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Research

Using species distribution models to assess the long-term impacts of changing oceanographic conditions on abalone density in south east Australia

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Warming from climate change and resulting increases in energy stored in the oceans is causing changes in the hydrodynamics and biogeochemistry of marine systems, exacerbating current challenges facing marine fisheries. Although studies have evaluated effects of rising temperatures on marine species, few have looked at these impacts along with other environmental drivers over long time periods. In this study, we associate long-term density of blacklip abalone to changing oceanographic conditions in a climate change 'hot-spot' off southeast Australia. We downscaled and hind-casted existing hydrodynamic models to provide information on waves and currents over 25 yr and used this information to run biophysical connectivity models. We combined the connectivity models with 21 yr of data on abalone density, temperature, seafloor habitat, and the effects of a disease outbreak in an machine learning modeling approach to develop a spatio-temporal model of abalone density. We found that the combination of temperature, connectivity, current speed, wave orbital velocity, fishery catch, depth, reef structure and a disease outbreak explain 70% of variation in abalone density and allowed us to create 30 m resolution predictive grids with 75% accuracy. An emerging hotspot analysis run on the individual predictive grids from each year detected a predominance of low-density grids across the region, with 49.5% of cells classified as cold spots, 14.3% as hotspots and 36.2% with no significant patterns observed. This type of spatio-temporal analysis provides important insights into how changing environmental conditions are impacting density in an important fishery species, allowing for better adaptive management in the face of future climate change.

Keywords: boosted regression trees, climate change, downscaled hydrodynamics, emerging hot-spots, *Haliotis rubra*, long-term analyses

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Introduction

Almost the entire Earth is experiencing increasing surface temperatures due to climate change with a global average warming of 0.85°C over the last century and projected increases of more than 2°C by 2100 (RCP4.5; IPCC 2013). The majority of the energy (90%) from these increases is stored in the world's oceans (IPCC 2013), elevating temperatures and causing changes in the hydrodynamics and biogeochemistry of marine systems (IPCC 2007, Diaz and Rosenberg 2008). These changes are already having a significant impact on marine biodiversity (Pauly et al. 2002, Srinivasan et al. 2010, Poloczanska et al. 2013). In particular, climate change poses a significant risk to commercial fisheries and the economies they sustain, with changes in species distribution, abundance and phenology already being reported for fisheries around the globe (Cheung et al. 2010, Rutterford et al. 2015).

Population dynamics of fishing stocks is often strongly associated with oceanography (Pauly et al. 2002, Portner and Knust 2007) and changes in oceanographic conditions can have significant effects (Sumaila et al. 2011). For example, many species are shifting their distributions in response to warming waters by either moving in a poleward direction (Beaugrand et al. 2002, Perry et al. 2005, Mueter and Litzow 2008, Pinsky et al. 2011, Poloczanska et al. 2013) or by inhabiting deeper depth ranges (Dulvy et al. 2008). While the effects of changing temperature on fisheries around the world are being studied at increasing rates (Cheung et al. 2010, Lam et al. 2016, Serpetti et al. 2017), other oceanographic factors associated with climate change can also affect marine species' distribution and productivity but are often overlooked (Harley et al. 2006). More recent studies are examining the effects of ocean acidification on marine fisheries (Stiasny et al. 2016, Fernandes et al. 2017) but more oceanographic information can help further understand the effects of climate change.

Additional impacts of climate change on marine ecosystems include alterations to global marine wind fields, which result in changing wave climates (spatial distribution of wave height, period and direction averaged over a period of time; Tokinaga and Xie 2011, Young et al. 2011) and ocean currents (Fyfe and Saenko 2006). The impacts of climate-induced changes in hydrodynamics are less well understood despite knowledge that the wave climate strongly influences the distribution of coastal and marine communities (Wernberg et al. 2005, Rattray et al. 2015, Young et al. 2015). Current patterns are also well-recognized as having significant influence on larval dispersal and recruitment processes in many marine taxa since the movement of pelagic larvae is often passive due to poor swimming capacity relative to the velocity of currents (Gaylord and Gaines 2000, Cowen and Sponaugle 2009, Stachura et al. 2014). Therefore, changes in those currents can have large effects on marine populations by altering patterns of population connectivity (Svensson et al. 2005, Cheung et al. 2009). Consequently, climate-induced changes in ocean circulation are likely to have strong impacts on fisheries (Moore et al. 2018).

Associating species distributions and local densities with spatial and temporal variability in oceanographic conditions can assist fisheries management through an improved understanding of stock structure, connectivity and factors influencing biomass distributions (Ianelli et al. 2011, Wilderbuer et al. 2013, Szuwalski and Hollowed 2016). Furthermore, these associations can help to predict how species are likely to respond to changing environmental conditions (Walther et al. 2002). One method for achieving an understanding of species' responses to their environment is through the use of species distribution models (SDMs), which have increased in applications over the past couple of decades (Guisan and Thuiller 2005, Phillips et al. 2006). Traditionally, SDMs have made static predictions, but temporal components are becoming more common in terrestrial systems (Nielsen et al. 2003, Ruegg et al. 2006, Flantua et al. 2007, Barrows et al. 2008) and a few recent examples have emerged in marine systems (Cheung et al. 2010, Tyberghein et al. 2012, Rutterford et al. 2015). Application to marine systems is challenging as spatiotemporal variability within the three-dimensional water column is often more limited at appropriate scales (Valavanis et al. 2008, Franklin 2010) and marine observation data is limited (Guinotte et al. 2006, Kaschner et al. 2006), especially over longer time frames (Hoegh-Guldberg and Bruno 2010). To effectively conserve species and achieve improved management outcomes for fisheries, the incorporation of temporally dynamic variables is needed to account for variations in species distributions and abundances due to changing conditions.

