatellite, LiDAR, GIS, genetic stock structure, fishery footprint modelling, hotspot analysis, recruitment patterns.

2 ACKNOWLEDGEMENTS

Funding for this project was provided by the Fisheries Research and Development Corporation, Western Abalone Divers Association, Department of Environment and Primary Industries and Deakin University. We would like to thank the managers, divers and investors in Victoria for their support throughout the project. In particular, we would like to thank the divers: David Forbes, Rob Torelli and Johno Rudge and their respective crews for their assistance with the fine and broad scale sampling undertaken as part of this project. Drs Matt Koopman and Fabian Trinnie provided expert assistance with collecting DNA samples in the field. We also thank Nicholas Gudkovs of the Commonwealth Scientific and Industrial Research Organisation, Animal, Food and Health Sciences, Mohan Raj (Lonimar Australia Pty Ltd) and Mark Touzeau (AFCOL Australia Ltd) for coordinating the collection of genetic samples from South Australia, and the Victorian Central and Eastern Zones, respectively. Thank you to Gail Schofield and the two anonymous reviewers whose comments improved this study.

3 BACKGROUND

The primary objective of this project was to integrate geospatial and genetic technologies to improve the current spatial management of the Western Zone abalone fishery of Victoria, Australia. The policy objective of sustainable exploitation of abalone stocks in the Western Zone has been enhanced in recent years with the adoption of a reef-scale assessment and management system developed in cooperation between Industry and Government. Unlike historical management strategies operating over large spatial scales, the system developed by the Western Abalone Divers Association (WADA) accounts for highly variable growth rates, resulting in variation in life-history parameters (size at sexual maturity and fecundity) and the historic productivity across reefs (Prince, 2005). Although this management approach is geared towards the sustainable harvesting of abalone stocks, more information on abalone population dynamics and available habitat is required to ensure sustainable harvesting. This study investigated the habitat connectivity and genetic stock structure of the blacklip abalone, *Haliotis rubra* (Leach), in the Western Zone fishery of Victoria using seafloor structure information derived from LiDAR (Light Detection and Ranging) technologies and population genetic measures.

Assessing the patterns of fisheries activity at a scale relevant to resource exploitation provides a new perspective for ecosystem based fisheries management. The recent availability of field instruments with global positioning system (GPS) data logging capability and their integration with GIS using a geostatistical approach provides opportunities to investigate patterns in productivity hotspots that might exist across fishing zones (Mundy, 2012). Habitat maps were combined with spatially explicit fishery-dependent data to provide a framework for analysing cumulative fishing effort and spatiotemporal changes through time. This study also provides valuable information on stock connectivity, spatial patterns of recruitment, and on the current genetic condition of abalone stocks affected by Abalone Viral Ganglioneuritis (AVG) in Victoria. This information enables fine tuning the current spatial management of the Western Zone fishery and guidance for stock recovery planning,

including stock augmentation activities. Although this study focuses specifically on AVG affected stocks within the Victorian Western Zone, the research outputs have management implications that will benefit Australian abalone fisheries management more broadly.

The nature of the seafloor structure has a profound effect on which aquatic communities are able to develop (Kostylev et al. 2001). It is widely recognised that species are not randomly distributed among varying habitats; instead, species show associations with the physical properties of the surrounding environment (Guisan and Zimmermann 2000). Species have evolved to recognise and utilise particular features of their environment for locating food, predator avoidance, courtship and reproduction. Their ability to perform these functions is dependent on cues from other organisms, features of their physical environment and their dispersal ability (Olenin and Ducrotoy 2006). Environmental complexity may be investigated via geospatial techniques. The state of Victoria is in a unique position as full coverage seafloor structure information has been captured using LiDAR to depths of ~25 metres for the entire open coast. Therefore, we may apply landscape metrics typically used in terrestrial studies to objectively assess environmental complexity in seascapes (Wilson et al. 2007). This information may be integrated with high-resolution fishery catch and effort data to provide opportunities to better understand the seafloor characteristics driving the extent of potential abalone fishing grounds. By identifying representative indicators of environmental complexity that influence targeted abalone habitat by divers, this information may be used as a surrogate to predict patterns beyond sampled locations. This project conducted innovative research to integrate independent datasets to better understand biological and geo-physical relationships for multi-scale predictive modelling of abalone-habitat associations and marine ecosystem resource assessment. These data facilitated investigations of abalone habitat suitability, identification of productivity hotspots, and reef characteristics that most influence these observed patterns.

The resilience of populations to environmental change, viruses (including AVG) and resource competition depends largely on genetic variation in quantitative traits, recruitment and gene flow in combination with levels of predation and exploitation. Genetic studies are increasingly becoming part of natural resource management because they either directly or indirectly estimate critical parameters that determine resilience. Genetic tools provide information about the evolutionary history, population size, current levels of genetic diversity and gene flow in species, along with other key factors contributing to the fitness of populations. Importantly, genetic studies may be used to provide insights into recruitment within and among populations. Understanding the levels of gene flow is critical for selecting appropriate management strategies to sustain any fishery. For example, reproductively isolated stocks characterised by unique genetic signatures or 'genotypes' require independent management consideration as these stocks effectively represent closed, self-recruiting population sub-units with unique environmental requirements and adaptive traits. The ability to develop effective response strategies and stock recovery plans following population collapse requires a detailed understanding about stock connectivity, in addition to the spatial patterns of recruitment, patterns of genetic diversity, effective population sizes and available habitat. To model stock recovery we must understand the patterns of larval dispersal and

recruitment in a given area. Further, the loss of genetic diversity is typically associated with population crashes and while biomass may respond relatively rapidly, stocks may remain highly vulnerable if genetic diversity has been significantly reduced. This phenomenon is compounded by the fact that the effective population size (Ne) of marine species is often several orders of magnitude lower compared to the census population size. In this case stocks are at risk of losing genetic variability, potentially resulting in reduced adaptability, population persistence, productivity and increased susceptibility to diseases. This project investigates patterns of gene flow, recruitment and genetic diversity in the Western Zone fishery, and provides several adoption pathways for future stock assessment, risk management, and effective recovery planning.

Pending outcomes from the genetic study if significant genetic structure is observed associations between genetic patterns and seafloor structure features will be assessed to identify physical features that might act as barriers to gene flow and influence stock structure in the Western Zone. This field, known as 'landscape genetics' is used widely in natural resource management and typically involves a combination of genetic and landscape ecological data using spatial statistics (Segelbacher et al. 2010). Given the uniqueness of the LiDAR spatial data available, this study is the first to use such an approach to investigate abalone benthic habitat at the scale at which the fishery operates. With high-resolution (5 metre cell size) three-dimensional full coverage seafloor structure information available from the shoreline to depths of ~25 metres, there is a unique opportunity to use these data to determine the spatial extent of individual reef systems, physical and biological connectivity between reef patches, and relationships with the spatially explicit fishery-dependent data that have been collected. In addition, these data provide a unique opportunity to design sampling protocols across isolated (island) reef patches to test multiple hypotheses regarding dispersal and relatedness.

4 NEED

Population dynamics, habitat availability and physical environmental features, all of which influence stock structure, must be considered to devise spatially effective management strategies. The need for demographic information at the genetic level is accentuated by the advent of Abalone Viral Ganglioneuritis (AVG) and associated stock depletions in the region in recent years. Spatial patterns of stock connectivity, recruitment and genetic diversity are needed to model stock recovery, identify vulnerable fishing stocks (where stock depletion has impacted levels of genetic diversity) and develop stock augmentation guidelines as the mixing of genetically differentiated stocks could potentially have negative fitness consequences. Besides the obvious need for genetic information to assist post-AVG management, it is anticipated this information will help improve the current spatial management of the Western Zone fishery through the identification of isolated and connected fishing stocks, in addition to estimates of gene flow that will assist future risk management. For the first time, detailed seafloor structure information to depths of ~25 metres for the entire abalone fishery of Victoria is available. Whilst this information has primarily been collected by the Department of Environment and Primary Industries Future Coasts Program for the assessment of coastal vulnerability, there is an opportunity to apply the data to determine the spatial extent of individual reef systems, connectivity between reef patches, and the relationships between seafloor structure information and genetic connectivity of abalone populations. The availability of these data also provides a unique opportunity to collate spatially-explicit, fishery-dependent data available for the Western Zone into a geographical information system (GIS) and integrate it with LiDAR-derived seafloor information using a range of spatial analysis techniques. These data are expected to facilitate investigations of potential abalone habitat suitability, identification of productivity hotspots to provide indications of productivity in relation to reef extent, and the reef characteristics and environmental variables that most influence abalone habitat suitability. Further, the integration of geospatial and genetic data provides long term benefits by producing information about patterns of physical and biological stock connectivity that will contribute to the WADA reef-scale assessment and management system.

5 **OBJECTIVES**

- 1. Investigate methodologies to integrate commercial catch data with LiDAR-derived seafloor structure information to identify the spatial connectivity of reef systems and abalone habitat suitability.
- 2. Conduct a population genetic assessment of *Haliotis rubra* in the Western Zone to determine stock population structure, spatial patterns of recruitment and the impact of AVG induced stock declines on genetic diversity.
- 3. Integrate population genetics, landscape ecology and spatial analyses, to elucidate how genetic variation in *H. rubra* is affected by landscape and environmental variables at both broad (Western Zone) and fine (Killarney, Petrel Point and Marlo) spatial scales.

6 METHODS

6.1 STUDY AREA

The main study area covers the Western Zone abalone fishery of Victoria, from Warrnambool to the South Australian border $(140^{\circ} 56' - 142^{\circ} 31' \text{ E} \text{ and } 38^{\circ} 06' - 38^{\circ} 26' \text{ S})$ (Figure 1). This region spans 200 km of exposed coast, ranging from 0.2 to 4 km width, and encompassing diverse coastal features. The region comprises a mosaic of reef and bare sediment, with large unconsolidated areas that are typically restricted to the nearshore zone. The shelf gradient is highly variable, being relatively shallow in the west, with very steep rocky regions in the vicinity of Port Fairy. The large proportion of low-medium profile reef in the area is attributable to intense wave energy, which prevails from the southwest and sweeps much of the sediment from the shallow shelf.

Structure is apparent in the exposed sandstone reef surface, including parallel beds and folds, particularly in the west. Rock type varies from bedded sandstone and limestone in the west and blocky, irregular basalt flows in the east. The spectacular among these occurs offshore from Tyrendarra (Julia Bank), where an elongate, sinuous lava tube bisects a broader, more viscous lava flow comprising large blocks separated by numerous crevices. Less distinct lava tubes and basalt flows also occur offshore of Warrnambool. A number of distinct, partially sediment-filled palaeochannels also occur along the coast. These represent seaward extensions of the Glenelg River, the Surry/Fitzroy River, Eumeralla/Shaw River (Lake Yambuk) and Hopkins River. These features are likely to have been cut during the last glacial period, and are exposed today due to the general lack of sediment supply along this exposed coast. The palaeochannels represent elongate 'corridors' of bare sediment, which extend relatively long distances offshore flanked by rugose reef.

Inshore, unconsolidated sediments prevail between rocky headlands, whereas more exposed coastal sections comprise rocky cliffs which drop directly to sand beds in >25 m water depth. Shallow reef systems in this region are macroalgae dominated, with offshore seagrass beds being observed in the sediments off Portland and Warrnambool.

In addition to the main study area, DNA sampling for genetic analysis included regions in the western and eastern ends of the Eastern Zone of the Victorian abalone fishery; within the Central Zone of the Victorian abalone fishery; and from Port Lincoln in South Australia.

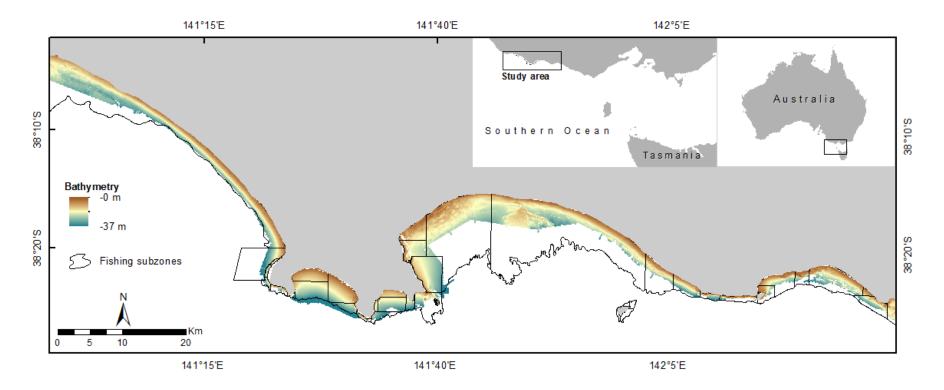


Figure 1. Study area encompassing the Western Zone abalone fishery, south west Victoria, Australia. Black solid lines represent boundaries for each subzone in the Western Zone. LiDAR derived shaded bathymetry is overlaid showing coverage for each subzone. LiDAR generally provided good coverage within diving depths across the zone. No LiDAR coverage available for the subzones surrounding Julia Percy Island.

6.1.1 GEOPHYSICAL DATA (LIDAR)

Inshore coastal bathymetric data were acquired from LiDAR collected in April 2007 using a LADS Mk II system coupled with a GEC-Marconi FIN3110 inertial motion sensing system and a dual frequency kinematic geographic positioning system (kGPS). LiDAR penetration into the water column was typically 2–3 times the Secchi depth (approximately 25 m). Penetration was impaired in some areas by turbidity and breaking waves. Point soundings were gridded to an optimal spatial resolution of 5 m, and an estimated spatial accuracy of ± 1 m.

To characterise local variation within LiDAR, a suite of products were derived from the bathymetry dataset, and are referred to as "derivatives" (Table 1). These derivatives were selected for their potential influence on the distribution of biological assemblages (Rattray et al. 2009), in terms of exposure to wave energy and benthic currents (aspect, Benthic Position Index), susceptibility to sediment accumulation (Benthic Position Index), complexity and surface area of reef structure (complexity, rugosity and maximum curvature).

Primary	Secondary	Definition	Potential habitat
derivative derivative			influence
Aspect		Aspect (azimuthal bearing of the steepest slope), separated into Eastness and Northness.	Exposure to wave energy and currents.
Curvature	Maximum and minimum curvature	Maximum curvature (convexity) and minimum curvature (concavity) at regions where the slope is zero, where plan and profile curvature remain undefined.	Exposure to currents; rock type.
	Bathymetric Position Index (BPI)	Variation among cells within a specified radius or annulus; it may be calculated at a variety of user-defined scales so as to capture local and broad-scale variations in bathymetric position.	Susceptibility to sediment accumulation; exposure; potential reef dwelling species habitat.
Terrain	Complexity	Second derivative of the slope surface; indicating the rate of change in slope values.	Defines potential reef dwelling species habitat.
	Rugosity	Ratio of the surface area to the planar area across the neighbourhood of the central pixel (rugosity = surface area of 3 x 3 neighbourhood / planar area of 3 x 3 neighbourhood).	Defines potential reef dwelling species habitat.

Table 1. Derivative products from LiDAR bathymetry.

6.1.2 HABITAT SUITABILITY MODELLING

A habitat suitability modelling approach was used to predict the potential footprint of the Western Zone fishery based on the location of all GPS logged abalone catch records for the years 2008–2011. The maximum entropy method (MaxEnt) is a general-purpose, machine-

learning method with a simple and precise mathematical formulation. It has a number of aspects that make it well-suited for habitat distribution modelling (Phillips et al. 2006).

