Persistence of marine species of the Australian South-east Marine Region under alternative fisheries management strategies

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Abstract

The marine environment is heavily affected by fishing pressure and knowing how different management strategies affect the persistence of marine species is crucial for ensuring sustainable fishing. Models used within the fisheries management strategies evaluation context have been implemented in the past decades from traditional single species methods to an ecosystem-based approach, but there are still uncertainties on the effectiveness of these models. This thesis aims to understand the drivers of marine species persistence coupling network-based methods and spatially explicit population viability analyses (PVA). This thesis focuses on marine species of south-eastern Australian waters, a region characterised by rich biodiversity and oceanographic complexity, supporting important Australian commercial fisheries sectors.

PVA is an approach not yet widely investigated in the context of fisheries management strategies evaluation, however understanding species viability and ensuring metapopulation persistence is fundamental to avoid overexploitation of the stocks. In this thesis is examined how spatially explicit PVA compares to other commonly used models, demonstrating that PVA is a powerful alternative, suitable to inform fisheries management. PVA is applied to estimate metapopulation persistence in a spatial context, analysing how persistence changes when modelling alternative fisheries management scenarios for important commercial fisheries species.

The knowledge of species distribution is very important for any spatially explicit population modelling and is needed when studying population viability and dynamics. A recent challenge in understanding and predicting species' distributions has been focused on the influence of population connectivity. This thesis explores how to integrate graph-based metrics, representative of seascape connectivity, into marine-based species distribution models (SDMs) to understand the contribution of connectivity to predict marine species spatial distribution.

Connectivity is a key determinant of metapopulation persistence of species inhabiting fragmented habitats. Larval connectivity is quantified using a biophysical model. Connectivity is visualized as networks, where habitat patches are represented by nodes and dispersal connections are represented by linkages. In this thesis graph-based metrics are calculated because of their significant role as indicator of metapopulation persistence, identifying key habitat patches for the overall persistence of the species.

The results of this thesis demonstrate how PVA is a valuable tool helping to inform fisheries managers on the effects of fishing on marine species. Habitat heterogeneity and movement ecology demonstrate to be critical model parameters, strongly influencing metapopulation persistence, suggesting that fisheries managers might benefit from better understanding of movement behaviour and habitat characteristics. This thesis results also provide insight on the role of connectivity to determine marine populations persistence and distribution. Hotspots of connectivity reveal to be key habitats, often enhancing habitat suitability, and strongly influencing metapopulation persistence. Managers and ecologists would benefit by employing similar approaches in making more efficient and more ecologically informed decisions and focusing more on local connectivity patterns to better understand and protect marine species.

Declaration of originality

This is to certify that:

i. The thesis comprises only of my own original work towards the PhD except where indicated in the Preface.
ii. Due acknowledgement has been made in the text to all other materials.
iii. The thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

Giorgia Cecino

November 2020

Preface

This thesis comprises of six chapters: a general introduction (Chapter 1), four research chapters, and a general discussion (Chapter 6). The work presented in this thesis is predominantly my own. It was conducted under the supervision of Dr Eric Treml and Dr John Morrongiello. In order to facilitate journal publication Chapters 2-5 have been written as independent studies. This will lead to some unavoidable repetition between chapters. Throughout the chapters I use the pronoun 'we' to be consistent with academic publishing convention and acknowledge the collaborative nature of this work.

The chapters status and the contribution of collaborators have been outlined below:

Chapter 2

Cecino, G., Treml, E.A. and Morrongiello, J.R. (in review), Linking spatial heterogeneity of habitat and population viability analysis to evaluate fisheries management strategies.

This chapter has been submitted for publication to the journal *Fish and Fisheries* on 24th November 2020. The manuscript corresponds to the version submitted to the journal and it has only been modified to adhere to the section numbering and style formatting of the thesis at large. Contents remains otherwise unmodified.

I conceived the idea of the chapter, undertook the data analysis and draft the chapter. Dr John Morrongiello assisted in the design of the chapter, assisting with editing of the manuscript. Dr Eric Treml assisted in the design of the chapter, helped to review and refine the chapter.