Abalone (*Haliotis* spp.) are marine molluscs that have undergone intensive fishing throughout the world resulting in stock depletion in most countries (Dichmont et al. 2000, Rossetto et al. 2015) and evidence suggests that climate change could cause further decreases (Caputi et al. 2016). Increased temperatures and decreases in dissolved oxygen caused by climate change are both associated with reduced growth and greater mortality in abalone (Boch et al. 2018), while ocean acidification can decrease thermal tolerance at the larval stage (Zippay and Hofmann 2010). Rising ocean temperatures from climate change can also increase the occurrences of disease outbreaks, resulting in mass mortality of abalone (Ben-Horin et al. 2013). Understanding how abalone populations respond to environmental conditions over long time periods can help to better manage these species in the future.

Australia's blacklip abalone *Haliotis rubra* fishery is the world's largest wild abalone fishery with a net value of US$65 million (Stobart et al. 2018). Australian abalone fisheries remain comparatively resilient to global fisheries and contribute around 50% of wild-caught abalone to the market, however, large decreases in catch quotas due to overfishing and disease have occurred (Mayfield et al. 2012). A large portion of the *H. rubra* fishery is located along the southeast coast of Australia, which is in a climate change 'hot-spot' where sea surface temperatures are experiencing rapid warming at rates 3–4 times the global average (Ridgway 2007, Frusher et al. 2013) with a 0.8°C increase observed since the

1960s (Miles et al. 2016). Additionally, an analysis of a 30-yr historical record shows that wave heights are increasing globally with the most significant increases (0.7 cm yr^{-1}) occurring off southeast Australia (Young et al. 2011, Young and Ribal 2019). Given the potential threats of climate change to the abalone fishing industry, there is a need to develop better predictive models of how changing environmental conditions may influence future persistence.

In this study we link long-term biomass in *H. rubra* fishing stocks to changing oceanographic conditions in Victorian coastal waters in southeastern Australia to understand the impact of spatial and temporal environmental conditions. We compiled both dynamic and static environmental spatial layers for the coastal region of Victoria, Australia including information on waves, currents, connectivity, sea surface temperature, fisheries catch, seafloor structure, reef characteristics, and the extent of an abalone virus outbreak. These environmental datasets were combined with *H. rubra* density from fishery independent diver observations from 1995 to 2015 in a machine learning model to understand how they drive variability in productivity. This analysis aims to understand how changing conditions are impacting density of an important fishery species, and inform better adaptive management of the fishery in response to future environmental change.

Material and methods

Study region

The study region for this project is within the coastal waters of Victoria, Australia extending along ~2000 km of coastline (Fig. 1). This coastline consists of a mixture of seafloor topography and a strong temperature gradient with warmer waters in the east (Hobday and Lough 2011) and cooler waters in the west (Frusher et al. 2013). Variation in orientation of the coast to dominant swell directions affects the distributions of marine communities and is subjected to persistent high energy swells (Porter-Smith et al. 2004).

The spatially-variable, dynamic and rapidly changing environment makes this region ideal for studying the potential effects of climate change on an important fishery species, *H. rubra*, and the resulting management implications. The fishery for *H. rubra* within this region is divided into three active commercial fishing zones (Western, Central and Eastern). Two of those zones (Western and Central) have suffered major recent declines due to disease (Abalone Viral Ganglioneuritis; Mayfield et al. 2011) and the third from range expansion of an urchin species (*Centrostephanus rodgersii*; Ling 2008). One primary objective for the fishery is to rebuild biomass through previously enacted and conservative

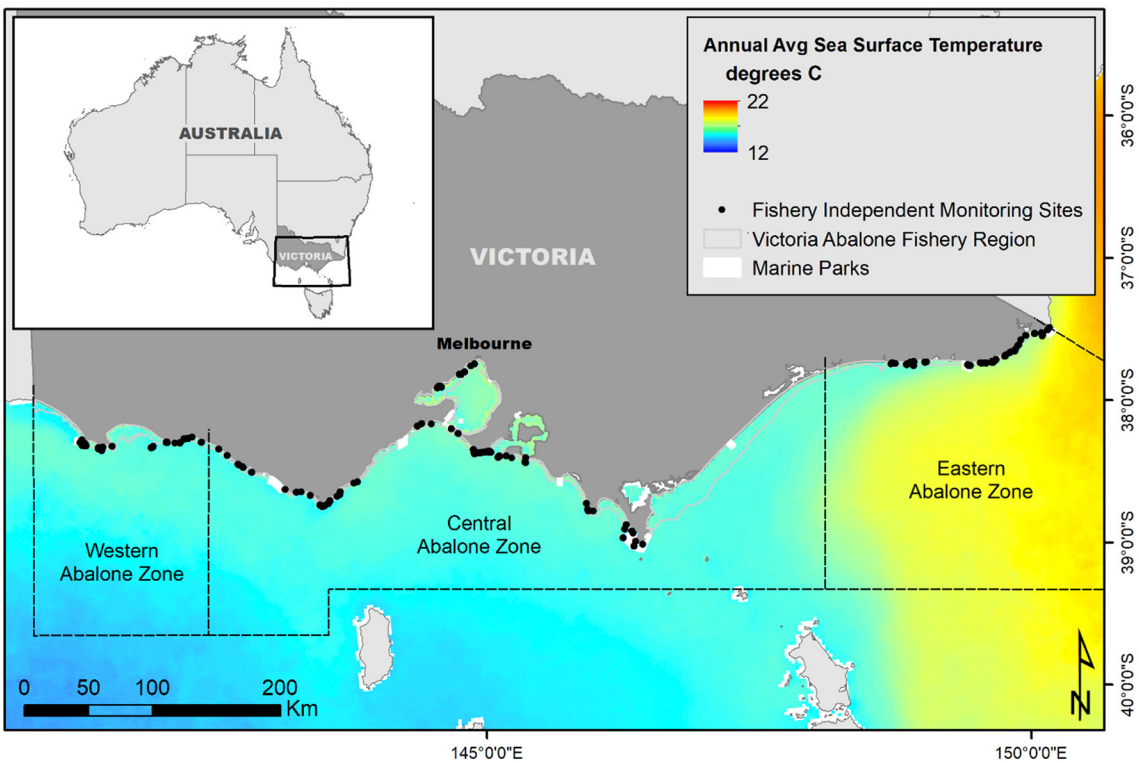

Figure 1. Study region along the nearshore coastal waters off Victoria, Australia. The *Haliotis rubra* fishery in Victoria is managed across three zones delineated by the dashed lines: Western, Central and Eastern. The light grey polygon shows the Victoria abalone fishery region, which is managed across smaller zones (not shown here), and the black points represent the 195 fishery independent monitoring sites for abalone. Marine parks (shown as white polygons) represent areas closed to fishing. The gradient in sea surface temperature across the study area is shown in the background.