To build the MaxEnt models, full-coverage LiDAR derived seafloor structure information was combined with GPS locations of logged abalone catches to extrapolate similar potentially suitable fishing areas across the Western Zone fishery. AbTrack GPS locations localities were summarised as presence records using a 1 ha (100 m x 100 m) grid for the Western Zone to take error associated the inherent accuracy of the GPS receiver (~20 m) into consideration, and ensure that the data represent the vessel track rather than the diver track (Mundy, 2012). Erroneous tracks associated with logged records whilst vessels were transiting between sites were removed from the analysis. Logged catch locations, occurring in \sim 15,000 1 ha presence cells, were randomly partitioned into two parts; 75% as training data and 25% for model validation. Models were trained using the following settings: convergence threshold (0.00001), maximum iterations (1000), auto features, regularisation multiplier (r = 1) and background points (100,000). Model performance was evaluated using the thresholdindependent AUC (area under curve) of the ROC (receiver operating characteristic). ROC plots the fraction of occurrence records that are classified as being present against the portion of absence points that are classified as being absent for all possible thresholds. In the case of MaxEnt, where no absence data are used, AUC is interpreted as a measure of the ability of the model to discriminate between a suitable environmental condition and a random analysis pixel (background), rather than between suitable and unsuitable conditions, as an AUC developed with measured absences is interpreted (Phillips et al. 2006). An AUC value of 0.5 implies that the model predicts species occurrence no better than random, and a value of 1.0 implies perfect prediction. The relative importance of the contribution of each explanatory variable to the probability distribution observed was determined using a Jackknife test. Response curves were also generated to show the relative influence of each topographic variable in the MaxEnt logistic prediction.

6.1.3 GEOGRAPHIC HOT SPOT ANALYSIS

Three sub-zones were selected for the assessment of effort distribution (Figure 2); Discovery Bay, Julia Bank and Lady Julia Percy Island. Approximately 220,000 records of AbTrack data (including length and GPS location) have been geo-referenced for spatial analyses, providing coverage across the Western Zone.

Commercial fishing effort data (AbTrack, Mundy, 2012) from all fishers in each zone were provided by WADA (Western Abalone Divers Association) for the years 2008–2011. All effort localities were geographically plotted. Fine-scale rectangular grids with 1 ha (100 m x 100 m) cell size were overlaid on each study area. After excluding outliers, the number of effort localities was joined to the grid polygon layers for further analysis.

Hotspot analyses were conducted independently in the three sub-zones of the Western Zone fishery to identify areas of reef within each zone that were preferentially targeted by fishers over the 4 years, 2008–2011. Three reef regions were selected for the hotspot analysis: (A) Discovery Bay (1066 ha), (B) Julia Bank (2714 ha) and (C) Lady Julia Percy Island (266 ha),

which are shown in Figure 2. No structured fishing was implemented in the three locations used for the hotspot analysis during the period of investigation. Hence, we propose the patterns observed are a reflection of characteristic diver harvest behaviour. An example of point localities for a Western Zone site (western end, Discovery Bay 2008–2011) overlaid on LiDAR data coverage is shown in Figure 3. Several issues were identified with the AbTrack data that needed to be taken into account prior to analysis. These issues include catch records in areas of no reef (potentially due to vessel drifting whilst catch is logged) and duplicate positions for catch records. These issues precluded the use of some data for the fine-scale analysis.

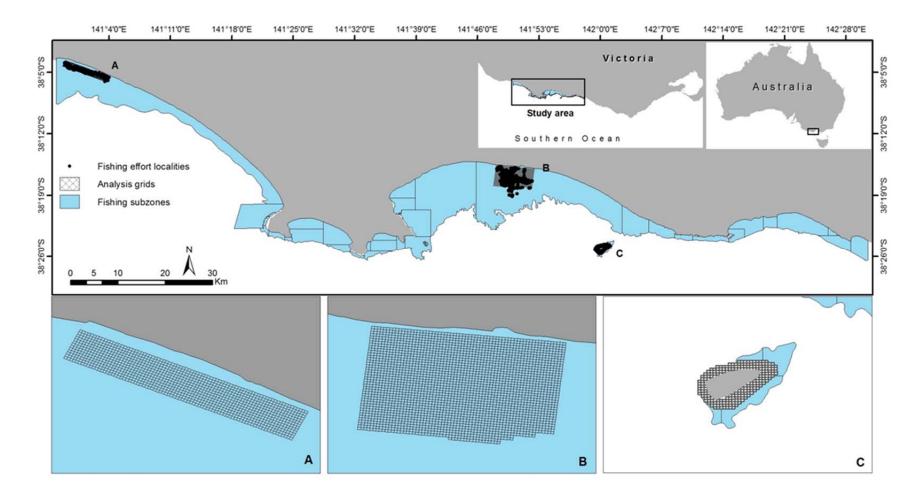


Figure 2 Map of the study area representing 1 ha analysis grids in (A) Discovery Bay (1066 ha), (B) Julia Bank (2714 ha) and (C) Lady Julia Percy Island (266 ha) used for the hotspot analysis, western Victoria over a 4 year period from 2008–2011.

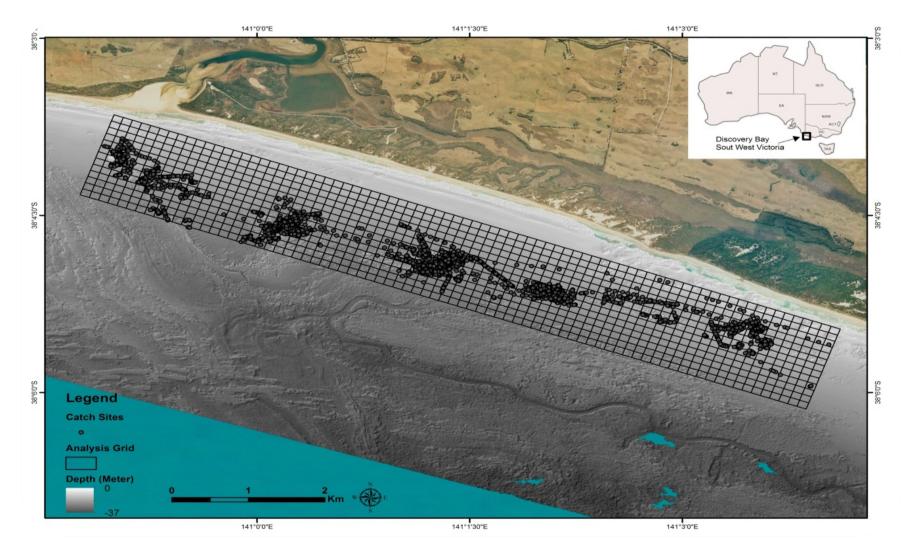


Figure 3 Fishing effort locations, analysis grid and LiDAR coverage for the Discovery Bay (west) site. Evidence of GPS logging observed during transits between sites were filtered prior to undertaking the hotspot analysis for each site

6.1.4 DATA ANALYSIS

Spatial statistics tools in ArcGIS Software (ArcGIS 10, ESRI®) were used to analyse spatial and temporal patterns in fishing effort data. Global Moran's I was applied to compute autocorrelation in effort data within the 1 ha analysis grids for each year. Using the distance, location and cell values, Moran's Index was calculated with values ranging between -1 (dispersed pattern) and +1 (clustered pattern), with values near zero indicating random distribution. Several distance classes (including 125, 250, 500, 750, 1000 and 1500 m) were considered to determine the distance band where autocorrelation and clustering patterns occur in fishing effort distribution. This approach evaluates whether fishing effort localities across the space of analysis grids occur non-randomly and, if so, whether they were dispersed or clustered. The fixed distance band and Euclidian distance technique were adjusted for autocorrelation analyses. The computation is based on the following formula:

$$I = \frac{n}{S_0} \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} w_{i,j} z_i z_j}{\sum_{i=1}^{n} z_i^2}$$
Eq. 1

where: $w_{i,j}$ is the spatial weight between features (grid cells) *i* and *j*, *n* is the total number of features, *z* is the deviation of an attribute for feature *i* from its mean and S_0 is the aggregate of all the spatial weights.

Once the global patterns in the dataset were determined, local Getis-Ord Gi statistic was used to determine the areas, with high values of effort being referred to as hotspots. This analysis determines statistically significant local autocorrelation and dependence of neighbouring cells. The 250-m distance band was chosen for hotspot analysis following the results of Global Moran's I. Local Getis-Ord Gi statistic uses the formula:

$$G_{i}^{*} = \frac{\sum_{j=1}^{n} w_{i,j} x_{j} - \bar{X} \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\frac{\left[n \sum_{j=1}^{n} w_{i,j}^{2} - \left(\sum_{j=1}^{n} w_{i,j}\right)^{2}\right]}{n-1}}}$$
Eq. 2

where: $w_{i,j}$ is the spatial weight between features *i* and *j*, *n* is the total number of features, x_j is the attribute value for feature *j*.

6.2 GENETICS

6.2.1 TISSUE COLLECTION AND DNA EXTRACTION

6.2.1.1 TIER 1 SPATIAL SAMPLING

Broad geographical sampling across the Western Zone was conducted to determine spatial patterns of stock connectivity and genetic diversity. Haliotis rubra sample collections held by the Department of Environment and Primary Industries (DEPI) were used for the broad scale population genetic analysis of the Western Zone fishery in this study. A total of 1264 whole specimens, representing eight Western Zone reef codes (The Craggs, Lady Julia Percy Island, The Water Tower, Murrels, Inside Nelson, Levies, South Bridgewater, and Whites) and 10 size classes (50 mm to 149 mm), were collected in 2009 by the DEPI as part of the post-AVG fishery surveys. Specimens from each site were collected within a 25 m radius of an anchored vessel, and subsequently preserved at -20 ° C. From these samples, we collected 50 mg biopsies from 320 individuals (40 per site), representing each of the reef codes and size classes, for genetic analysis. Dissection tools were sterilised between samples to avoid cross contamination. The biopsied material was transferred to 2 ml microcentrifuge tubes containing 100% ethanol and transported to the laboratory. The sampling of multiple size classes was critical to avoid sampling single cohorts (potentially related individuals), which might lead to ambiguous estimates of gene flow and genetic structure. A total of 30 samples per site (reef code) were used for the genetic analysis.

Additional samples from South Australia and the Central and Eastern Zone Victorian fisheries were also included, to gain insights into the broader spatial patterns of stock connectivity. These samples included: 33 samples from Port Lincoln (South Australia) supplied by Nicholas Gudkovs (CSIRO Animal, Food and Health Sciences); 30 samples from Apollo Bay, Point Addis, Shallow Inlet, and 28 samples from Point Cook (Victorian Central zone), supplied by Mohan Raj (Lonimar Australia Pty Ltd) and David Forbes (commercial and research diver); and 30 samples from Marlo, Mallacoota, and Gabo Island (Victorian Eastern zone), supplied by Harry Gorfine (DEPI) and Mark Touzeau (AFCOL Australia Ltd). Biopsies were performed following the procedures described in the previous paragraph. Details concerning the sampling sites and numbers for the broad scale population genetic assessment are provided in Table 2 and Figure 4.

Site	Site Code	Latitude	Longitude	n
Bridgewater	В	-38.3931	141.3967	27
Whites	W	-38.3487	141.3836	30
Murrels	М	-38.4068	141.5243	30
Inside Nelson	Ν	-38.4091	141.5582	30
Lady Julia Percy Island	LJ	-38.4215	141.9940	30
Craggs	С	-38.3879	142.1419	30
Water Towers	WT	-38.3948	142.2062	30
Levies	L	-38.3850	142.4353	30
Port Lincoln	PL	-35.0600	135.8046	33
Apollo Bay	А	-38.7500	143.6500	30
Point Impossible	PI	-38.3126	144.3759	30
Port Phillip Bay	PP	-38.1014	144.8883	28
Wilsons Promontory	WP	-38.8203	146.1533	30
Marlo	М	-37.8033	148.7941	30
Mallacoota	MA	-37.7319	149.6005	30
Gabo Island	G	-37.5591	149.9114	30

Table 2. Collection details for *Haliotis rubra* samples used in this study, including the site codes used throughout the study and the number of individuals from which microsatellite genotypes were obtained (n).

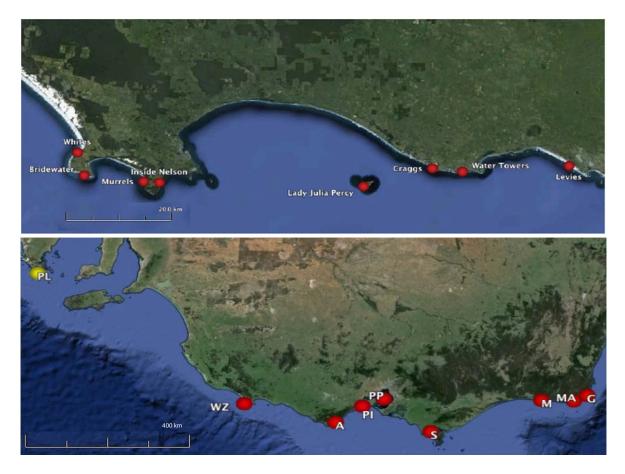


Figure 4 Map of the *Haliotis rubra* collection sites for the broad scale genetic survey from the Victorian Western Zone (upper image), and across fishing jurisdictions (lower image; Western Zone, labelled WZ). The colour coding of collection sites corresponds with the genetic clusters identified by Bayesian analyses (red = population 1; yellow = population 2).

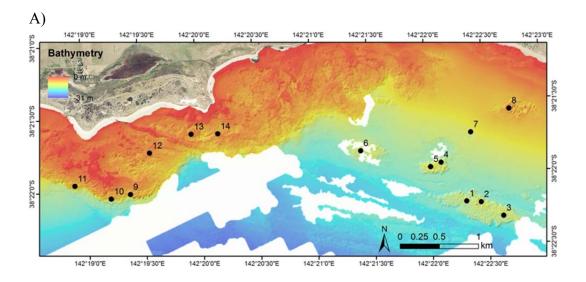
6.2.1.2 TIER 2 SPATIAL SAMPLING

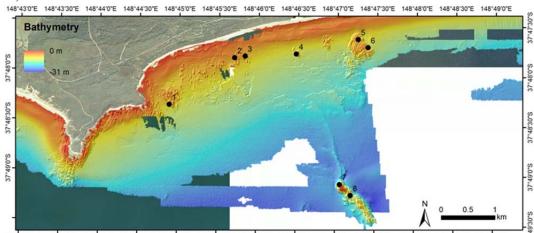
Replicated hierarchical sampling at fine spatial scales was also conducted to assess the extent of larval recruitment among Western Zone reef patches, and to test the hypothesis that abalone larval movement is limited (<100 m), with stocks being largely self-recruiting units (Prince et al. 1987, 1988; McShane et al. 1988). Under a local recruitment model, significant correlation between relatedness and geographic distance is expected (individuals separated by distances of <100 m will be more related than individuals separated by distances of >100 m). Using LiDAR habitat mapping, a variety of isolated, continuous, exposed and protected reef structures with historically variable fishing productivities were identified from the Killarney area in the Western Zone fishery (Table 3). Abalone specimens were subsequently sampled across a range of spatial scales (0–6.6 km), with 10 individuals being collected within a 20 m radius from 16 randomly distributed sites representing six reef structures (Figure 5A). A 50 mg non-lethal tissue biopsy was collected from each of the 160 live specimens following the previously described protocol, and the specimens were returned to the point of collection. This procedure was repeated at two additional sites from the Eastern Zone fishery for comparative purposes, with eight sites distributed across six reef complexes being targeted in

the Marlo area (spatial scales 0-3.5 km; Figure 5B), and four sites representing three reef complexes at Petrel Point (0-5.0 km; Figure 5C).