Chapter 3

Cecino, G., Valavi, R. and Treml, E.A. (in review) Testing the influence of seascape connectivity on marine-based species distribution models.

This chapter has been submitted for publication to the *Journal of Biogeogra*phy on 15th November 2020. The manuscript corresponds to the version submitted to the journal and it has only been modified to adhere to the section numbering and style formatting of the thesis at large. Contents remains otherwise unmodified.

I prepared the study design with input from Dr Eric Treml. I performed the least cost paths analysis, and I developed the code for the biophysical model, based on the original code of Dr Eric Treml. Roozbeh Valavi provided assistance in developing the species distribution models code. All authors contributed to the interpretations of the results. I drafted the chapter, Roozbeh Valavi and Dr Eric Treml assisted with reviewing the chapter.

Chapter 4

Cecino, G. and Treml, E.A. (in press). Local connections and the larval competency strongly influence marine metapopulation persistence. *Ecological Applications*.

This chapter has been accepted for publication on 5th October 2020 and it is now in press with the journal *Ecological Applications*. Computational support was provided by the University of Melbourne's High Performance Computing system, Spartan. I designed the study with Dr Eric Treml. I collected the data and performed the analysis, with support from Dr Eric Treml, and Dr Treml contributed to the interpretation of the results. I wrote the entire code for most of the analyses presented in this chapter. The code of the biophysical model is based on the original code of Dr Treml biophysical model. Stella Fulton and Martin Ingram provided assistance with the eigenanalysis. I drafted the chapter with extensive input from Dr Eric Treml. The chapter was improved by comments and suggestions from reviewers and the editors at *Ecological Applications*.

As per University regulations, the author-accepted version of the manuscript has only been modified to adhere to the section numbering and style formatting of the thesis at large. Contents remains otherwise unmodified.

Chapter 5

Cecino, G., Treml, E.A., and Morrongiello, J.R. (in prep), Individual movement behaviour determines the impact of management strategies for a commercially harvested fish.

This chapter is now in preparation for submission to a fishery journal. I designed the study, collected the data, I wrote the code and performed the analyses. Dr Eric Treml and Dr John Morrongiello provided assistance in the design of the chapter, editing and reviewing this chapter.

Appendices

A substantial amount of data and information have been generated to support the conclusions of this thesis. This material is made available in this thesis because it is essential for understanding the methods and conclusions of each chapter, and it is included in separates Appendices.

Funding support

My PhD candidature has been supported by a Melbourne Research Scholarship. Conference travel has been supported by a Science Abroad Travelling Scholarship and a School of BioSciences Travel Grant.

Acknowledgements

I would like to thank my incredible supervisors, Eric Treml and John Morrongiello, for their support and their advice. Their contribution has been fundamental for this thesis. They shared with me their knowledge, they encouraged me, and they always believed in my abilities. But, most importantly, I would like to thank my supervisors for being kind and listening to me when I needed support. I would also thank my advisory committee, Pia Lentini and Mick Keough, for their valuable advice through my PhD.

This thesis would not have been possible without the support of many people. I would like to thank my two great labs. All the past and current members of the MSEaC Lab. They have been next to me through the ups and downs of my PhD. Thank you for being my friends and always giving the best advice. This thesis would not be the same without the ideas and the support from this amazing group of scientists. Clare, Jutta, Kay, Ben, Roberto, Kelsey, Molly, Trish, Fran, Stella, I thank you all. I would like to thank all the Morrongiello Lab. You welcomed me as part of your group, I learnt so much from you, and I found so many good friends. Thank you for all our interesting discussions and your support in the past years.

I am incredibly grateful to have had support from many great scientists. I would like to thank Roozbeh, a great scientist, but first of all, a dear friend. Thank you for solving my coding issues, thank you for sharing your time and knowledge to improve my science. Also, I would like to thank Stella and Martin, who helped me understanding matrices, eigenvalues and other mathematical concepts that I would have never believed I could understand. I had the opportunity to interact with many members of the QAECO Lab, who adopted me as part of their group and involved me in their activities. In particular, I would like to thank Erica, talking to you helped me to finally understand how a PVA works.