management measures including reduced catch quotas, increased size limits and a reduction through attrition in the number of commercial abalone divers (DEDJTR 2016), and it is recognised that a changing climate is likely to limit the extent of rebuilding that could occur (DPI 2015).

Abalone biomass sampling

Density data from fishery independent diver surveys of *H. rubra* across 195 monitoring sites (Fig. 1), conducted by the Victorian Fisheries Authority, were collated from 1995 to 2015. At each of these sites, divers count all abalone within six 30 m by 1 m transects set at random cardinal directions from the central site coordinates and randomly collect 25 abalone from the end of each transect for shell length measurement. We used these data to compute total biomass per site for each year using the allometric relationship:

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

where W is weight in kilograms; L_s is maximum abalone shell length in centimeters; and a and b are regression constants with specified values of 0.000412 and 2.76, respectively (McShane et al. 1988a, b). The transect data were then used to calculate the total biomass (kg) per 900 m^2 to conduct all further analyses at 30 m resolution.

Seafloor structure data

Light detection and ranging (LiDAR) data were collected across the coastal waters of Victoria (Quadros and Frisina 2010). The LiDAR dataset provides bathymetry information at 5 m resolution and extends from elevations of +10 m to ocean depths around −25 m (Quadros and Frisina 2010). Using this LiDAR bathymetry, we derived characteristics of the seafloor including depth, slope, vector ruggedness measure (VRM), multiple scales of bathymetric position index (BPI), substrate type and reef areas (Supplementary material Appendix 1 Table A1). These variables were derived from the 5 m resolution bathymetry and then averaged at a 30 m scale with the Focal Statistics tool within ArcGIS Spatial Analyst (ESRI 2011) to match the site scale of abalone sampling, and then clipped to the 20 m depth contour to restrict all analyses to the diver depth range.

Downscaled oceanography

We downscaled oceanographic parameters likely to be important to the distribution and productivity of abalone. First, processed sea surface temperature (SST) datasets were sourced from the Integrated Marine Observing System (IMOS 2017). Annual and seasonal (summer and winter) means in SST were computed from 1995 to 2015 for use in the geospatial models. These data were then downscaled to 30 m resolution using Empirical Bayesian Kriging (EBK) in ArcGIS to create SST maps at the same spatial scale as the other variables. The EBK interpolated SST results were significantly correlated ($r = 0.74$, $p < 0.001$) to an independent dataset of SST observations (<www.surf-forecast.com/>).

Wave and current information were derived from a coupled hydrodynamic and spectral wave model (DHI 2016). More detailed information on the development of these hydrodynamic models can be found in Supplementary material Appendix 1. The hydrodynamic models were run as annual simulations from 1990 to 2015, starting in July of one year and ending in July of the next to allow for an annual, seamless model during the *H. rubra* spawning period over austral summer (December–February; McShane et al. 1988a, b). Annual outputs describe ocean currents at 5 min timesteps using a triangulated mesh with a spatial resolution of ~500 m at the shoreline to ~30 km in the open ocean. These outputs are used in the biophysical modelling (see below). For the spatial analyses, monthly 500 m grids for each of the model attributes (current speed, wave orbital velocities, significant wave height, wave power, current direction, wave direction) were further summarized into annual and seasonal (summer and winter) averages for each year and downscaled to 30 m using EBK.

Biophysical modelling

We used habitat, oceanographic and biological data within a biophysical dispersal model (Treml et al. 2015) to quantify patterns of *H. rubra* population connectivity across the study area (more details on this approach can be found in Supplementary material Appendix 1). A cloud of larvae was released fortnightly from each habitat patch (reef area) within dispersal simulations that allowed larvae to be transported downstream by currents. Ocean current velocities, turbulent diffusion and larval behaviour move the larvae through the seascape at each modelled timestep. The abalone dispersal simulations were modelled for up to a 20-d larval duration period with potential settlement from 2.5 d, providing a conservative larval duration.

These simulations allowed us to develop potential population connectivity matrices via larval dispersal for each year to show the likelihood of movement through the seascape and the relative influence on downstream populations. These dispersal structure matrices were then used to generate spatially and temporally variable measures of replenishment and connectivity (Supplementary material Appendix 1; Treml et al. 2015).

Fisheries catch data

Annual *H. rubra* catch and effort data from 1995 to 2015 were obtained from the Victorian Fisheries Authority. Using these data, we calculated annual CPUE (kg h^{-1}) for each of the major fishing zones: Western, Eastern and Central.

Disease outbreak

We also took into account a disease outbreak during the time period of this study. Between 2006 and 2010, AVG caused

by the abalone herpes virus (AbHV), spread along the western coastline of Victoria, devastating wild and farmed abalone stocks, with mortalities exceeding 90% in some areas (Gorfine et al. 2009). To account for AVG, we created a categorical grid with the following classifications: 0 = areas prior to the outbreak and those areas not affected by the outbreak, 3 = active period of the virus, 2 = 2 yr following outbreak and 1 = 3–5 yr following outbreak.

Spatio-temporal modelling of abalone biomass

To identify which of the above factors best explain the distribution of productive abalone reefs, we combined assessments of annual, fishery independent *H. rubra* density with the dynamic and static environmental variables described above (Supplementary material Appendix 1 Table A1) using boosted regression trees (BRT). Rather than providing a single 'best' model, such as in traditional regression methods, the BRT method utilises a large number of relatively simple tree models to develop associations between response and explanatory variables and allows for more robust predictions (Elith et al. 2006, 2008, Leathwick et al. 2006).