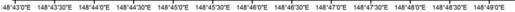
Site	Site Code	Latitude	Longitude	n
<u>Western Zone</u>				
Killarney	Site 1	-38.3699	142.372	10
	Site 2	-38.3701	142.3741	10
	Site 3	-38.3718	142.3773	10
	Site 4	-38.3654	142.3685	10
	Site 5	-38.3658	142.367	10
	Site 6	-38.3636	142.3569	10
	Site 7	-38.362	142.3731	10
	Site 8	-38.3595	142.3788	10
	Site 9	-38.3673	142.3231	10
	Site 10	-38.3677	142.3202	10
	Site 11	-38.366	142.315	10
	Site 12	-38.3626	142.3261	10
	Site 13	-38.3607	142.3323	10
	Site 14	-38.3608	142.3362	10
Eastern Zone				
Marlo	Site 1	-37.8094	148.7577	10
	Site 2	-37.8072	148.7695	10
	Site 3	-37.8066	148.7728	10
	Site 4	-37.8057	148.7798	10
	Site 5	-37.8018	148.7906	10
	Site 6	-37.8033	148.7941	10
	Site 7	-37.8195	148.7847	10
	Site 8	-37.8228	148.7887	10
Petrel Point	Site 1	-37.7918	149.3875	10
	Site 2	-37.7930	149.4053	10
	Site 3	-37.7919	149.4366	10
	Site 4	-37.7934	149.4414	10

Table 3. *Haliotis rubra* tissue collection sites for fine-scale, genetic spatial autocorrelation analysis in the Western (Killarney) and Eastern (Marlo and Petrel Point) Zone abalone fisheries





B)



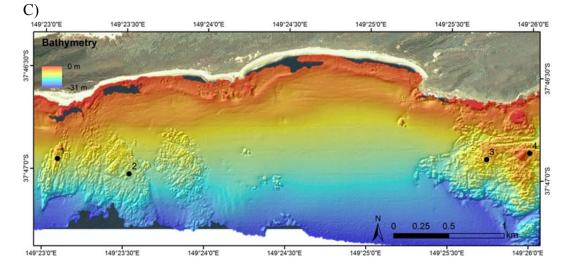


Figure 5. Map of *Haliotis rubra* collection sites from the Killarney (A), Marlo (B) and Petrel Point (C) sampling regions. Pairwise comparisons of multilocus genotypes from 10 abalone specimens at each site were used for spatial autocorrelation analysis. Each region was analysed independently. Site code positions are listed in Table 3.

Approximately 10 mg of muscle tissue from each *H. rubra* specimen was used for DNA extraction. Total genomic DNA was extracted using a modified Chelex® extraction protocol (Walsh et al. 1991). Individual samples were macerated using a sterile scalpel blade, and placed into separate 0.5 ml microcentrifuge tubes, also containing 3 μ L proteinase K and 200 μ L of 5% Chelex® solution. Samples were subsequently digested at 55 °C for 60 min, followed by a final incubation at 95 °C for 15 min, with periodic vortexing. Extractions were stored at -20 °C until required. Prior to Polymerase Chain Reaction (PCR) amplification, extractions were spun at 13,000 rpm for 2 min. Aliquots from the bottom half of the supernatant from above the Chelex ® resin was used for PCR amplification.

6.2.2 MICROSATELLITE ANALYSIS

6.2.2.1 POPULATION STRUCTURE

The frequency variation of nuclear microsatellite alleles was assessed to determine the patterns of gene flow and population genetic structuring across H. rubra sample sites. Particular care was taken with our selection of microsatellite markers, as this aspect is critical for obtaining reliable results, and has been a common issue with previous genetic studies of marine molluscs, including H. rubra (Huang et al. 2000; Conod et al. 2002; Astanei et al. 2005; Temby et al. 2007; Brownlow et al. 2008; Appleyard et al. 2009; Miller et al. 2009). Marine molluscs appear prone to influences from null alleles at microsatellite loci, which may bias estimates of genetic structure (Hedgecock et al. 2004; Brownlow et al. 2008; Lemer et al. 2011; Miller et al. 2013). To avoid this potential source of bias, we assessed the performance of 27 microsatellite loci developed by Evans et al. (2000) and Baranski et al. (2006), some of which have been previously used for population genetic studies. This procedure was achieved by genotyping 30 individuals from two sample sites (Whites and Bridgewater) at each of the 27 loci, and measuring their respective conformity to Hardy-Weinberg expectations. Those that differed significantly were regarded as potentially problematic, and were excluded from further analysis. A total of 15 polymorphic microsatellite loci were selected for subsequent population genetic analysis of H. rubra (Table 4). These loci were amplified by multiplex PCR using Eppendorf Mastercycler S gradient units, and following the protocol described by Blacket et al. (2012). Microsatellite profiles were examined and scored manually using the program GeneMapper version 4.0 (Applied Biosystems).

6.2.2.2 TIER 1 SPATIAL SAMPLING

Descriptive statistics were calculated for the microsatellite data using FSTAT, version 2.9.3 (Goudet 1995), including allelic richness per population averaged over loci, Weir and Cockerham's measure of F_{IS} , a global estimate of F_{ST} (with 95% confidence limits) (Weir and Cockerham 1984), population pair-wise measures of F_{ST} and their significance determined using permutations (10,000), and pairs of loci tested for linkage disequilibrium using a log-likelihood ratio test. To overcome potential limitations of F_{ST} calculations using multiallelic

loci (Jost 2008), additional estimates of population differentiation, D_{est} , were obtained using SMOGD version 1.2.2 (Crawford 2010) and GenAlex version 6.41 (Peakall and Smouse 2006). The software MICRO-CHECKER (Van Oosterhout et al. 2004) was used to assess microsatellite loci for null alleles and for scoring errors. The frequency of null alleles per locus was obtained using the 'Brookfield 1' formula, as evidence of null homozygotes across loci was not observed (Brookfield 1996). The sequential Bonferroni procedure (Rice 1989) was used to adjust significance levels when performing multiple simultaneous comparisons.

Estimates of observed (H_o) and expected (H_E) heterozygosity were determined using the Excel Microsatellite Toolkit (Park 2001) and deviations from Hardy-Weinberg equilibrium (HWE) were tested using Genepop version 3.4 (Raymond and Rousset 1995). An analysis of molecular variation (AMOVA) was performed in GenAlEx version 6.41 (Peakall and Smouse 2006) by using pairwise F_{ST} as the distance measure, with 10,000 permutations and missing data for loci set at 10%. The model for analysis partitioned variation among and within sample sites. Regression and Mantel tests of Slatkin's linearized F_{ST} transformation [$F_{ST}/(1 - F_{ST})$] (Rousset 1997), with the natural log of geographical distance were calculated using GenAlex (Peakall and Smouse 2006). The significance of Mantel tests was determined by permutation (10,000 randomisations). A factorial correspondence analysis (FCA), implemented in GENETIX version 4.05 (Belkhir et al. 2004), was used to summarise patterns of genetic differentiation between individuals across sample sites. The first two underlying factors that explain the majority of variation in multi locus genotypes across loci were plotted. Table 4. The 15 microsatellite loci included in this study, and the remaining 11 loci excluded after preliminary screening revealed significant deviations from Hardy-Weinberg expectations. Locus name, repeat motif(s), primer sequence and corresponding reference and Genbank accession numbers are provided. Asterisks indicate that a primer sequence had been modified from those provided by the author.

Locus	Repeat motif(s)	Primer sequences (5'–3')		Reference	Genbank accession
Multiplex 1					
Hrub2.B01	(AAC)N	CCTCGACAACATGGAAAGGT	TTGATGTAGCGTCTTGGCAG	Baranski et al., 2006	DQ278057
Hrub11.E05	(GTT)N	GTTGGTGTCGTTTCTTCCGT	ATTTGTCCCGACAATCCGTA	Baranski et al., 2006	DQ278016
Hrub6.CO4	(CTGT)N	CGTTGGTGGGTTCTCTTGA	GGATGCTAGGGCATTATCCA	Baranski et al., 2006	DQ278083
Hrub1.H08a	(AC)N	TTGACGATTTAGGGGTTTCG	TCAGTTTATGATGCTGATTGACG *	Baranski et al., 2006	DQ277997
Hrub10.B11 a	(AC)N	CGAGTTGTGTCCCCTTGTCT	TAGGTTAGCAACCCCCGTCT*	Baranski et al., 2006	DQ278000
Multiplex 2					
Hrub8.F11	(CA)n	CCCTTGGCATCAGGATAAGA	TTTGCCTTATGAAATTCCCG	Baranski et al., 2006	DQ278099
Hrub1.H07	(ACTC)N	TCACTTCCAAGACCCGATTC	CCTGAAATGGCCTTTACGAA	Baranski et al., 2006	DQ277996
Hrub9.B05	(TG)N	AATCCGGAATACTGCACTGG	AGGTCATATTGTCCACCGGA	Baranski et al., 2006	DQ278104
Hrub17.E04	(TG)n	CGCAAAGCATGAAACAGAAC	CTCCCCACATCCATGTTACC	Baranski et al., 2006	DQ278054
Hrub9.H11	(GACA)N	TGACAATTCGTGGCAGAGAG	GGCCAGTTGCCTTTTACTGA	Baranski et al., 2006	DQ278115
Multiplex 3					
Hrub11.A07	(TG)n	CAGCATGACCAAAACACCTG	AAAGAACTTCTCGCCGAACA	Baranski et al., 2006	DQ278009
cmrHr2.14	(GAGT)8(GAGT)5	GTCCTCCAGTGAGACCCAAA	AGCATGGGTATTGTTGACTG	Evans et al., 2000	AF194957
Hrub12.E10	(GATG)N	TGCAGCATAACACTTGCTCA	CGTAGCTGCCTTCATCCTTC	Baranski et al., 2006	DQ278024
Hrub13.F06	(GT)N	GACAGGTGCTCCCCTATTCA	CCAGGTGTCAACATGACCTG	Baranski et al., 2006	DQ278037
Hrub13.C12 a	(TGC)N(GTT)N	TCAGACTGCATGACAACAGG*	CGTATCAGTGGCCAAATCAG	Baranski et al., 2006	DQ278035
Excluded loci					
cmrHr1.14	(GT)13TT(GT)2GA(GT) 3	CTACGTACACTTTAATGTGCTC	CTGCCTAAAAGTTCAATCC	Evans et al., 2000	AF194952

cmrHr1.24	(AT)8	TCTAGCATGTCTGAGGGAGG	TGTGTCATTGTGGTCGAAAG	Evans et al., 2000	AF194953
Hrub11.D08	(GT)n	ACGTAACGACCTCCTGCAAA	CCACAAGCACATAAACACAACC	Baranski et al., 2006	DQ278015
Hrub12.A02	(CA)N	CCGACGGTGTTAAAACGACT	ACTGCTCCAATACGGCAAGT	Baranski et al., 2006	DQ278017
Hrub12.E07	(GA)N(GT)N	CTGCACTAATTCAGTTCCATGTT	CGCTCAGTGAGGTAAAGCTG	Baranski et al., 2006	DQ278023
Hrub13.A02	(AC)N	TCGATTTACAAGACAAGTCTCCA	ACGCTGAGTCACTCCCATTT	Baranski et al., 2006	DQ278032
Hrub13.B04	(TG)N	TCTTCCCATTCTATGTTGAGTCAG	TCGGACCTATACAAGCAACG	Baranski et al., 2006	DQ278033
Hrub13.C11	(TG)N	TGCACAAAGAAGTTAATAAAAACC A	TGAGTGAAACAATTGCTCGG	Baranski et al., 2006	DQ278034
Hrub17.E12	(GT)n (GCGT)n	GTCGGCACCGCATTATTATC	GTCGGCACCGCATTATTATC	Baranski et al., 2006	DQ278055
Hrub2.G01	(GT)n	GGTGTTACCGGTCAACTTGG	TTATGTCACAGGGGGCCAAAC	Baranski et al., 2006	DQ278060
Hrub3.F03	(CAG)N(CAA)n	GTCTTTTGGTGTGACTGCGA	CTGGTGTCCTGAAACGCAAT	Baranski et al., 2006	DQ278066
Hrub4.E05	(CA)N	GTTTTGAAACCCGTTGCTGT	CAATGCTCATTCCCACTCAC	Baranski et al., 2006	DQ278073

Independent analyses of population structure were conducted using Bayesian analyses. Based solely on genetic data, STRUCTURE (Pritchard et al. 2000) identifies the number of distinct clusters / populations, assigns individuals to clusters and identifies migrants and admixed individuals. To determine the number of populations (*K*), five independent simulations for K = 1-16, with 100,000 burn-ins and 1,000,000 data iterations were run. Analysis was performed using the admixture model of population structure (i.e. each individual draws some fraction of their genome from each of the *K* populations) and allele frequencies correlated among populations (i.e. allele frequencies in the different populations are likely to be similar, due to factors such as migration or shared ancestry). The most likely *K* was estimated using Evanno's ΔK (Evanno et al. 2005), which was implemented in Structure Harvester (Earl and Vonholdt 2012).

A second Bayesian analysis of population genetic structure was performed using the *R* package software GENELAND (Guillot and Santos 2009). This method uses a geographically constrained Bayesian model that explicitly takes into account the spatial position of sampled multilocus genotypes, without any prior information about the number of populations and degree of differentiation between them. The inference algorithm was launched by a single step approach (Guillot 2008) using the Dirichlet distribution, as used previously for allele frequencies, and where *K* was allowed to vary from 1 to 16. Five independent runs of 1,000,000 MCMC iterations were performed, with a maximum of 300 nuclei and a 50,000-interation processing burn-in that was consistent with recommendations (Guillot 2009; Guillot and Santos 2009).

6.2.3 SPATIAL AUTOCORRELATION

6.2.3.1 TIER 2 SPATIAL SAMPLING

Spatial autocorrelation was used to assess the spatial genetic structure of *H. rubra* at fine spatial scales among the Killarney, Marlo and Petrel Point sampling replicates, to test for evidence of localised stock recruitment. Spatial autocorrelation analysis was performed using SPAGeDi 1.2 (Hardy and Vekemans 2002), using a dataset containing multilocus genotypes for 149 individuals from 16 Killarney sample sites, 80 individuals from eight Marlo sample sites and 40 individuals from four Point Petrel sites. We estimated the Queller and Goodnight (1989) relatedness coefficient among pairs of individuals belonging to the same *a priori* defined distance classes. For each class, random permutations in the spatial locations of individuals (10000 permutations) were then used to assess deviations of the relatedness coefficient *R* from 0. Distance classes were chosen so that they contained more than 100 pairwise comparisons, had a participation index >50% and a coefficient of variation of participation of less than 1 (Hardy and Vekemans 2002). Deviation from 0 means that individuals within a given distance class are significantly more (positive values) or less (negative values) related than random. To assess the reliability of the results obtained with

the Queller and Goodnight (1989) relatedness coefficient, we repeated the analyses using two other relatedness estimators; namely, Lynch and Ritland's (1999) relatedness coefficient (r) and the kinship coefficient of Loiselle et al. (Loiselle et al. 1995). In all cases, similar results were obtained; therefore, we only present the results for the Queller and Goodnight (1989) relatedness coefficient.

7 RESULTS AND DISCUSSION

7.1 SPATIAL ANALYSES

7.1.1 HABITAT SUITABILITY MODELLING

The MaxEnt model was able to predict reef areas of high fishery suitability at a fine-scale (5 m resolution) across the entire Western Zone fishery. Reef features smaller than 100 linear metres were resolved from the surrounding soft sediments (Figure 6) (larger scale maps are provided in Appendix 3). The AUC for the training data and test data (0.89 in both cases) indicated a good performing model. It is important to note that the model presented is a representation of the fishery footprint based on logged catch locations, rather than the habitat suitability of *H. rubra*. Understanding the realised niche of the species would require a systematic sampling regime across the broader geographical range of the species (i.e. at depths greater than those typically targeted by fishers).

The Jackknife test of variable importance showed that bathymetry, rugosity and complexity contributed 41.5%, 29.3% and 18.3%, respectively. Remaining predictors had relatively small contributions; maximum curvature (9.1%), BPI 300 (6.6%), BPI 100 (1.1%) and aspect (0.5%). The response curves indicated that highly suitable regions were characterised by highly rugose seafloor structure (i.e. high profile reefs), with the most suitable areas occurring at depths of around 10 m, and a gradual decline in suitability to depths of 20 m.