I am immensely grateful to my writing group. Joining this group was the best decision I have taken during my PhD. My-Linh, Mel, William, Cassie, Van, Aruska, Kate, Jamie, Michelle, Christopher, you have a special place in my heart. Thank you for being my support, for never judging me, and always encouraging me. Thank you for all the fun we shared during our writing days. I learnt so much from you, especially how to floss dance.

I am grateful to have found true friendship in Melbourne. To Tara, Thy, Trish, Laura, Sedi, Roozbeh, Juanma, Maita. You are special to me and I am grateful to have met you and share my PhD journey with you. I am thankful to have crossed my path with yours. My life would not be the same without you.

Thank you to everyone in the Office G06, G01 and all my friends around Biosciences 4. I missed so much seeing you in the office every day during 2020. We laughed so much together, and you made my days on campus fantastic. To Sandra, my first friend in Melbourne, who understood the struggle of being an international student and supported me in the early stages of my PhD. To Sere, for your true friendship and for sharing all the food. To Francesco, the IT champion of the house, who tolerated to live with me and his brother for two years. I am also particularly grateful to my extended Australian family, without whom I would have never moved to Melbourne.

To Carlo, Emiliano, Michele, mum, and dad thanks for your unconditional support even if thousands of kilometres separate us, I miss you every day. To all my friends and family in Italy and around the world, who supported me during the past years.

And last, thank you Giorgio, for your love and for supporting me during this crazy journey.

Thank you, all.

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Chapter 1

General introduction

The understanding of marine species distribution and dynamics has been of great interest to marine ecologists and managers for decades. Recently, significant improvements in our knowledge of the habitat structure, population distribution and dynamics have been made through spatially explicit approaches, leading to innovation in spatial management tools for conservation and fisheries management. Fish, as well as the associated fishing industry, are inherently geographically structured, and therefore require spatial approaches, such as area closures and regional plans (Punt et al. 2016). Similarly, conservation actions are often associated with spatial protected areas to ensure the persistence of important marine species and habitats (Di Franco et al. 2016). Together, these common place-based management and conservation approaches in the marine environment strongly suggest a spatial approach would be most appropriate.

The Australian commercial fishery is an important sector for Australian economy, generating an estimated value of over 3 billion dollars in 2019 (Brown et al. 2020). However, associated activities of non-selective fishing practices such as trawling, dredging, trapping and gillnetting may have a significant, yet heterogeneous, impact on fished populations and the marine environment in general (Foster et al. 2015). As a result, effective management that takes a spatially explicit approach may help maintain stocks, as well as help protect the environment.

Spatial and non-spatial models simulating marine population growth and dynamics are key tools used in marine conservation and commercial fisheries management. A variety of models have been applied for decades to understand the viability of marine species, describing the ability of species to persist for future generations (Akçakaya 2000,

Burkhart and Slooten 2003, Winship and Trites 2006). Although many of these models predict the growth of the whole population without considering spatial heterogeneity, those that do include space explicitly can help identify key habitat patches and/or important subpopulations to the long-term viability, which can inform marine spatial planning and the design of marine protected areas (Gerber et al. 2003). These management actions, which aim to conserve local populations and/or ensure sustainable fishing, should be tested for effectiveness. Only then these accurate and reliable models can evaluate the impact of management actions on marine biodiversity and marine ecosystems functioning. Advancements in computer hardware and modelling approaches have allowed for improved realism and complexity (Bunnefeld et al. 2011) but many challenges remain due to limited knowledge around early life stages and movements (Bruce et al. 2002), the spatial structure of populations (Hutchinson 2008, Ying et al. 2011) and models and parameters uncertainties (Hill et al. 2007).

This thesis provides a critical and spatially explicit assessment of several common conservation and fisheries models, comparing the strengths, weaknesses, and complexities in realistic seascapes. It explores why spatial approaches may be essential to understand the implications of fisheries management and marine conservation actions. I propose that spatially explicit models are preferred to more traditional models (either non-spatial or spatially-implicit), allowing integration of the spatial variability in habitat characteristics, as well as ocean dynamics, which is particularly significant for species threatened by habitat loss and climate impacts. In this thesis, I cover a number of important fisheries management approaches, including Population Viability Analysis (PVA), connectivity and metapopulation dynamics, and predicting species distributions. Together, these complementary approaches help to develop a more comprehensive and geographic view of fisheries management strategies, the role of connectivity, and the influences on marine species distributions and persistence.