To reduce overfitting the data and optimize model parameters, we used the BRT tuning functions in the caret package. We used a learning rate of 0.002, an interaction depth of 3, 16 000 trees, and a 10 k-fold cross validation method (Leathwick et al. 2006) within R statistical software (R Core Team) and the 'gbm' package (Ridgeway 2017). We ran a series of BRTs with varying combinations of explanatory variables until we developed a model with high variance explained and accurate predictive ability. The BRT was trained using 70% (n = 2143) of the density observations while the remaining 30% (n = 919) were held in reserve for evaluating the predictive ability of the resulting best model. The final BRT model was used to predict the density from the evaluation dataset and those predictive values were compared to the observed density values using a Pearson correlation analysis. We also bootstrapped the predictions by randomly selecting 70% of the data 50 times each year to develop standard deviation maps of the annual predictions and averaged those across all years to provide an overall uncertainty map. The final model was used to predict and extrapolate density across the coastal zone within the Victoria state waters with a separate 30 m resolution predictive grid for each year, resulting in 21 predictions from 1995 to 2015.

To determine which areas along the coast are experiencing positive or negative changes in density of *H. rubra*, we used the Emerging Hot Spot Analysis (EHSA) tool in ArcGIS. EHSA incorporates both space and time into a clustering analysis of densities (Getis and Ord 1992) and classifies the region into 'hot' or 'cold' spots. Statistically significant hot spots are defined as those features that have high values and surrounded by features also with high values while cold spots have the opposite pattern (Ord and Getis 1995). To assign the spatio-temporal bins for the density analysis, we chose a neighbourhood size of 2500 m based on the clustering of the data (Moran's *I*) and five year time-step intervals to account for temporal correlation associated with abalone size classes.

Results

Biophysical modelling

A total of 217 dispersal simulations were run over the 25-yr study period, revealing a general west-to-east connectivity of *H. rubra* larvae (Supplementary material Appendix 1 Fig. A4). The primary sources of abalone larvae are from large populations in the west half of the state, with a few sources in the east and Tasmania (Supplementary material Appendix 1 Fig. A5) resulting in patchiness across the state (Supplementary material Appendix 1 Fig. A6). The number of significant connections supplying a reef (in-degree) tends to increase moving east along the coast, following the dominant dispersal direction from west-to-east with a drop in dispersal in the central areas and embayments. Self-recruitment is also patchy throughout the study area (Supplementary material Appendix 1 Fig. A6B) with many reefs in the east mostly reliant on outside sources for recruitment.

Spatio-temporal modelling of abalone productivity

The parameters for the final BRT model along with results from the cross-validation are shown in Table 1. The final BRT model used 16 000 trees across 11 explanatory variables. The performance statistics show that the model performed relatively well at explaining variation in density of *H. rubra* across the study area and time period. The R-squared of the fitted model specifies that the BRT explains 70% of the spatial and temporal variation in density. Additionally, when we used the BRT model to predict density from the evaluation dataset and compared those predictions to the observed densities, we found that the BRT model was fairly accurate in predicting across both space and time. The Pearson correlation from this comparison was 0.750 and statistically significant (p-value < 0.001; Supplementary material Appendix 1 Fig. A7).

The nature and relative magnitude of influence from each explanatory variable used in the final BRT is shown in Fig. 2. Summer SST had the highest relative influence of 21.9% on

Table 1. Model parameters and performance statistics from the final boosted regression tree (BRT) model used to associate abalone biomass with spatial and temporal explanatory variables.

BRT model parameters	Abalone biomass model
Error distribution	Poisson
Learning rate	0.002
Interaction depth	3
Number of trees	16 000
Mean residual deviance	18.992
Training data correlation	0.838
R-squared (fitted model)	0.702
Pearson correlation with evaluation data (p-value)	0.750 (p < 0.001)