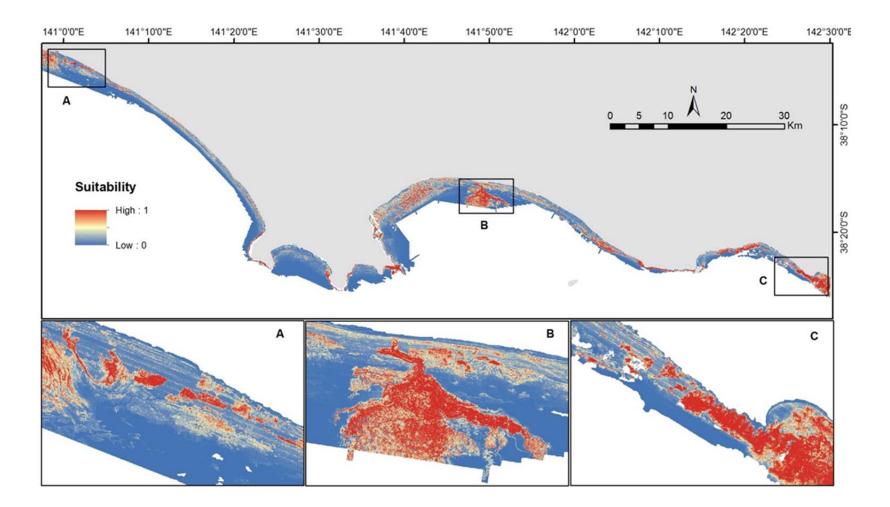


Figure 6. Blacklip abalone habitat suitability map from the Maxent Species Distribution model (based on fishing activity). Insets show suitability maps for fishing subzones: (A) Discovery Bay (B) Julia Bank and (C) Warrnambool. Detailed maps for the Western Zone are provided in Appendix 3

7.1.2 GEOGRAPHIC HOT SPOT ANALYSIS

Moran's I analysis revealed clustering patterns in fishing effort distribution, with strong clusters using shorter distances measures. High clustering was observed at 125, 250 and 500 m distance bands (Figure 7). Moran's index and the z-score were found to be higher in 2010 and 2011 compared to 2008 and 2009, indicating stronger spatial clustering of effort in these years (Figure 8). As observed in this study, some investigations suggest that spatial autocorrelation may decrease with increasing distance bands (McGarvey 2006). Lower values with increasing distance bands might be indicative of the patchy distribution of available fishable reef.

The results of the Getis-Ord Gi* analysis revealed statistically significant z-scores, identifying spatial clusters of high values (hot spots) (Osei and Duker 2008). The high effort clusters are situated near the central area of the analysis grids that overlap major reef extensions, as identified by the LiDAR data (Figure 9, 10, 11). The results indicate spatial variation in fishing effort across years (2008–2011).

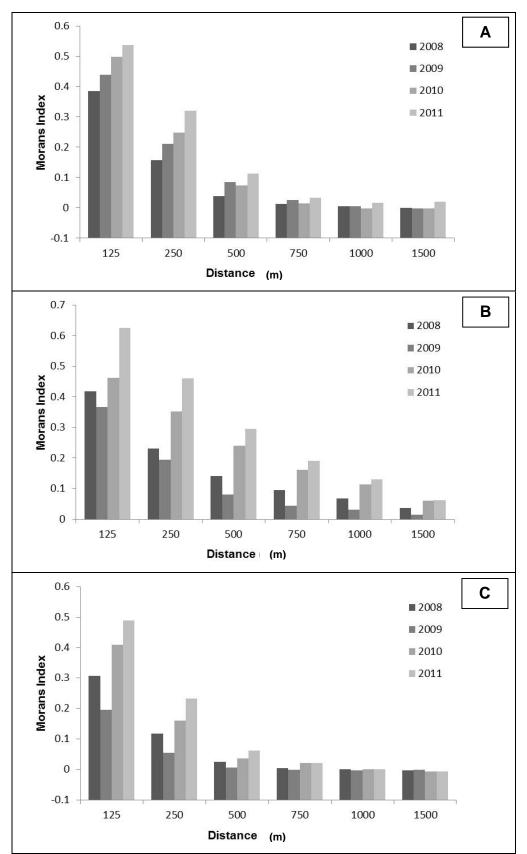


Figure 7. Results of Moran's index across increasing distance bands calculated for each year in the (A) Discovery Bay, (B) Julia Bank and (C) Julia Percy analysis grids. Values greater than zero indicate the clustering of fishing effort (positive spatial autocorrelation), whereas values less than zero indicate dispersed fishing effort (negative spatial autocorrelation).

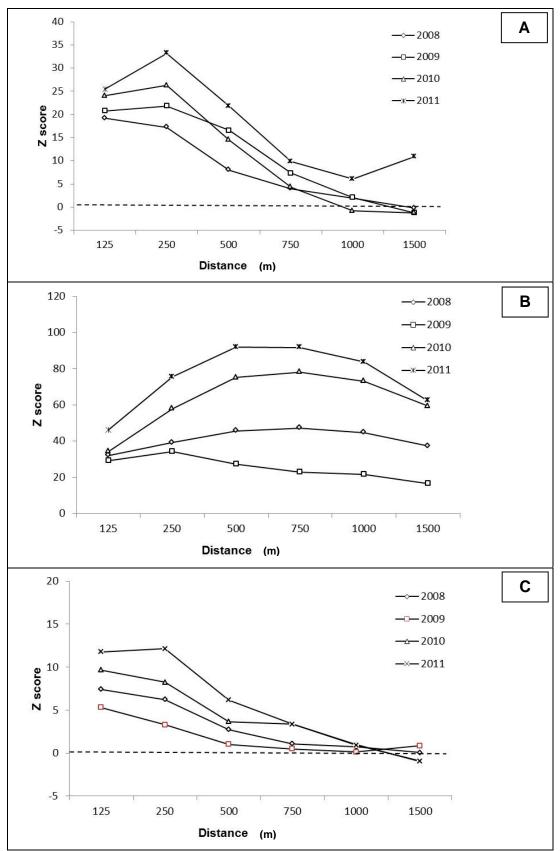


Figure 8. Moran's *I* spatial autocorrelation analysis (z-score) for each year in the (A) Discovery Bay, (B) Julia Bank and (C) Julia Percy analysis grids. Moran's I analysis showed that the distribution of fishing effort was clustered. Where significant clusters occurred, most

clusters were found at shorter distance measures. For instance, high clustering was often observed at 125, 250 and 500 m distance bands, with Moran's Index decreasing at larger distance thresholds. Moran's Index and z-score values were higher in 2010 and 2011 compared to 2008 and 2009 for all three sites. In addition, higher Moran's z-score values were obtained at Julia Bank compared to the other two study sites (C).

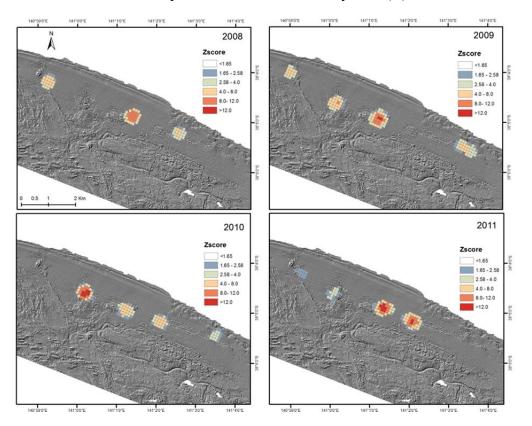


Figure 9 Hotspot analysis of fishing effort distribution from 2008 to 2011 at Discovery Bay over artificially illuminated LiDAR bathymetry. Values >1.65 indicate significant clustering (hotspots).

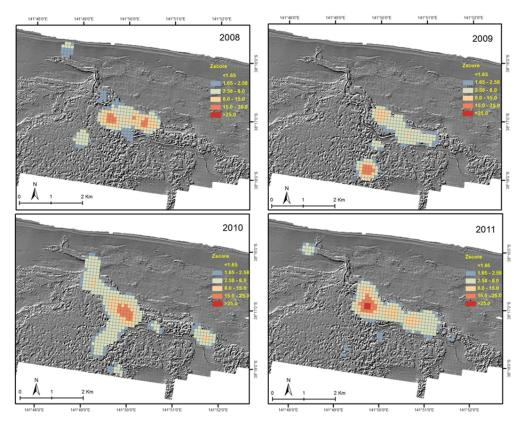


Figure 10. Hotspot analysis of fishing effort distribution from 2008 to 2011 at Julia Bank over artificially illuminated LiDAR bathymetry. Values >1.65 indicate significant clustering (hotspots).

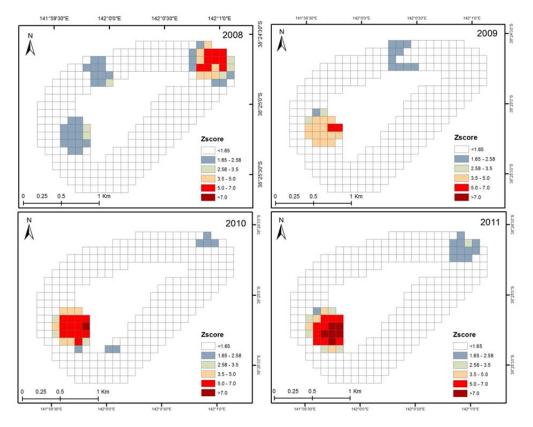


Figure 11. Hotspot analysis of fishing effort distribution from 2008 to 2011 at Julia Percy Island (detailed bathymetry not currently available). Values >1.65 indicate significant clustering (hotspots).

7.2 GENETICS

7.2.1 POPULATION STRUCTURE

7.2.1.1 TIER 1 SPATIAL SAMPLING

A total of 475 *H. rubra* specimens from 16 sampling sites were successfully genotyped at 15 microsatellite loci. Marker independence was confirmed across all sampling sites, with linkage disequilibrium analyses indicating no significant linkage between loci; however, MICROCHECKER analyses indicated the potential influence of null-alleles at loci Hrub10.B11a, Hrub1.H07, Hrub6.CO4, Hrub12.E10 and Hrub9.B05. All subsequent analyses were conducted including and excluding these potentially problematic loci. Each analysis was congruent, indicating that the exclusion of these loci had no significant effect on the overall results. Nonetheless, we present and discuss the results based on the analyses of the10 reliable loci only. A total of 138 alleles were detected, with a mean of 8.17 alleles per locus at all sites. Allelic richness of all loci and across all sites ranged from 6.28 to 7.53 (Table 2), while expected heterozygosities ranged from 0.66 to 0.73 (mean $H_E = 0.70$). Significant departures from the Hardy–Weinberg Equilibrium (HWE) were observed (P < 0.05) at four sampling sites (Table 5), two of which were also accompanied by significant F_{IS} values,

indicating a significant deficit of heterozygotes. These estimates were influenced by single different loci when HWE estimates at the locus and population level were assessed.

Table 5. Statistics for the *Haliotis rubra* sampling sites screened with 10 microsatellite loci. Mean values over loci are presented for the number of alleles (*a*), allelic richness (*r*), expected (H_E) and observed (H_O) heterozygosities, Hardy-Weinberg equilibrium (HWE) *P* values and inbreeding coefficients (F_{IS}) (significance after corrections for multiple comparisons is indicated by bold text).

Code	а	r	H_E	H_O	HWE	F_{IS}
В	8.70	7.53	0.73	0.70	>0.05	0.05
W	7.90	6.92	0.70	0.65	>0.05	0.07
М	8.50	7.29	0.72	0.70	>0.05	0.02
Ν	8.40	7.17	0.70	0.69	>0.05	0.02
L	8.10	7.39	0.71	0.58	<0.001	0.19
С	8.00	6.79	0.69	0.64	>0.05	0.08
WT	8.60	7.22	0.68	0.64	<0.001	0.07
L	8.40	7.23	0.71	0.69	>0.05	0.02
PL	8.30	6.73	0.66	0.64	<0.001	0.03
AP	7.00	6.28	0.68	0.63	>0.05	0.07
PA	9.00	7.42	0.71	0.66	>0.05	0.06
РР	7.80	6.79	0.69	0.69	>0.05	0.01
WP	8.30	7.32	0.72	0.73	>0.05	-0.01
М	7.50	7.10	0.69	0.65	>0.05	0.07
MA	8.30	7.21	0.69	0.59	<0.001	0.15
G	7.90	6.85	0.69	0.68	>0.05	0.01

Global estimates of F_{ST} and D_{est} across all loci were significantly different from zero ($F_{ST} = 0.020$; 95% CI = 0.012–0.030; $D_{est} = 0.051$; 95% CI = 0.028–0.077), indicating limited gene flow and genetic structuring amongst sampling locations. This result appears to be largely driven by a single divergent population from South Australia, PL. All pairwise comparisons of F_{ST} and D_{est} with PL were found to be highly significant, indicating limited gene flow between PL and the Victorian sample sites. Following the exclusion of PL, global estimates of F_{ST} and D_{est} across all loci were weak, but significantly differed from zero ($F_{ST} = 0.007$; 95% CI = 0.004–0.009; $D_{est} = 0.017$; 95% CI = 0.009–0.031), with nearly all pairwise F_{ST} and D_{est} esimates being found to be weak and generally non-significant. This finding incidates the presence of high levels of gene flow across reefs within the Western Zone fishery, and between the Western, Central and Eastern zone fishing stocks in Victoria.

AMOVA analyses were consistent at indicating limited genetic variation among sites. The majority of variation across microsatellite loci was explained by variation within sites (98%; P < 0.001), while between site variation was 2% (P < 0.001). The within site variation was further enhanced by the exclusion of PL from the analysis (99%; P < 0.001). These results indicate that there is very little structuring within the dataset, particularly within Victoria. The

FCA was also highly consistent, indicating limited genetic structure (Figure 9), with the first two factors representing just 4.12% of the total variation between samples (2.24% and 1.88%, respectively). Figure 12 shows little differentiation between individuals from the Victorian sample sites, with only individuals from the South Australian site (PL) being genetically differentiated and forming a distinct cluster.

Regression analyses and a Mantel test indicate moderate isolation by distance. There was significant association between genetic distance and geographic distance, with the Mantel test showing a weak relationship between Slatkin's linearized F_{ST} and the natural log of geographic distance (Mantel r = 0.53, P < 0.05). Regression showed this relationship to be positive and linear ($R^2 = 0.28 P < 0.05$). This signal is reduced when the PL site was removed from the analysis (mantel r = 0.47, P < 0.05: regression $R^2 = 0.22$, P < 0.05), indicating potentially high levels of gene flow across Victorian sample sites.

Both Bayesian clustering analyses provided consistent results, despite the different approaches used to identify the number of populations (K) within the dataset. Both analyses identified two populations (K = 2), with all individuals from the South Australian population PL being assigned to the first population, and the remaining individuals from all Victorian sample sites being assigned to the second population. These findings are highly consistent with the F_{ST} and D_{est} estimates, indicating high levels of genetic connectivity among Victorian sample sites, but potential isolation from the PL site. Population assignment based on each of the Bayesian clustering analyses for each sample site is presented using site colour codes in Figure 12.