This first chapter establishes the core ecological and technological context for the research presented in this thesis. Limitations and challenges of commonly used models are also presented, highlighting the potential advantages of using alternative models like spatially explicit PVA. Following, the significance of considering connectivity in the study of the spatial distribution of marine species is explained. Finally, I follow with an outline of my research aims, and the specific thesis structure.

1.1 Complexity and limitations of modelling tools used in fisheries management

Fishery data, such as catch per unit of effort (CPUE) and maximum sustainable yield, have been traditionally recorded to quantify the effectiveness of fisheries management and analyse stock abundance trends using single species modelling approaches (Botsford et al. 2009a). The analysis of these data became the primary instrument for the evaluation of the success of the fisheries management plans (Botsford et al. 2009b). However, in some instances the stock assessment showed limited ability to predict or prevent the collapse of fish stocks from excessive fishing (Botsford et al. 1997). For example, the now infamous case of the northern cod, where a single species stock assessment failed causing the collapse of the North Atlantic stock (Walters and Maguire 1996). Proposed causes of this failing include errors in data, such as disagreements between trends of catch rates and exploited biomass estimates, and inaccuracies in fishery survey results and landings data (Butterworth and Punt 1999). In addition, the effect of geographic heterogeneity was usually not included in these stock assessments, thus excluding the spatial variability of growth, recruitment, maturity, fishing pressure and natural mortality (Hutchinson 2008, Botsford et al. 2009a). The rapid decline of fish stocks in many locations around the world, despite ongoing management attempts, highlights the urgent need for better management tools (Botsford et al. 1997, Cowan et al. 2012, Hilborn et al. 2020).

Ecosystem-based approaches to assess and manage fisheries have been suggested as an appropriate alternative to single species assessment (Pikitch et al. 2004). Although specific details are often debated (Trochta et al. 2018), it is broadly accepted that using Ecosystem-Based Fisheries Management (EBFM) has led to positive outcomes for the conservation of marine resources (Di Franco et al. 2016). The goal of this approach is to maintain the whole ecosystem in a healthy condition, build productivity and resilience, and ensuring its structure and functions (Norse 2010). Specifically, EBFM approaches focus on food web resilience, and this has resulted in the development of important reference points for marine communities, such as changes in trophic network structure, changes in biomass or shifting predator-prey dynamics (Babcock et al. 2005, Metcalfe et al. 2015). In addition, the spatially explicit framework of the ecosystem-based approach was a major improvement in the conservation of species, integrating the true biophysical geography of the marine environment into the decision context (Norse 2010). Similarly, choosing an appropriate spatial scale for the management of species, as well as identifying subregions particularly vulnerable to over-exploitation, has led to the inclusion of metapopulation dynamics and dispersal or migration patterns between populations to be incorporated into the EBFM approach (Fogarty and Botsford 2007). Many tools within EBFM have been developed to assess the impact of alternative ecosystem-based fisheries management strategies and are characterised by high levels of complexity. Despite EBFM being considered as an ideal approach for sustainably managing fisheries, it has also been criticised for being time demanding and expensive, for the lack of flexibility in its framework and the ecosystem models' complexity (Bunnefeld et al. 2011). Critics of EBFM argue that it is difficult to translate EBFM principles into management actions, it is extremely context-specific and therefore not applicable to many fisheries (Trochta et al. 2018). The limitations of the EBFM approach reduces its applicability, leading to many fisheries still managed as a single and spatially homogeneous fish stock. For this reason, a spatially explicit approach of intermediate

complexity could provide a flexible and transferable approach to assess the impact of fisheries management on marine species across various seascape contexts.