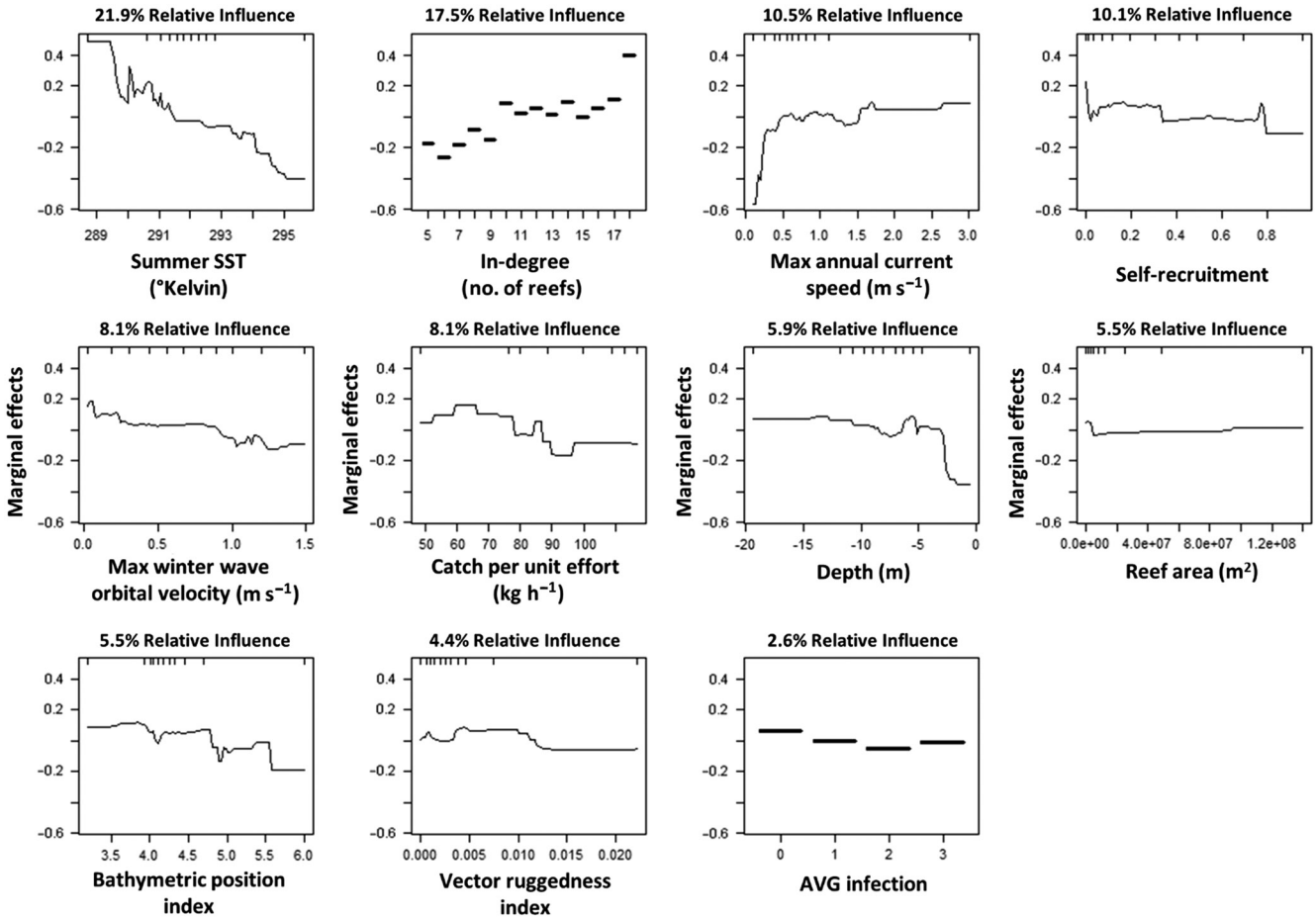

Figure 2. The nature and relative magnitude of the influence of each explanatory variable on the boosted regression tree (BRT) for *Haliotis rubra* density. Each graph represents the relationship between the variables and the marginal effects from the BRT. All relationships are shown for median values of the other variables in the model. The relative influence of each of the variables to the best BRT model as a percentage of the explained variance is shown above each plot.

the BRT. The relationship with summer SST is negative, with higher densities generally associated with areas of cooler temperatures. The number of significant connections providing larval supply to a particular location (in-degree) is the second most important variable in the BRT at 17.5%. As the number of reefs supplying larvae increases, density increases. Current speed has an asymptotic relationship with density and *H. rubra* density increases dramatically with increasing current speeds up to about 0.5 m s^{-1} with only a slight positive relationship after that threshold. Self-recruitment had a relative influence of 10.1% in the BRT. The relationship with self-recruitment is complex but there is an overall negative relationship with higher density values associated with lower values of self-recruitment. Maximum winter wave orbital velocity is the fifth most influential variable. The highest values of density are found in areas where wave orbital velocity is the lowest and then a slight but steady decrease as wave orbital velocity increases. Density has a negative relationship with CPUE, which has an 8.1% relative influence on the BRT. Depth has an asymptotic relationship with density with higher densities from 5 to 20 m depth and a steep decline in depths shallower than 5 m. Reef area has a 5.5% relative influence on the overall model but there is only a slight increase in biomass with increasing reef area. Bathymetric position index (BPI) at the 50 m scale was also influential (5.5%). Higher *H. rubra* density is correlated with regions of lower bathymetric position (e.g. valleys in the terrain). Complexity of the seafloor, calculated using VRM (4.4% relative influence), showed that abalone density increases with increased complexity up to a value of around 0.010 (moderate complexity) and then decreased from that point as complexity continued to increase. Finally, the categorical variable for AVG infection had a 2.6% influence on the final BRT. Highest *H. rubra* densities were observed in areas unaffected by the virus (AVG_Inf = 0). The lowest biomass was observed during the 1–2 yr following the outbreak (AVG_Inf = 2). During the outbreak (AVG_Inf = 3) and 3–5 yr after the outbreak (AVG_Inf = 1), moderate densities relative to the other categories were observed.

The relationships between *H. rubra* density and each of the explanatory variables used in the final model allowed us to develop predictive maps of abalone density over all the

reefs in the study area (Fig. 3). These maps were produced at 30 m resolution and can be used to evaluate spatio-temporal patterns in predicted abalone density. The standard deviation maps show that there is more uncertainty within the deeper depth ranges of the study area (Fig. 3b).

The results from the EHSA showed that predicted abalone density is experiencing an overall negative trend across Victoria (Fig. 4). From the 2500 m neighbourhood analysis, 36.2% had no detectable pattern, 14.3% were classified with hot spot patterns and 49.5% were classified as cold spots (Fig. 5).

Discussion

Understanding how species are distributed throughout their environment and factors that influence their distribution is essential for effective management of commercial fisheries. In this study, we characterized temporal and spatial variability in oceanographic conditions along the coast of Victoria in southeastern Australia, and identified key environmental factors likely influencing the distribution of *H. rubra*. Our results identified a variety of influential environmental factors that, when combined, can accurately predict *H. rubra* distributions and indicate how distributions are changing through space and time.