	В	W	Μ	Ν	LJ	С	WT	L	PL	Α	PI	PP	WP	Μ	MA	G
В	*	0.00	-0.01	-0.01	0.00	-0.01	0.01	0.00	0.25	0.04	0.00	0.04	-0.01	0.04	0.02	0.05
W	0.00	*	0.01	-0.01	0.00	0.01	0.01	0.01	0.25	0.03	0.00	0.04	0.02	0.03	0.03	0.06
Μ	-0.01	0.00	*	-0.01	-0.01	-0.01	0.00	-0.01	0.26	0.01	-0.01	0.02	0.00	0.02	0.01	0.01
Ν	0.00	0.00	0.00	*	-0.01	0.00	0.00	-0.01	0.22	0.03	0.00	0.04	0.02	0.04	0.01	0.04
LJ	0.00	0.00	0.00	0.00	*	0.01	0.00	0.00	0.27	0.00	0.00	0.03	0.01	0.01	0.02	0.0
С	0.00	0.00	0.00	0.00	0.00	*	0.00	0.01	0.24	0.03	0.00	0.04	0.00	0.04	0.02	0.03
WT	0.01	0.00	0.00	0.00	0.00	0.00	*	0.00	0.24	0.02	-0.01	0.05	0.02	0.03	0.02	0.03
L	0.00	0.00	0.00	0.00	0.00	0.01	0.00	*	0.22	0.04	-0.01	0.03	0.02	0.03	0.02	0.04
PL	0.10	0.11	0.10	0.10	0.11	0.10	0.10	0.09	*	0.30	0.22	0.29	0.28	0.32	0.32	0.37
A	0.02	0.01	0.00	0.01	0.00	0.01	0.01	0.02	0.13	*	0.02	0.04	0.04	0.03	0.01	-0.0
PI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.01	*	0.03	-0.01	0.01	0.03	0.04
PP	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.01	0.12	0.02	0.01	*	0.05	0.06	0.07	0.06
WP	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.01	0.11	0.02	0.00	0.02	*	0.02	0.04	0.05
Μ	0.02	0.01	0.01	0.02	0.01	0.02	0.01	0.01	0.13	0.01	0.01	0.03	0.01	*	0.05	0.0
MA	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.13	0.01	0.01	0.03	0.02	0.02	*	-0.0
G	0.02	0.02	0.01	0.01	0.00	0.01	0.01	0.01	0.15	0.00	0.02	0.03	0.02	0.01	0.00	*

Table 6. Pairwise estimates of F_{ST} (lower diagonal) and D_{est} (upper diagonal) among 16 *Haliotis rubra* collection sites. Values shown in bold are significant (P < 0.001) after 10,000 permutations and corrections for multiple comparisons

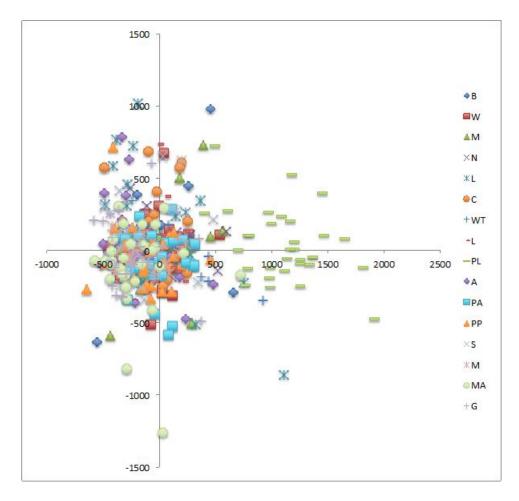


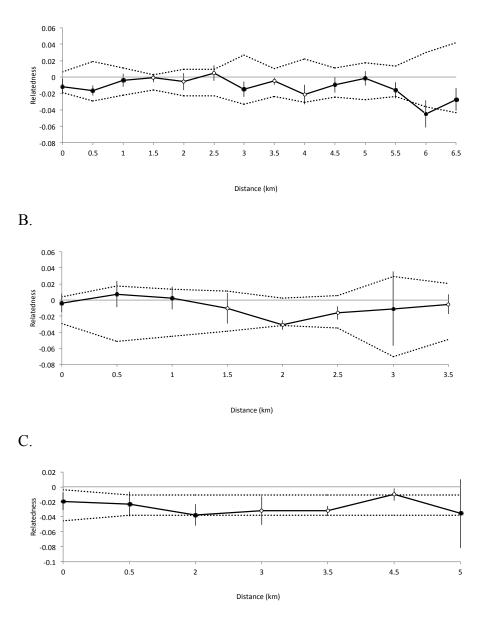
Figure 12. Two-dimensional scatter plot showing the relationships among *Haliotis rubra* sampling sites based on a factorial correspondence analysis of 10 microsatellite loci for 16 sampling sites. The first factor (x-axis) explains 2.24% of the variance, whilst the second factor (y-axis) explains 1.88% of the variance.

7.2.2 SPATIAL AUTOCORRELATION

7.2.2.1 TIER 2 SPATIAL SAMPLING

A spatial autocorrelation analysis was performed using the mutiliocus genotypes of 149 *H*. *rubra* specimens from 16 sites and six reef complexes from the Western Zone Killarney area. The Queller and Goodnight (1989) relatedness coefficient (R) was calculated for all pairs of individuals, involving 11,036 pairwise comparisons across 11 distance classes, ranging from 0 to 6,600 m. Identical independent analyses were also conducted in the Eastern Zone for 80 individuals from Marlo (3,160 pairwise comparisons across eight distance classes, ranging from 0 to 3,500 m) and 40 individuals from Petrel Point (741 pairwise comparisons across seven distance classes, ranging from 0 to 5,000 m). Each analysis indicated no significant association between relatedness and geographic distance (Figure 13). Estimates of R were not

significantly greater at reef scales, or even at the 100 m distance class, indicating that recruitment is unlikley to be localised at reef scales within these regions of the Western and Eastern Zone fisheries. Instead, these results indicate that migration between reef patches is likley to be extensive across generations.



A.

Figure 13. Spatial auto-correlograms of Queller and Goodnight's relatedness coefficient (R) in relation to distance for pairs of individuals for the Killarney (A), Marlo (B) and Petrel Point (C) sampling sites. The solid black line represents the observed correlation coefficient (R) as a function of distance. Error bars represent the standard error around R (calculated by jackknifing). The permuted 95% confidence intervals (dashed lines) around the null hypothesis of a random distribution of individuals (average coefficients after random permutations; solid grey line) are also shown.

7.3 DISCUSSION

The present study presents the first attempt at integrating LiDAR imagery with precisely positioned individual fishing records to better understand the extent and connectivity among reefs supporting commercial fishing grounds for the marine molluse, *Haliotis rubra*. Application of LiDAR high-resolution topography for interpreting GPS tracked fishing records in fishery footprint modelling of abalone in Australia is unprecedented.

Most commercial fisheries data do not have precise geographic coordinates to define the spatial location of catches. More often, a system of coarse scale grids (kilometres) is used for fishers to record catch locations (Morris and Ball 2006). Existing management strategies employing GPS positions for individual abalone catches provide a far greater level of detail (metre-level resolution) regarding fishing effort locations. Importantly, environmental data have not been generally available at a comparable scale to fisheries data. In a recent study, Mellin et al. (2012) modelled the distribution of blacklip and greenlip abalone across Victoria and South Australia, using a coarse scale national bathymetry model (250 x 250 m cell size). In comparison, the high resolution afforded by LiDAR technologies applied in this study (5 x 5 m cell size) provides fine-grained bathymetric variation to categorise habitat information at a resolution closer to the scale of exploitation. In addition, the availability of both bathymetric LiDAR and accurately positioned fishing locations facilitate the development of fishable habitat models that better reflect the scale at which variability in the resource occurs. This allows for an improved understanding of the likely distribution of important fisheries habitat, which is critical for managing a stock that varies considerably over relatively small spatial scales.

Here, we focussed on LiDAR derived data layers that provide a limited geophysical view of the drivers of suitable fisheries habitat. Oceanographic parameters, such as temperature, salinity and currents are also potential drivers of stock distribution and productivity; however, these data types are often not available at an appropriate resolution for fine (reef) scale studies (Brown et al. 2012). Similarly, geospatial parameters of reef patch size and accessibility may be important determinants in the commercial viability of a fishing ground, neither of which is represented in this study. This limitation is reflected in the suitability model, which identifies very small reef patches as highly suitable fisheries habitat, but which are unlikely to hold commercially fishable stocks. The model may also exclude potentially productive areas of reef that have been accessed historically, but which are not currently fished due to greater depth or closure. Nevertheless, the model outputs provide an effective snapshot of fishing grounds under the current harvesting regime at a resolution that informs management at the scale of individual reefs. In addition, the modelling process has the capacity to be refined, as new environmental or fisheries data become available.

Previous studies have reported success in modelling sessile or slow moving infaunal or epifaunal species that show a close correlation with the presence of certain substratum characteristics (Degraer et al. 2008). Brown et al. (2012) indicated the usefulness of fishing activity datasets, and the performance of the MaxEnt modelling approach, to spatially predict habitat suitability for sea scallop (*Placopecten magellanicus*) in the south west fishing area of

Nova Scotia, Canada. In our study fishery habitat suitability was defined using nine LiDARderived environmental variables combined with effort locations. Rugosity, bathymetry and complexity were identified as the three most important variables contributing to the distribution model. Most suitable areas were around 10 m, with suitability declining with depth. Highly suitable grounds were also predicted in reef areas with higher values of rugosity and complexity. These variables are highly similar to the determinants contributing to abalone occurrence, distribution and components determining abalone habitat preferences (Chick et al. 2012). Rugosity, as a measure of topographic complexity, provides an indicator of potential shelter for marine organisms, particularly benthic species. Measuring rugosity over broad geographical regions has been identified as a valuable tool in conservation planning, as it defines the physical structure of the reef that has been shown to correlate positively with the abundance and biomass of reef fish (Kuffner et al. 2007; Pittman et al. 2007).

GIS-based spatial statistics models were used to determine the spatial trends and hotspots in the distribution of fishing activity from 2008 to 2011. The analyses of effort data using hotspot analyses allowed the concentration of effort through time to be determined, and provided an opportunity to analyse the spatial dynamics of the fishery at the reef scale. No structured fishing was implemented in the three locations used for the hotspot analysis. As such, we propose the patterns observed are a reflection of characteristic diver behaviour. Understanding habitat use at scales relevant to resource use may also assist interpreting structured fishing designs, diver movements, and fishing preferences. Trends in fishing effort with significant clusters of effort were observed. The clustering of fishing effort indicates the patchy distribution of abalone stocks within their habitats, particularly across the short distances (10s-100s m) observed in this study. When fishery effort hotspots were overlaid on the predicted habitat suitability models and data on reef extent, a patchy distribution of effort throughout the reef complexes was observed. High effort was often associated with reefs of high rugosity/complexity, indicating associations between particular reef structures and habitat preferences of the species. The application of the hotspot analyses may provide a useful tool for the spatial management of the abalone fishery. For example, a consistent hotspot through time may be an indication of a highly productive ground. An increase in a region's hotspot value may indicate an intensification of effort, as observed in the southwest region of Julia Percy Island (Prop Bay). A management decision may be required to determine whether this increase in effort may be maintained and, if not, support a downward revision of total allowable catch (TAC) for this reef code. Conversely, the decline of a hotspot might indicate that an area is becoming less productive, or that there has been a translocation of effort to a different location. Changes in the aggregate number and effort intensity of hotspots can indicate how the resource is performing under a specific management strategy, thereby facilitating refinement or revision of the chosen strategy. Under all of these scenarios, hotspot analysis provides an insight into the spatial patterns of fishing effort over time, with the value increasing with the temporal time step available. Interpreting observed patterns is a complex process. Rather than being used "standalone", it is more likely that the value in these analyses will be realised when implemented as a tool during stakeholder consultation. Two key limitations on the interpretation of the logger data

are the inherent accuracy of the GPS receiver (~20 m), and that the data represent the vessel track rather than the diver track (Mundy, 2012). It was necessary to edit logger data to remove duplicate records and erroneous tracks associated with logged records whilst vessels were transiting between sites from the analysis. By using an analysis grid cell size of 1 ha (100 m x 100 m), quantitative data may still be obtained at a scale appropriate to the patch size of abalone, but without overstating the spatial accuracy of the data, given the stated limitations (Mundy, 2012).

The genetic structure of *H. rubra* across the eight Western Zone reef codes was assessed using allele frequencies from 15 polymorphic microsatellite loci. A two-step analysis of the microsatellite data was implemented to avoid biases associated with heterozygote deficits at some loci. Heterozygote deficits are common in marine molluscs (Brownlow et al. 2008); however, the cause of this phenomenon remains uncertain. It may be caused by a range of factors, such as non-random mating, selection, Wahlund effects and null alleles (Brownlow et al. 2008). Heterozygote deficit due to non-random mating or Wahlund effects is unlikely in this case because deficits were heterogeneous across loci (significant and non-significant F_{IS} values). The potential influence of selection is more difficult to determine. Microsatellite loci are typically recognised as neutral genetic markers; however, it is possible that some loci are linked to genes under selection (Astanei et al. 2005). Yet, like previous genetic studies of H. rubra (Huang et al. 2000; Conod et al. 2002; Appleyard et al. 2009; Miller et al. 2009), our analyses indicate that a number of loci are potentially influenced by null alleles. This phenomenon appears to be a common problem, generally driving heterozygote deficits in marine molluscs (Hedgecock et al. 2004; Astanei et al. 2005; Brownlow et al. 2008; Lemer et al. 2011; Miller et al. 2013), and has been attributed to high mutation rates (Bierne et al. 2003). It is important that population genetic analyses account for potential biases associated with null alleles, as failure to account for potentially problematic loci risks returning false signals of genetic structure. In the present study, all analyses were conducted inclusive and exclusive of loci that were potentially affected by null alleles. We observed consistency across the datasets, indicating that the null alleles had little effect on the overall results.

The results from each analysis were consistent, providing confidence in the patterns that have emerged. All independent analyses revealed that the abalone stocks from the eight Western Zone, four Central Zone and three Eastern Zone reef codes are genetically homogeneous, indicating a single interbreeding population. Despite barriers to adult dispersal (soft sediment barriers between reef patches), it appears that larval movement is capable of homogenising the gene pool across broad geographical distances. These findings are highly consistent with previous population genetic investigations of *H. rubra* (Brown 1991; Conod et al. 2002; Li et al. 2006; Miller et al., 2009) and other abalone species (Evans et al. 2004; Tang et al. 2005; Gutierrez-Gonzalez et al. 2007), which have also reported evidence of extensive gene flow and limited genetic structure over large geographic distances. Interestingly, the only South Australian sample included in this study (PL) appears to be genetically distinct, indicating potential stock isolation. Recent unpublished findings from genetic research on greenlip abalone (*Haliotis laevigata*) indicates the potential isolation of some South Australian and

Victorian stocks (Mundy pers. comm.); however, further genetic surveys of South Australian *H. rubra* from intermediate geographical locations are needed to determine whether this pattern of uniqueness is accurate, or simply an isolation by distance effect (Brown 1991).

Our results indicate panmixia across the Victorian coastline; however the genetic homogenisation of stocks may theoretically be achieved by the movement of only a small number of effective migrants per generation (Frankham et al. 2009). The weak relationship between genetic and geographic distance indicates that larval movement is unlikely to be localised. Replicated hierarchical spatial sampling at fine spatial scales is necessary to effectively test whether Victorian stocks are largely self-recruiting units. This information is critically important for understanding the resilience of abalone stocks to environmental stress, including fishing pressure, and for modelling stock recovery following major disturbances such as AVG. Ecological studies indicate that the dispersal of *H. rubra* larvae is likely to be highly localised (Prince et al. 1987; McShane et al. 1988). These findings have been supported by genetic studies on *H. rubra* from Tasmania, indicating that recruitment is primarily local, while low levels of gene flow across generations prevent genetic differentiation (Temby et al. 2007; Miller et al. 2009). Similar patterns of local-recruitment have also been reported in genetic studies of another abalone species on the east coast of Australia (Piggott et al. 2008).

In this study, we have demonstrated the integration of newly available LiDAR derived patterns of reef connectivity combined with population genetic data to conduct landscape genetic analyses in a marine environment, to better understand the recruitment of a commercially important species. This study provides the first evidence suggesting that recruitment is not exclusively localised across the H. rubra fishery. Our results indicate that abalone stocks from the Killarney, Marlo and Petrel Point regions are highly connected, and migration between neighbouring and more distant reef patches (up to 6,000 m separation) is likely to be extensive across generations. The replicated hierarchical sampling and analytical approach used here is substantially similar to the genetic study of Miller et al. (2009). Hence, the inconsistent results between these two studies are likely to driven by geographic effects. Also, there is a weight of ecological evidence suggesting that recruitment is localised in various regions of the fishery (Prince et al. 1987; McShane et al. 1988). Consequently, we propose that patterns of recruitment are spatially variable and largely determined by certain factors, such as wave exposure and current intensity. Stocks inhabiting protected or semiprotected habitats are more likely to be self-recruiting compared to those inhabiting exposed habitats; although our surveys found no direct evidence of this phenomenon, despite sampling abalone from a complex of exposed and protected isolated reef patches in the Killarney region. Also, recruitment is likely to be temporally variable depending on coinciding spawning times and ocean current intensities, potentially leading to fluctuating patterns of recruitment through time and space. Nonetheless, these findings provide new insight into the biology and ecology of the species, and the integrity of local fishing stocks. Further studies will be extremely beneficial for describing the spatial patterns of recruitment

across the fishery more broadly, and assisting fisheries managers by providing a better understanding of the resilience / vulnerability of abalone stocks from specific reef codes.