The BRT analysis suggests that summer SST is the most important variable correlated with the density distribution of *H. rubra* across Victoria. Based on this relationship, increasing summer SST is likely to have a negative influence on density. These findings are consistent with the literature describing fitness reductions in Haliotids following exposure to chronic or acute thermal stress (Raimondi et al. 2002, Rosenblum et al. 2005, Vilchis et al. 2005) and Jalali et al. (2018), which found that areas of higher average SST were associated with lower average abundance of *H. rubra*. A review of blacklip abalone responses to summer SST also corroborated our results showing that smaller sizes and lower catches occur with warmer temperatures (Pecl et al. 2014). Based on these results and future projections for increased SST in southeast Australia

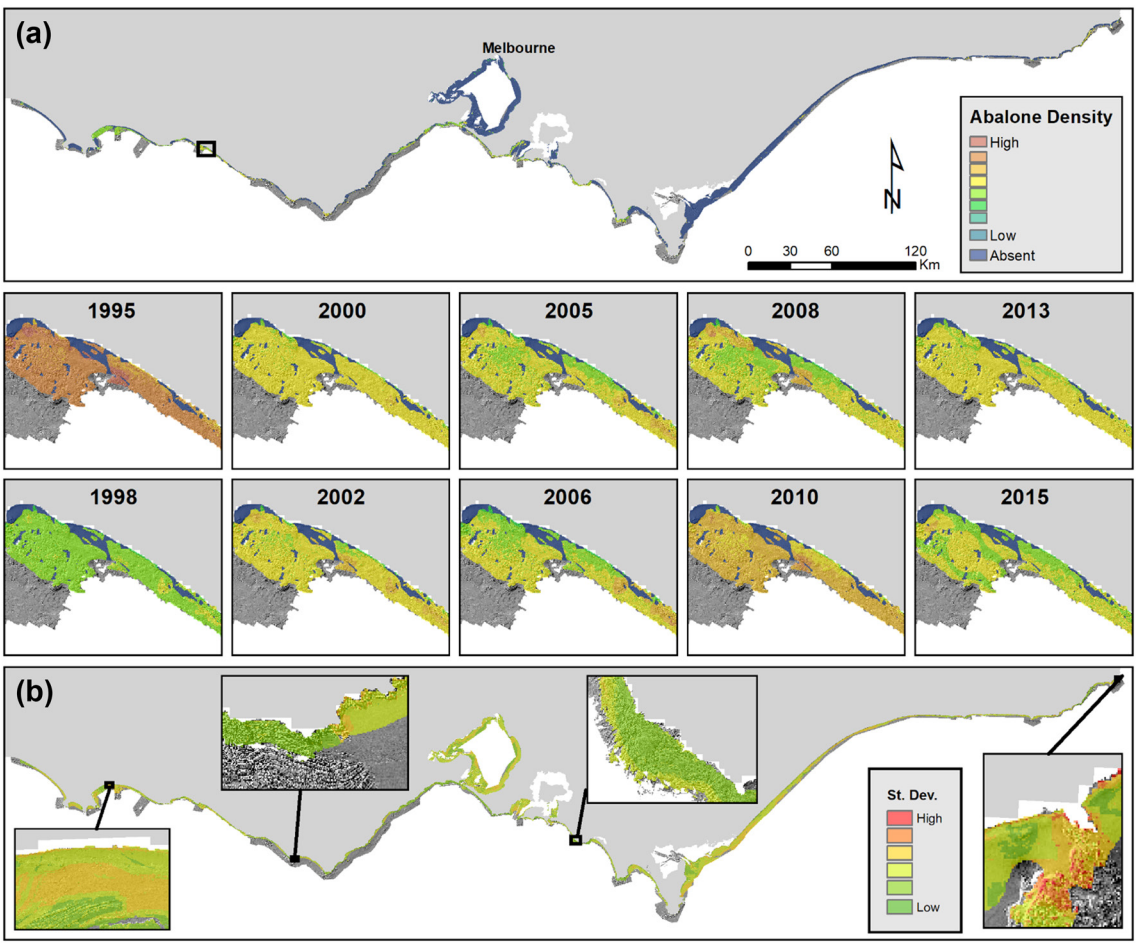

Figure 3. Predicted density of *Haliotis rubra* from the boosted regression tree (BRT) model across Victoria. The extent indicator in the statewide map of density predictions (a) corresponds to the section of the coast shown in the time series below. There is a clear change in density through time, which is driven by changes in the oceanographic variables, as shown by the time series. The map of standard deviation values across the state waters (b) provides an indication of the variation in predictions from the bootstrapping.