The findings of this study provide immediate benefits for the Western Zone fishery through multiple adoption pathways. First, these results may be used effectively to guide future stock augmentation programmes. Stock augmentation activities, such as reseeding and translocation are being explored as an option for promoting the recovery of stocks in heavily AVG affected areas. These interventions generally require careful genetic management because the mixing of stocks from isolated gene pools may jeopardise the integrity of local stocks through the introduction of maladaptive genotypes (Weeks et al. 2011). Although our data indicate that neutral genetic diversity across the Western Zone is homogenous, possible locally adaptive genetic differences at more localised scales need to be taken into consideration. Under strong selection, adaptive differences may be maintained among populations despite high levels of gene flow (Ribeiro et al. 2011). Highly variable growth rates among stocks from different reef complexes indicate that selective pressure at local scales may be strong, with some genotypes having adaptive advantages in specific environments. Although previous research indicates that growth variation is possibly an example of phenotypic plasticity, and driven by environmental factors (Saunders et al. 2009), a conservative approach would be to source abalone for augmentation purposes from different reef complexes, ideally characterised by different phenotypic traits (e.g. growth rates). Assuming that some genotypes will succeed and others will fail, this 'composite mixing' approach would provide genetically robust stocks for translocation. We advise that fisheries managers refer to the genetic guidelines for effective translocations described by Weeks et al. (2011) for further details before proceeding. The results from this and previous studies demonstrate that patterns of recruitment are likely to be spatially and temporally variable, indicating that some stocks will recover naturally overtime without intervention, while others will benefit greatly from augmentation activities to 'kick-start' their recovery. Determining populations that require intervention is a challenging task; however, temporal catch data at the reef scale could be used as an indicator of local recruitment dependency (e.g. stocks that are slow to recover from disturbance are more likely to be largely dependent on local recruitment), and to help identify stocks that would benefit from enhancement through translocation/reseeding.

Our results indicate that AVG has had no obvious impact on the genetic health of Western Zone abalone stocks. In this study, we included sites that had been heavily impacted by AVG (e.g. Craggs and Murrells) and sites that had not been affected by the virus (Lady Julia Percy Island). Estimates of genetic diversity (allelic richness and heterozygosity) within the Western Zone are relatively homogenous. Consequently, reef codes that should be treated as priority areas for stock augmentation are not apparent. However, these findings must be treated with some caution, as the effects of rapid stock declines on genetic diversity may take multiple generations to become detectable (Frankham et al. 2009). This issue is particularly true given that the age of some individuals included in our analysis pre-date the virus outbreak. Therefore introducing a potential source of bias to our contemporary diversity estimates. Given that this study indicates gene flow among Western Zone stocks is likely to

be extensive (at least in some regions), it is likely that natural gene flow will alleviate any stress of genetic diversity reductions in AVG depleted stocks. Nevertheless, the genetic diversity estimates generated in this study will provide valuable baseline data for monitoring the health of *H. rubra* populations into the future.

Our results indicate that abalone larvae are potentially capable of travelling across large geographic distances. This implication is supported by our findings of panmixia over broad spatial scales, and non-significant associations between genetic and geographic distance (in both tier 1 and 2 genetic datasets). This information provides a valuable framework for predicting the spread of potential heritable diseases, and the adaptive potential of the species to various environmental pressures, such as climate change. Under this model it would be expected that heritable diseases have the potential to spread very quickly throughout the Western Zone fishery, and even over larger distances crossing fishing zones and state boundaries. More positively, these findings also suggests that stocks are likely to be resilient to environmental pressure due to high levels of gene flow, and large population sizes that are capable of maintaining adequate genetic diversity that may facilitate the adaptive process by natural selection. Further genetic sampling of stocks across the species distribution will enhance our understanding of the broader spatial patterns of stock connectivity, and provide a basis for managing fisheries at broader scales. For instance, translocations offer a powerful management tool, and could be used routinely as a management option for replenishing stocks that have been depleted due to fishing or environmental pressure (i.e. urchin barrens, Johnson et al. 2001; Strain and Johnson 2009). Decisions to undertake translocation should nevertheless be risk-based and take into account costs relative to expected benefits. Understanding broad patterns of stock connectivity across fishing jurisdictions will provide the necessary framework for establishing translocation management guidelines within the Australian blacklip abalone fishery.

A specific objective of this study was to estimate Ne (effective population sizes) for Western Zone reef codes. This measure was deemed no longer applicable once extensive gene flow and a lack of genetic structure across the Western Zone fishery was discovered. The population appears to be very large, and spans a large geographic distance encompassing multiple fishing zones. Consequently Ne is likely to be large, even if it is several orders of magnitude less that the census population size. Efforts to calculate Ne based on the current dataset provided non-informative results (Ne = infinity); therefore additional spatial and temporal sampling is needed to obtain reliable estimates. Another major objective was to integrate genetic and geospatial data to determine how genetic variation is affected by landscape and environmental variables. Detailed analyses were not conducted, as *H. rubra* stocks were found to be genetically homogenous, indicating that there are no barriers to gene flow.

8 **BENEFITS**

The findings of this study provide benefits for the administrators of the Western Zone fishery, and follow-on benefits to the scientific and fishing communities. Outcomes from geospatial and genetic analyses conducted in this study will feed directly into the WADA reef-scale assessment and management system, and provide a framework for devising post AVG recovery plans. These data enhance our knowledge of the biology and ecology of *H. rubra*, and provide a framework for implementing effective management strategies that promote the productivity and sustainability of *H. rubra* stocks in the Western Zone fishery.

This study provides a better understanding about the spatial distribution patterns of fishing areas, which is necessary for planning fisheries strategies, long term profitability and ecosystem-based management of abalone stocks throughout the entire Western commercial fishing zone. The use of the fishery GPS logger data allowed us to determine the spatial trends and the concentration of effort through time. This information provides an opportunity to analyse the spatial and temporal dynamics of the fishery at the reef scale, providing benefits to administrators of the Western Zone fishery. Through participation in WADA quota allocation workshops, we found additional benefits in communicating spatial patterns of effort to the fishers. Whilst the hotspot analysis alone has the potential to provide valuable information regarding trends in fishing effort, it provides little information about the structural complexity of the targeted habitats and how they vary across the management zone. The LiDAR data provides the first detailed information about seafloor structure. Suitability analysis shows the extent of grounds with fishable characteristics across zones based on relationships derived from existing AbTrack GPS localities and variations in seafloor structure. Having access to LiDAR derived habitat information provides direct benefits to users and managers of a fishery where the stock varies across extremely small spatial scales. 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 reefs, which were identified through aerial photography and 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. This approach is 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. Diver consultation is generally only effective when there have been relatively consistent catches over a lengthy time period, i.e. a decade or more. In the absence of such information, the capacity to predict potential productive habitat is essential for stratification. It is also important to note that reef codes used for catch reporting are simply statistical blocks that only take limited account of habitat boundaries. The high resolution afforded by the LiDAR technologies applied in this study provides fine scale bathymetry information that may be used to categorise suitable fishing grounds at a resolution closer to the scale of resource use. This information provides fishers and managers with an effective snapshot of fishing grounds under the current harvesting regime at a resolution that informs management at the individual reef scale. The integration of LiDAR

data provides estimates of potential fishable reef extent with each management subzone. For example, by using the suitability output, we may estimate that approximately 1% of the Discovery Bay Marine National Park was identified as fishable habitat; equating to approximately 28 ha. Importantly, categorising reefs according to their structural complexity provides a basis for selecting specific reefs for tag-release-recapture and sampling to estimate growth and maturation. Detailed information about reef physiographic characteristics provides not only a means for targeting data collection, but also enables better interpretation of the results of analyses of those data. Abalone, as with many related gastropods, exhibit high levels of plasticity in their growth and size at maturity, both of which are important for assessment and management. Acquiring this information, especially growth, is costly. Thus, sampling is necessarily limited to relatively few reef complexes. Having access to this information now provides the potential for broad scale management. There is opportunity to account for variation in biological characteristics related to productivity rather than averaging across parameters from sites that may not reflect the overall productivity of a formal management unit (e.g. zone). Overlaying underlying fishable habitat models also provide new insight about resource use. The effective visualisation and communication of this data provided a useful feedback mechanism for integrating fisher knowledge into the fishery management system.

Prior to commencing this project, the genetic stock structure of the blacklip abalone fishery within the Victorian Western Zone, and across the Central and Eastern zones, was unclear. This knowledge gap was of concern, as failure to detect the underlying population structure may lead to the overexploitation and depletion of localised subpopulations. This information also provides the necessary foundation for guiding stock augmentation activities aimed at catalysing the recovery of AVG affected stocks, as the inappropriate mixing of genetically divergent stocks would have detrimental fitness consequences. This study demonstrates that *H. rubra* stocks within the Western Zone, and across the Central and Eastern Zone fisheries comprise a single genetic unit. Further to this finding, we demonstrate for the first time that the recruitment of *H. rubra* larvae is unlikely to be localised in some areas of the Western and Eastern Zone fisheries. This is contrary to the belief that recruitment is exclusively localised in this species. Instead, these data indicate that larval dispersal is extensive, and capable of homogenising gene pools over large geographic distances (>700 km).

The benefits of the genetics study are largely positive. This information simplifies the management process, suggesting the Western Zone fishery does not need to be modulated on genetic grounds. It also suggests there is minimal risk of mixing stocks through translocation activities, however potential adaptive differences need to be considered. Fortunately, there does not appear to be any apparent impact of the AVG virus on related levels of genetic diversity in affected stocks, suggesting stocks are likely to remain genetically resilient. Although, as previously discussed, more time may be needed for impacts to become detectable. The data in this study will act as valuable baseline for future monitoring purposes. A high level of stock connectivity also suggests that *H. rubra* is likely to have high adaptability to environmental pressures, which is driven by large population sizes (census and effective) capable of maintaining genetic diversity. Less positively, extensive larval

movement across large geographic distances indicates that if encountered in the future, heritable diseases have the potential to move rapidly through the Western Zone fishery and across Central and Eastern Zone fisheries. Conversely, in the face of emerging environmental stressors, such as disease and climate change, the spread of resistance genes throughout Victorian fisheries is likely to be a rapid process.

The benefit to fishers, administrators, researchers, recreational fishing communities and conservation groups is that the population structure in the Western Zone fishery can now be inferred with greater certainty, aiding decision making processes about fishery management policy. The results of this study also benefit the scientific community, by enhancing our current understanding about the biology and ecology of *H. rubra*.

9 FURTHER DEVELOPMENT

This study provides a proof of concept for the integration of LIDAR derived seafloor information with fishery dependent data.

A range of issues that require further development are listed below.

9.1 SPATIAL ANALYSES

- GPS data logger information. Fisher logger information provided in this study had some errors indicative of a combination of user and hardware failure. Single locations with up to 3000 abalones records were observed in some instances. GPS location is only indicative, as it records vessel position as a proxy for abalone harvest location. Some records were observed via transiting between reef patches. With the advent of high-resolution imagery, the precise positioning of fisher locations becomes even more critical, particularly if attempting to derive relationships for a patchily distributed resource.
- Providing an indication of productivity in relation to reef extent. Further development of spatial analyses approaches are required to connect temporal patterns in fishing effort and available fishing grounds.
- With the availability of bathymetric LiDAR data for the entire coast of Victoria, there are opportunities to expand the current analytical approach to the Central and Eastern management zones.
- Detailed seafloor information was not available for the Julia Percy Island reef codes. Opportunities to fill this knowledge gap should be considered in future data collection initiatives.
- Oceanographic parameters, such as temperature, salinity, currents and exposure, are also likely drivers of stock distribution and productivity; although these data types are often not available at an appropriate resolution for fine (reef) scale studies. The downscaling of oceanographic regional models may provide an opportunity to include these variables in the modelling approaches conducted in this study.

9.2 GENETIC ANALYSES

• The results from genetic spatial autocorrelation analyses suggest that recruitment is unlikely to be localised within some regions of the Western Zone fishery. These findings are inconsistent with previous studies that describe abalone stocks from separate reef complexes being largely self-recruiting units in other regions of the fishery. These inconsistencies suggest that patterns in recruitment are likely to be spatially and temporally variable, and could be driven by a number of potential physical factors including exposure, current intensities and spawning times. Understanding the spatial patterns of recruitment is critical for management

processes. This situation provides the basis for understanding the resilience of abalone stocks to environmental stress, including fishing pressure, and for modelling stock recovery following major disturbances, such as AVG. Further genetic studies are needed to test the generality of these findings across blacklip abalone fisheries.

- Modern population genomic approaches using state of the art genotyping technologies (e.g. RadSeq) facilitate genotyping across populations for large numbers of anonymous genetic markers (hundreds to hundreds of thousands). These advances provide unprecedented power for estimating patterns of neutral diversity within species populations that may be used to determine spatial patterns of relatedness and recruitment. A benefit of this technology is that patterns of adaptive diversity may also be estimated in the absence of any prior information on either molecular or quantitative trait variation. This approach would be valuable for determining whether variable phenotypes across reef codes (e.g. growth rates) have a genetic basis, and whether selection pressure plays a role in recruitment and colonisation success. This information would provide a valuable resource for guiding future stock enhancement investments.
- Further genetic sampling of stocks across the species distribution will enhance our understanding of the broader spatial patterns of stock connectivity, and provide a basis for managing fisheries at broader spatial scales. For instance, translocations offer an important management tool, and could be routinely used as a management option for replenishing stocks that have been depleted due to fishing or environmental pressure (i.e. urchin barrens). Understanding broad patterns of stock connectivity across fishing jurisdictions will provide the necessary framework for establishing translocation management guidelines within the Australian blacklip abalone fishery.
- The integration of geospatial and genetic data from the Western Zone fishery provides a valuable insight into the drivers of fishing productivity. Our data indicate that productivity is unlikely to be limited by reef availability or larval movement. Instead, colonisation success and productivity is likely to be driven by various ecological factors such as resource availability, competition and exposure. The integration of fishing knowledge and further surveys of reef structure, exposure modelling and ecological compositions will help identify potential drivers of colonisation success and fishery productivity.

Data will be held by Deakin University, University Of Melbourne and WADA pending the establishment of a National Data Storage facility. Information relating to the catches of individual fishers is confidential, and will remain so. No commercially sensitive material will be released. All raw data will be stored on secure servers, with password-protected access.

10 PLANNED OUTCOMES

The planned outcomes of the current study were divided into three research components. The first component involved the application of geospatial technologies to map the extent of reef structure and connectivity, and the integration of fisheries catch data to determine productivity hotspots and reef characteristics that determine habitat suitability. The second component was to conduct a comprehensive population genetic analysis to determine patterns of gene flow and population structure in the Western Zone fishery, determine impacts of AVG on the genetic diversity from affected reef codes, and attempt to calculate effective population size for isolated Western Zone stocks. The third component was to integrate landscape ecology, population genetics and geo-spatial statistics to conduct a landscape genetic analysis to identify barriers to gene flow and drivers of genetic structure.

By investigating GPS AbTrack logger locations with GIS, we were able to analyse the spatial distribution and intensity of fishing effort through time. Together with existing quota, reporting this information provides a valuable opportunity to understand changes in fishing patterns.

The predictive modelling approach of this study provides an improved understanding of the spatial distribution patterns of suitable fishing areas necessary for planning strategies and ecosystem-based management of abalone stocks throughout the Western commercial fishing zone. This approach presents an effective method for defining the extent of the available fishery. In the absence of suitable fishery-independent monitoring data, the approach described here provides a means to develop spatial models to define fishery habitats at a high resolution across the entire fishery. These models provide a detailed picture of habitat extent, reef patch size and connectivity, which are informative for refining the WADA reef-scale assessment and management system.

The genetic analysis indicated that *H. rubra* stocks within the Western Zone comprise a single genetic unit, interbreeding over large spatial scales, which possibly encompass the Central and Eastern Zone fisheries. These findings provide immediate benefits to the Western Zone fishery. This information indicates that there is likely to be minimal risk of mixing stocks through translocation activities aimed at catalysing the recovery of local stocks following AVG associated stock depletions. While we provide direct evidence of neutral gene flow across reef codes, we also recognise and discuss the importance of considering potential adaptive differences across reefs when sourcing stock for translocation.

Given the high level of gene flow, it is not surprising that no detectable impacts of AVG on the genetic health of local fishing stocks were recorded. Estimates of genetic diversity were relatively homogenous across AVG affected and unaffected reef codes; consequently, no reefs were identified as being particularly vulnerable. These findings need to be interpreted with some caution, as the impacts of inbreeding on genetic diversity may take multiple generations to become apparent. Therefore, the data generated in this study will provide a valuable baseline for future population monitoring. Until now, the spatial extent of larval recruitment within *H. rubra* fisheries has been expected to be highly localised. This information is critically important for understanding the resilience of abalone stocks to various environmental stresses, including fishing pressure, and for modelling stock recovery following major disturbances, such as AVG. We provide evidence of extensive migration across reefs in the Western and Eastern Zone fisheries. Spatial autocorrelation analyses indicated no significant association between relatedness and geographic distance, suggesting that migration between reef patches is likely to be extensive across generations in these regions. Combined with evidence from previous studies, patterns of recruitment are likely to be spatially and temporally variable. This study raises questions about the integrity of local fishing stocks, with further studies being needed to test the generality of these findings across the abalone fishery more broadly.

Evidence of panmixia over broad spatial scales and non-significant associations between genetic and geographic distance suggests that individual larvae are potentially capable of moving across large distances. This implies that heritable diseases may potentially sweep rapidly through Western Zone stocks, and possibly across Victorian fishing zones. This information also suggests *H. rubra* is likely to have high adaptability to environmental pressures such as disease and climate change. Stock resilience is likely to be driven by high levels of gene flow, and large population sizes that are capable of maintaining adequate genetic diversity to facilitate the adaptive process by natural selection.

Given that the Western Zone fishery was found to harbour a single large interbreeding population, the calculation of effective population sizes (*Ne*) for individual reefs was deemed no longer applicable. Efforts to calculate *Ne* based on the entire panmictic dataset encompassing Western, Central and Eastern zones produced non-informative results. Further sampling is needed to determine the geographical boundaries of this population to generate more reliable estimates. Additional temporal sampling would also enable heterozygosity discrepancies across generations to be measured, and would tighten the error margins around these estimates.

Evidence of panmixia across the Western Zone also impeded our ability to conduct meaningful landscape genetic analyses. Extensive gene flow indicates there is no apparent barrier to dispersal, despite habitats being highly fragmented in the region.

For the first time, we demonstrate the effective integration of high-resolution habitat mapping and population genetic data to conduct landscape genetic analysis in a marine environment. Geospatial data were used effectively to develop experimental designs at fine spatial scales based on high definition maps, depicting patterns of reef connectivity and isolation. This analysis suggests that despite reef habitats being highly fragmented in the Western Zone fishery, these parameters do not act as barriers to gene flow. Gene flow appears to be extensive at broader spatial scales, and does not follow an 'isolation by distance' model; suggesting the notion of long distance larval dispersal.

The results of this study have been communicated on regional radio and newspapers in Victoria. Presentation at the 2011 and 2012 WADA quota allocation workshops has also

provided an avenue to disseminate the research findings, and obtain feedback from stakeholders. Components of the work have been presented at the Malacological Society of Australasia 'Mollusc 2012' conference (Melbourne), and were also presented at the Marine Geological and Biological Habitat Mapping (GeoHab) conference in May 2013 (Rome, Italy).

11 CONCLUSIONS

All three project objectives were met in this study. Firstly we investigated methodologies to integrate commercial catch data with LiDAR-derived seafloor structure information, and identify the spatial connectivity of reef systems and abalone habitat suitability. Using a species distribution modelling approach, we were able to provide fishers and managers with a prediction of available fishing grounds under the current harvesting regime at a resolution that informs management at the individual reef scale. Furthermore, analyses of the fishery GPS logger data allowed for the determination of spatial trends, such as the changes in the concentration of fishing effort through time. Another aim was to conduct a population genetic assessment of *H. rubra* in the Western Zone. This objective was also achieved with *H. rubra* stocks within the Western Zone being found to comprise a single genetic unit, and preliminary evidence of stock connectivity spanning the Western, Central and Eastern Zone fisheries.

Second, population genetic analyses confirmed that the Western Zone abalone fishery is a single inter-breeding population. Estimates of genetic diversity were relatively homogenous across AVG affected and unaffected reef codes, indicating there is no apparent impact on the health of affected abalone stocks. As discussed previously, these findings need to be treated with some caution. Further fine scale population genetic analysis indicated that migration between reef patches is likely to be extensive across generations in, at least, some parts of the Western Zone fishery. These findings challenge the current literature that suggests *H. rubra* stocks are exclusively self-recruiting units.

Finally, integration of geospatial and genetic data from the Western Zone fishery has provided valuable insight into the drivers of fishing productivity. Our data suggests that productivity is unlikely to be limited by reef availability or larval recruitment. Instead, colonisation success and productivity is likely to be driven by certain ecological factors, such as resource availability, competition and exposure. Landscape genetic analysis indicates that there are no apparent barriers to gene flow in the Western Zone, despite reef habitats being highly fragmented. Gene flow appears to be extensive, and does not follow an isolation by distance model, suggesting long distance larval dispersal. Combined, these data provide a comprehensive framework guiding stock augmentation activities to catalyse the recovery of AVG affected reefs, as well as contributing towards improving our understanding of the spatial patterns of connectivity and recruitment across reef codes, and predicting the spread of heritable diseases and adaptability of abalone stocks to environmental pressures (e.g. disease and climate change).

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13 APPENDIX 1 – INTELLECTUAL PROPERTY

No commercially valuable intellectual property arose from this research. Information relating to the catches of individual fishers is confidential, and will remain so. No commercially sensitive material will be released. Whilst data access to the LiDAR data in this project was available for the spatial analyses component, future data access beyond the project will need to be negotiated with the data custodians and the Department of Environment and Primary Industries.

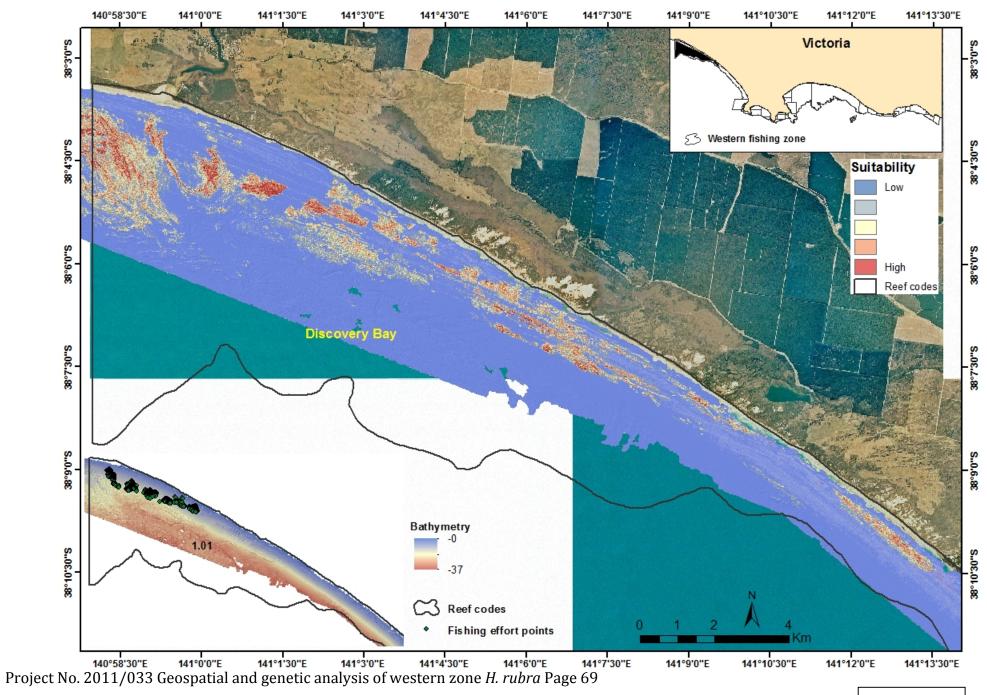
14 APPENDIX 2 – STAFF INVOLVED IN PROJECT

Dr Adam Miller (University of Melbourne) Dr Andrew Weeks (University of Melbourne) Dr Daniel Ierodiaconou (Deakin University) Dr Alex Rattray (Deakin University) Mohamed Ali Jalali (PhD student , Deakin University) Dr Harry Gorfine (DPI Fisheries) Dr Justin Bell (DPI Fisheries) Harry Peeters (WADA) Dr Duncan Worthington (Ambrad Consulting Pty) Dr Craig Mundy (UTAS) Professor Gerry Quinn (Deakin University)

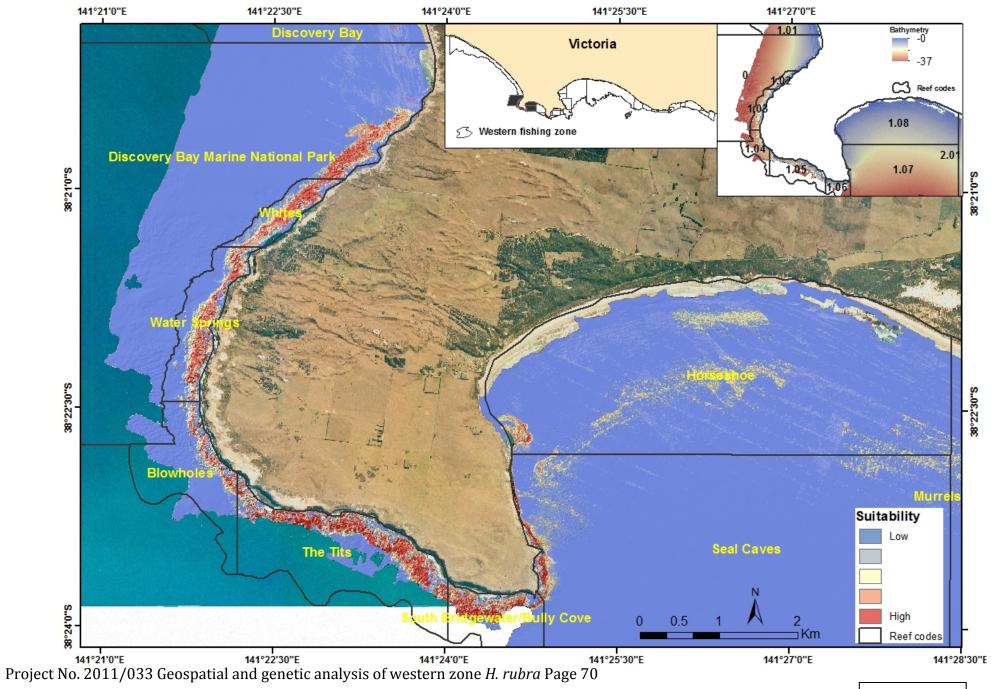
15 APPENDIX 3 – MAP SET OF SUITABILITY MODELS

The attached maps are derived from the habitat suitability modelling detailed in section 6.1.2.

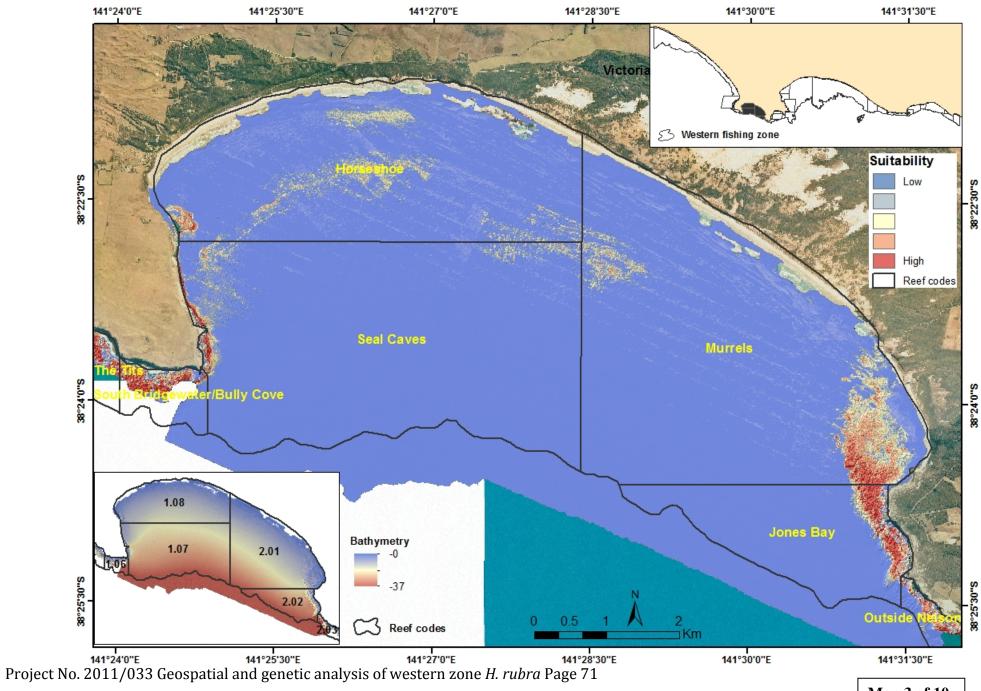
Maps are organised from the west of the Western Zone abalone fishery (Discovery Bay, Map1 of 10) to its eastern extent (Hopkins River, Map 10 of 10). A habitat suitability modelling approach was used to predict the potential footprint of the Western Zone fishery based on the location of all GPS logged abalone catch records for the years 2008–2011. The maximum entropy method (MaxEnt) is a general-purpose, machine-learning method with a simple and precise mathematical formulation, and it has a number of aspects that make it well-suited for habitat distribution modelling (Phillips et al. 2006). LiDAR derived seafloor structure information was combined with GPS locations of logged abalone catches to extrapolate similar, potentially suitable fishing areas across the Western Zone fishery. AbTrack GPS locations were summarised as presence records using a 1 ha (100 m x 100 m) grid for the western zone, to take into consideration any error associated with the inherent accuracy of the GPS receiver (~20 m), and, that the data represent the vessel track rather than the diver track (Mundy, 2012). Erroneous tracks associated with logged records whilst the vessels were transiting between sites were removed from the analysis. Logged catch locations, occurring in ~15,000 1 ha presence cells were randomly partitioned into two parts; 75% as training data and 25% for model validation. The MaxEnt model was able to predict reef areas of high fishery suitability at a fine-scale (5 m resolution) across the entire Western Zone fishery. Reef features smaller than 100 linear metres were resolved from the surrounding soft sediments (Figure 6) (larger scale maps are provided in Appendix 3). The AUC for the training data and test data (0.89 in both cases) indicated a good performing model. It is important to note that the model presented here is a representation of the fishery footprint based on logged catch locations, rather than the habitat suitability of H. rubra. Understanding the realised niche of the species would require a systematic sampling regime across its broader geographical range (i.e. greater depths compared to those typically targeted by fishers).