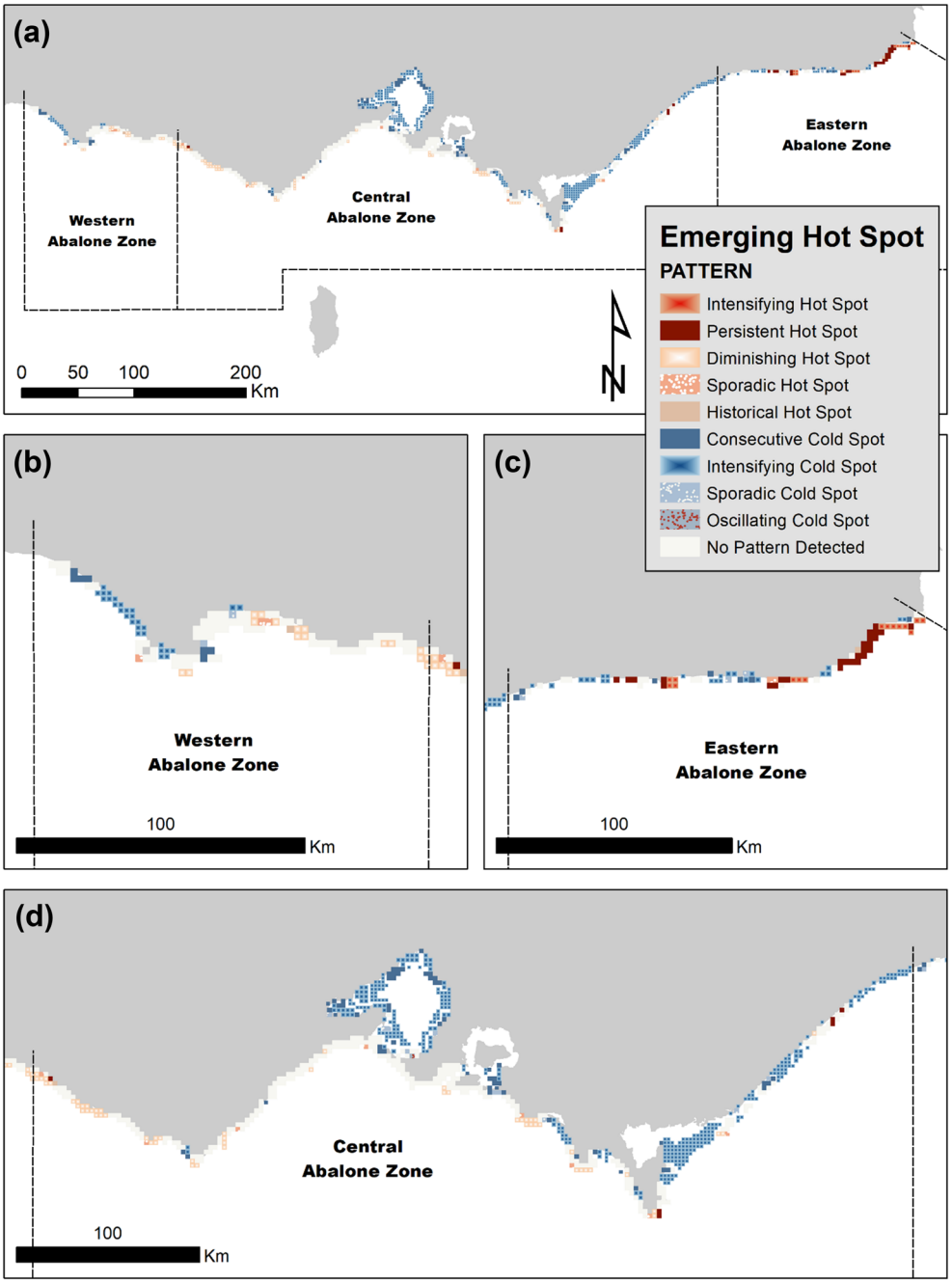

Figure 4. Results from the Emerging Hot Spot analysis for the predicted density of *Haliotis rubra*. The 2500 m spatial zones from the analysis are classified into one of the emerging hot spot patterns and coloured based on those patterns. The results for all of Victoria are shown (a) along with those for the Western Abalone Zone (b), the Eastern Abalone Zone (c) and the Central Abalone Zone (d).

at rates higher than average (Butler et al. 2007), temperature could have a negative effect on future productivity throughout the abalone fishery in Victoria.

Our biophysical model indicates a positive association between density and the number of incoming connections to individual reef habitats as the second most important variable. While several biological and physical parameters remain uncertain and have not been factored into our models (e.g. larval mortality, maximum competency, reproductive output), the scale of dispersal is consistent with the results of a drift tube study simulating the dispersal of abalone in California (Tegner and Butler 1985). Traditionally, abalone stocks were considered to be predominantly self-recruiting with larval movement limited to < 100 m (McShane et al. 1988b, Prince et al. 1987, 1988a, b). More recently, population genetics research has found a lack of genetic structuring at local spatial scales, indicating recruitment is not predominantly local in Victorian fisheries (Miller et al. 2016). In fact,

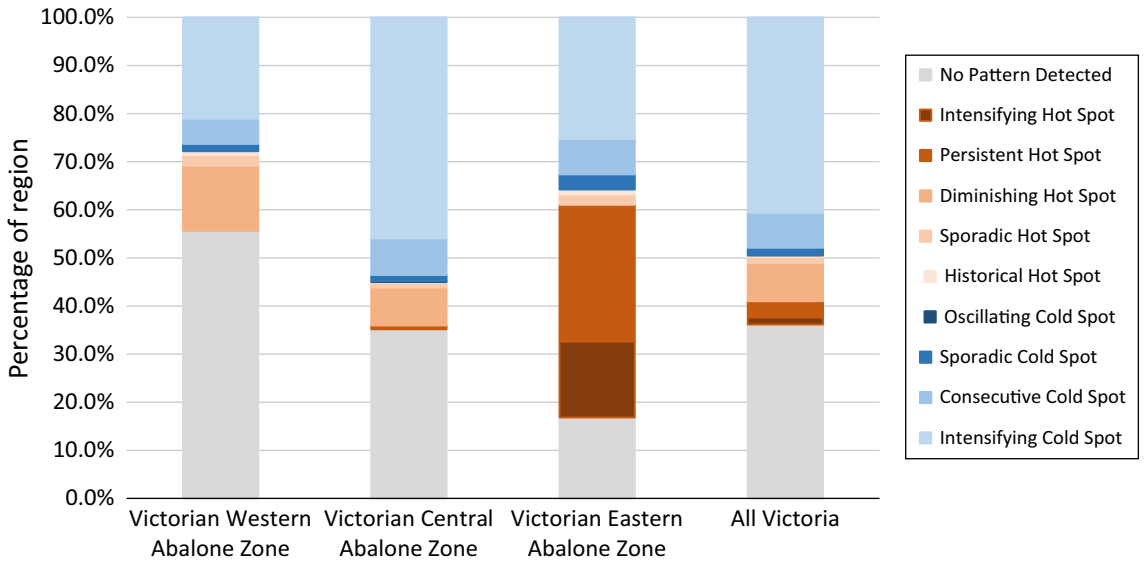

Figure 5. Summarized results from the Emerging Hot Spot analysis for the predicted density of *Haliotis rubra*. The fishing zones are along the x-axis (Western, Central and Eastern) along with the summary for the state of Victoria with the percentage of the region within each of the categories along the y-axis. Light grey represents those areas with no detected pattern while the warmer colors represent the 'hot spots' and the cooler colors represent the 'cold spots'.

our model suggests that annual self-recruitment, the fourth most influential variable, has a negative relationship with abalone density.