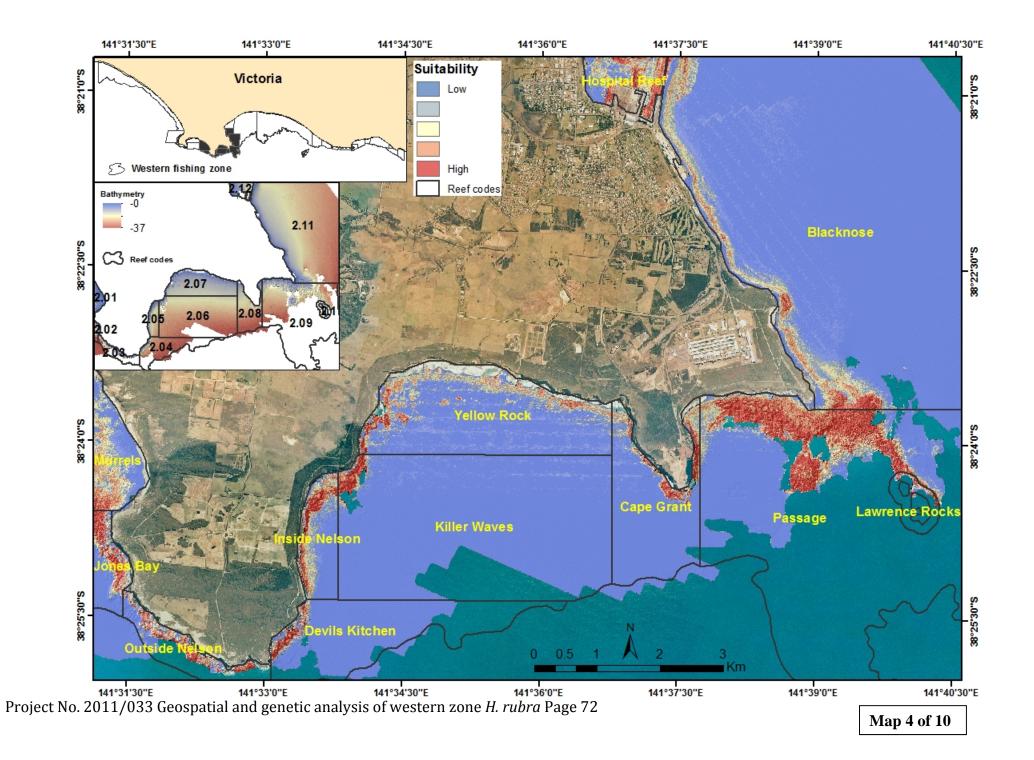
Map 1 of 10

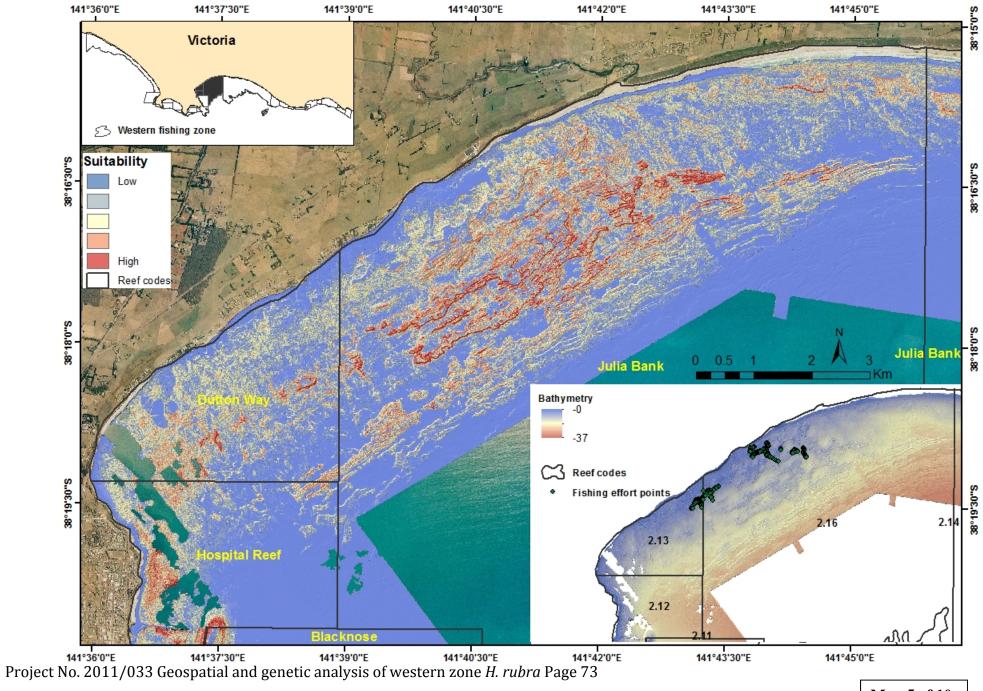


Map 2 of 10

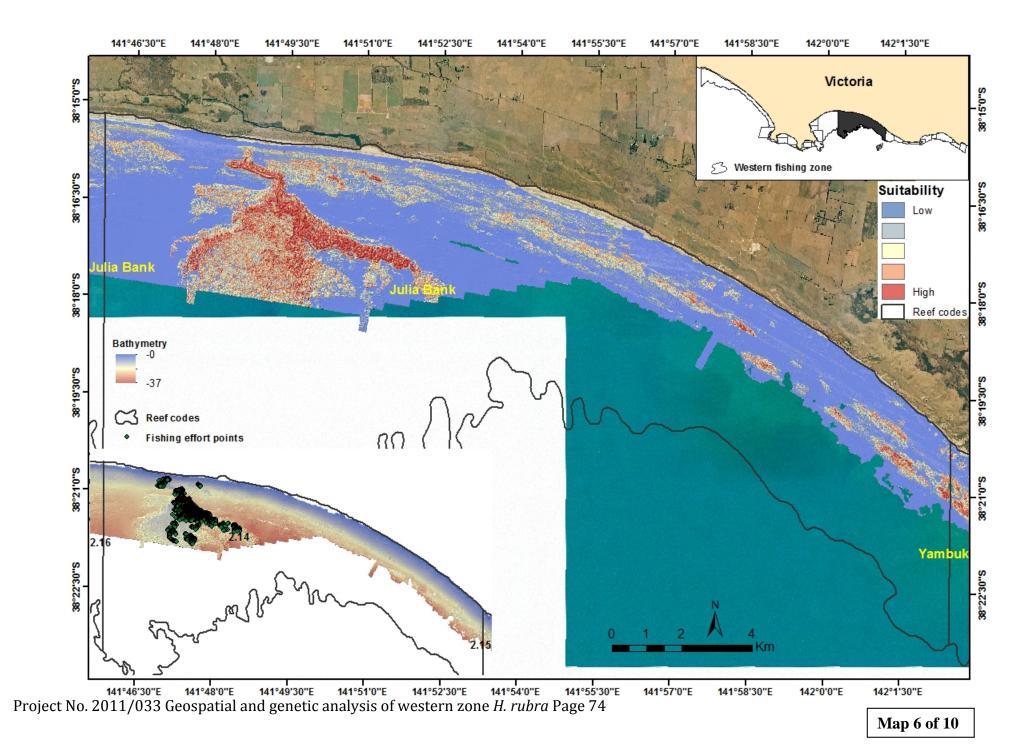


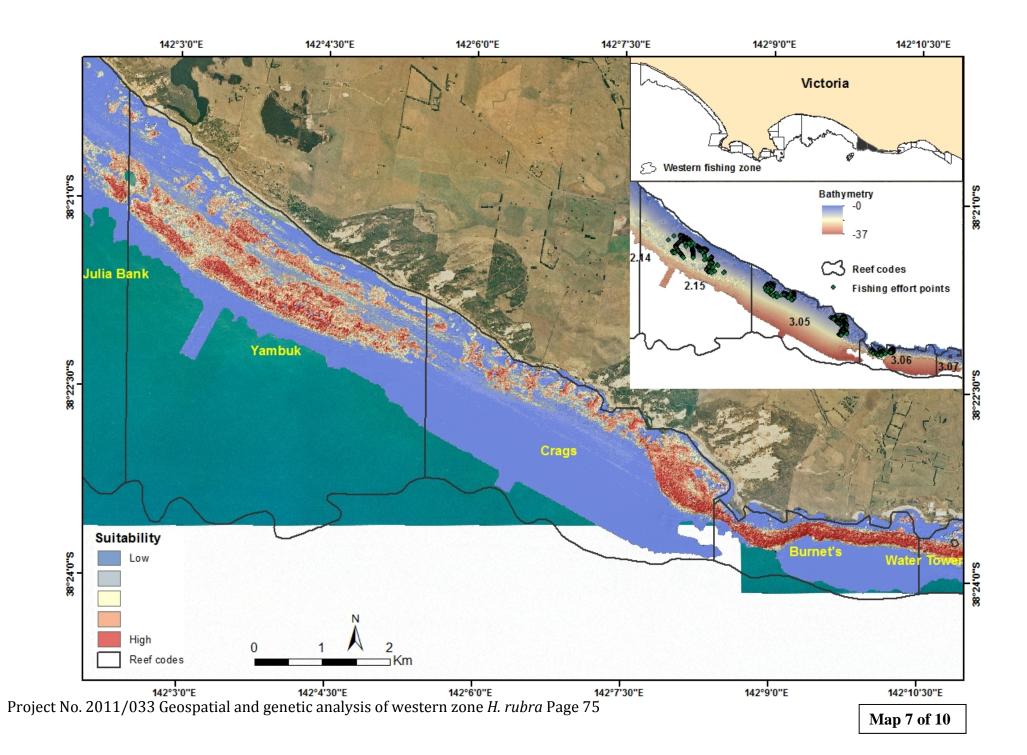
Map 3 of 10

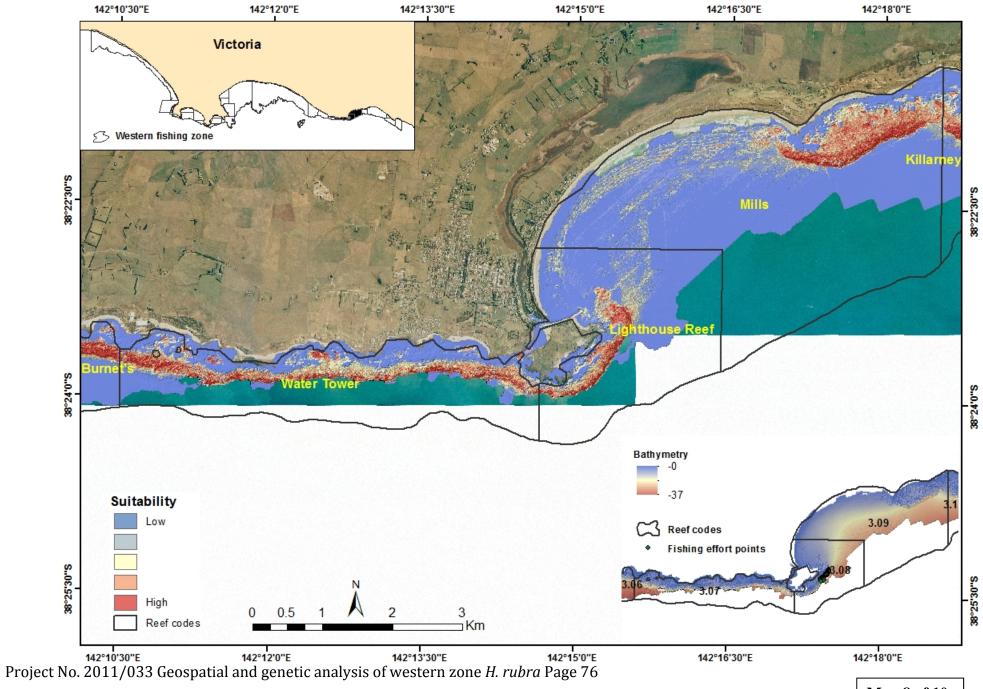




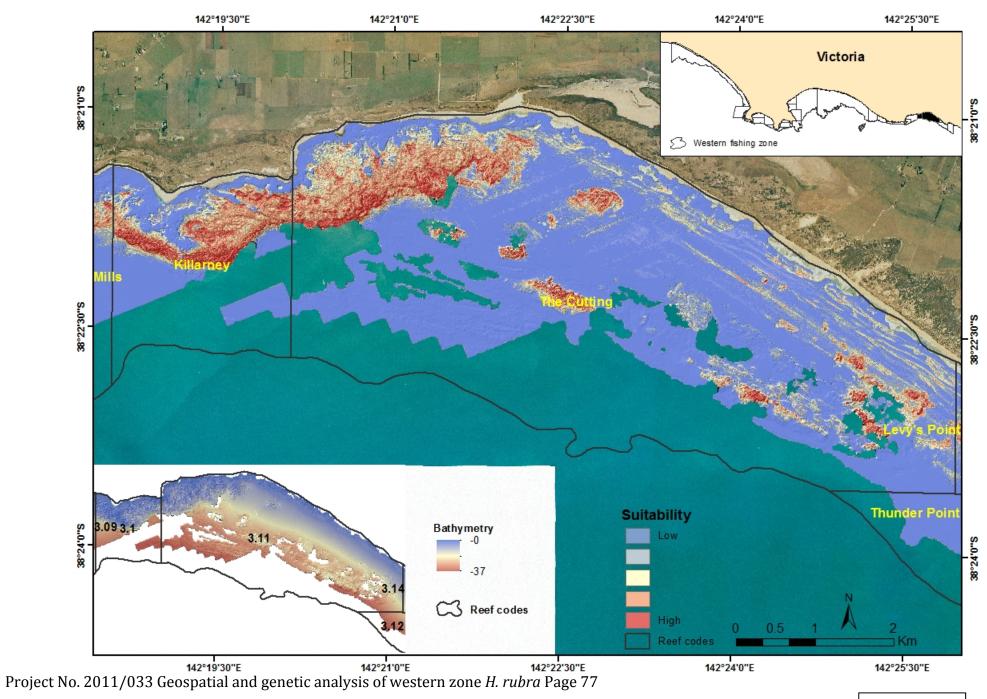
Map 5 of 10



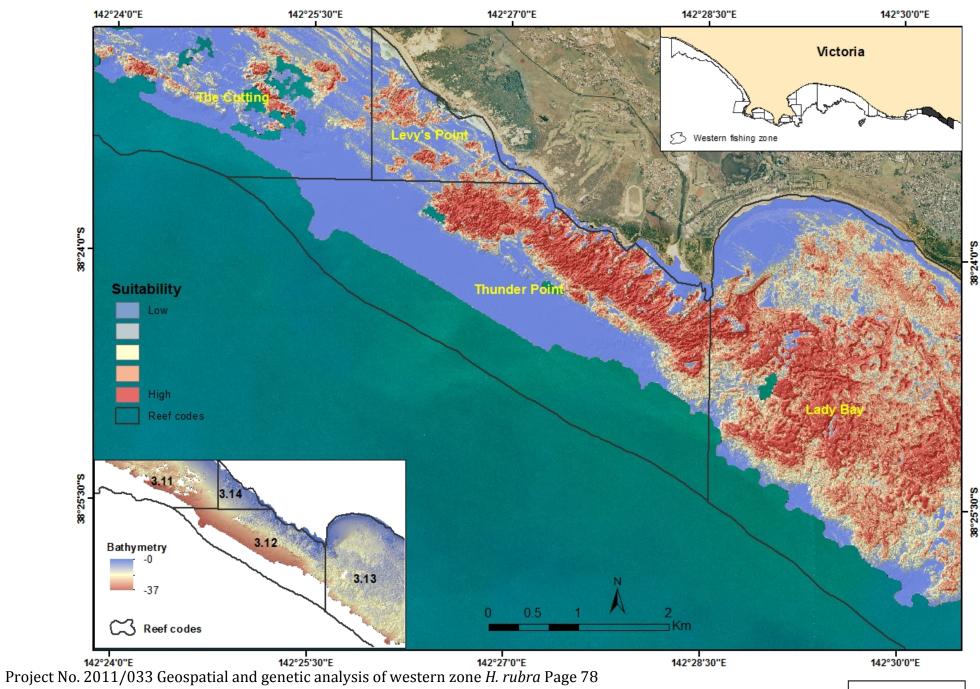




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