Spatio-temporal distribution of abalone density also appears to be influenced by hydrodynamic variables such as annual current speed and maximum winter wave orbital velocities. This is consistent with the sedentary nature of abalone and their reliance on opportunistic feeding on drift algae (Gorfine 2002), which is likely more available in habitats exposed to higher current speeds (Biber 2007) or faster wave orbital velocities. In addition, exposure to faster current speeds could also enhance larvae supply from non-local sources, contributing to higher biomass (Poore 1973, Stephens et al. 2006).

Our model indicates that CPUE from the commercial abalone fishery is the sixth most influential variable for explaining abalone density. As CPUE increases past around 70 kg h^{-1} of effort, density tends to decrease. It has long been recognized that CPUE may not accurately reflect changes in abundance (Beverton and Holt 1957). For abalone fisheries, CPUE at large spatial scales may be hyper-stable due to known aggregating behaviour (Abraham and Neubauer 2015) and the heterogeneity of suitable habitat. In addition, serial depletion may occur where fishers fish down a stock sequentially across productive habitat with no apparent decline in CPUE (Abraham and Neubauer 2015).

Environmental variables associated with the structure of the seafloor were secondary to those describing oceanographic processes when explaining patterns of variation in abalone density across the Victorian coastline but were important for explaining finer, reef-scale variations in density, with depth having the strongest influence. Although our fishery-independent sampling data of *H. rubra* is not across an extensive depth range, density tends to be lowest in depths < 5 m. Our results could be explained by greater water movement causing smothering or dislodgement of recruits in shallow habitat as was found by McShane and Naylor (1995) during their study on *H. iris*. We also observed a positive relationship between reef area and density consistent with predictions from island biogeography (MacArthur and Wilson 1963), where larger 'islands' are more likely to support larger populations and potentially provide bigger targets for larval settlement (Gilpin and Diamond 1976).

Within reef structures, abalone density appears to be greatest in lower elevations of the terrain (e.g. valleys and crevices). Crevice spaces provide relative shelter from high wave energy for juvenile abalone and protection from predatory species (Naylor and McShane 2001) as well as concentration of macroalgal drift (Gorfine 2002). Vector ruggedness measure (VRM) was also influential and has been previously associated with increases in diversity and abundance of benthic organisms (Holmes et al. 2008, Galparsoro et al. 2009), providing sheltered habitats that are suitable for feeding, breeding and juvenile development (Kuffner et al. 2007, Alexander et al. 2014). Our model suggests a parabolic relationship between VRM and density, indicating that density is greatest in terrain of moderate complexity.

Infection of abalone by AVG was the final variable included in the BRT. Between 2006 and 2010, AVG caused by the abalone herpes virus (AbHV) spread along the western coastline of Victoria, devastating wild and farmed abalone stocks, with mortalities exceeding 90% in some areas (Gorfine et al. 2009). Density continued to decrease following the active period of the outbreak, and fisheries are still on a recovery trajectory from these losses. Our model suggests there are slight increases in density in recent years. Based on the strong

influence of connectivity in our model, these increases could be attributed to those areas with a large proportion of reefs supplying larvae.

Although the BRT model does not explain all the variation in density, the model accounted for 70% of the variation and produced relatively accurate predictions when tested against a validation dataset. This affords confidence in our model for providing guidance to managers on which habitats are most suitable for supporting productive and resilient abalone populations with reasonable accuracy. In addition, by extrapolating those predictions over the entire study area across multiple years, we can use these predictions to help understand how habitat and changing oceanographic conditions are affecting these populations. The resulting predictive grids showed that there is both temporal and spatial variability in the density distribution of *H. rubra* within the coastal zone of Victoria, which we were able to analyse for emerging hot spots and cold spots. While 36.2% of the predicted abalone habitat shows no notable trend and 14.3% show an increase in abalone density, the remaining 49.5% indicates a declining trend. These data provide a glimpse into probable spatial change in density across the fishery over a long-term (21 yr) period.

The importance of this information is pertinent given the threat of climate change and uncertainty surrounding the likely impacts on the trajectory of commercial fisheries around the world. In this study, we used CPUE estimates at broad spatial scales with ~2000 km of coast reported in three broad sectors, which has a negative relationship with biomass. To more accurately inform stock management, understanding the spatial distribution of a stock as well as fishing effort is critical. Spatially-explicit fisheries data capture would provide new opportunities in understanding patterns of change in spatial allocation of fishing effort and the productivity of the resource. We have shown the benefits of spatially-explicit commercial fishing effort data (e.g. AbTrack; Mundy 2012) in the Western Zone of the fishery for evaluating patterns in fishing effort (Jalali et al. 2015). The availability of these data across the resource, through the use of vessel monitoring systems, would be beneficial for understanding harvesting behaviour and accurate assessment of whether serial depletion is occurring at the reef scale. This is currently not possible because the catch data are not spatially explicit or being reported at the scale of resource exploitation.

Globally, marine ecosystems are experiencing rapid environmental transformations from climate change, posing a direct threat to fisheries (Glantz 1990, Perry et al. 2005, Poloczanska et al. 2013). Spatially-explicit fisheries catch along with SDMs can be powerful tools for understanding how marine species are responding to these changes. In this study, the combination of long-term observation data and downscaled temporal datasets allowed us to determine how dynamic oceanographic conditions are affecting abalone density within Victorian coastal waters. In fact, these dynamic variables were the top five most important variables in the BRT, with 6 out of 10 variables in the final model capturing dynamic conditions. With SST off southeastern Australia rising at a rate 3–4 times that of the global average (Ridgway 2007, Ling 2008, Wernberg et al. 2011) and hydrodynamics changing faster than other areas (Young et al. 2011), these changes are already shifting species ranges in this region (Walther et al. 2002, Ridgway 2007, Suthers et al. 2011). The density maps developed in this study could help to more effectively manage the abalone fishery through informing quotas, especially if combined with spatially-explicit catch information. Also, the development of future predictions of hydrodynamic conditions could aid in the setting of quotas for future fishing seasons.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sj3tx9622> (Young et al. 2020).

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Supplementary material (available online as Appendix ecog-05181 at <www.ecography.org/appendix/ecog-05181>). Appendix 1.

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