1.2 Spatially explicit Population Viability Analysis (PVA), a powerful approach to assess impacts of fisheries management strategies

Choosing the best model to simulate the impact of fisheries management on marine species is critical for fisheries scientists. Managers use the results of these models to evaluate different management strategies and make optimal and sustainable decisions. Many tools exist to help fisheries managers explore management scenarios and assess their impact on fishing stocks and ecosystems. Popular tools used by fisheries scientists within the EBFM context are Ecosim with Ecopath and Ecospace (Christensen and Pauly 1992, Pauly et al. 2000, Christensen and Walters 2004) or the Atlantis ecosystem model (Audzijonyte et al. 2019), but these tools have limitations due to their high complexity and substantial costs.

Another powerful method that can be implemented to evaluate management effectiveness and explore alternative approaches for managing fisheries is population viability analysis (PVA). This risk assessment method has been successfully used in conservation biology for diverse terrestrial (Lahaye et al. 1994, Menges 2000, Haines et al. 2006, Menges et al. 2006, Aiello-Lammens et al. 2011), freshwater (Jarić et al. 2010) and marine systems (Ellner and Fieberg 2003, Sweka and Wainwright 2014). PVA has the goal of quantifying the persistence of populations and studying their vulnerability to both relative and absolute risk of extinction (Akçakaya et al. 2004). The main value of PVA is its ability to efficiently assess and compare the relative efficacy of various management strategies (Boyce 1992), rather than the absolute impact, of management decisions on subpopulations or regions (Akcakaya 2005). Additionally, spatially explicit PVA approaches can effectively accommodate the spatial and temporal structure of harvesting (i.e., fishing) and assess extinction vulnerability on the sub-population level

(Akçakaya et al. 2004). Having information on extinction risk on a sub-population level provides a clear advantage giving managers the ability to plan with more flexible and local-scale measures. This method can inform both demographic and genetic-based questions related to fisheries, such as spatial prioritization, recovery planning, management strategy comparisons, and effects of movements between stocks (Akçakaya et al. 2004, Sweka and Wainwright 2014). Using spatially structured approaches is critical where habitat patch characteristics vary through time due to natural and/or human environmental change (Larson et al. 2004). Yet, it appears clear that incorporating the fundamentals of ecology, habitat use, and the spatial context is necessary, for example the spatial dynamics between sub-populations, when determining effective population sizes (Fahrig and Paloheimo 1988). Therefore metapopulation approaches integrating ecologically significant dispersal patterns, should be included in the analysis of the species' persistence and patch occupancy rates (Boyce 1992, Akçakaya et al. 2004). That said, the addition of these spatial processes adds complexity to the models (Boyce 1992), so care should be taken to minimise the additional uncertainty while maintaining ecological realism.

Fisheries scientists use modelling tools to understand how fisheries management strategies influence the viability of species, expressed as variation in stock biomass, to help inform managers of the most sustainable strategies. Importantly, these models benefit from including animal movement data, critical for the implementation of spatial management tools, such as marine protected areas (Botsford et al. 2009a). PVA has been developed for decades and metapopulation dynamics describing how individuals move are largely implemented within spatially explicit PVA models, making this approach suitable to address the needs of fisheries scientists.

The applications of spatially explicit PVA for fisheries management are limited, and few examples can be found in the literature where this approach is used to evaluate fisheries management strategies (Akçakaya et al. 2004, Sweka and Wainwright 2014). Critics of

PVA argued that PVA outcomes are not reliable if data are not accurate (Coulson et al. 2001) – an important and fair criticism of all models. However, it has been demonstrated that PVA is a rigorous method with high predictive accuracy (Brook et al. 2000), that is both reliable and repeatable (Morrison et al. 2016). The potential of using PVA beyond its traditional use and applying spatially explicit PVA to the evaluation of fisheries management strategies is explored in this thesis, highlighting how this approach compares to other fisheries management modelling tools. To demonstrate the use of spatially explicit PVA, I present a case study for blacklip abalone, *Haliotis rubra*, in Victoria, south-east Australia (Fig. 1.1). Besides fisheries, the main stressors experienced by the Victorian blacklip abalone stock are habitat loss, due to interactions with invasive species, and the occurrence of viral diseases. In this thesis I demonstrate how PVA can efficiently incorporate these additional stressors, together with fishery-specific data, into spatially explicit models that estimate the impact of fisheries management strategies.

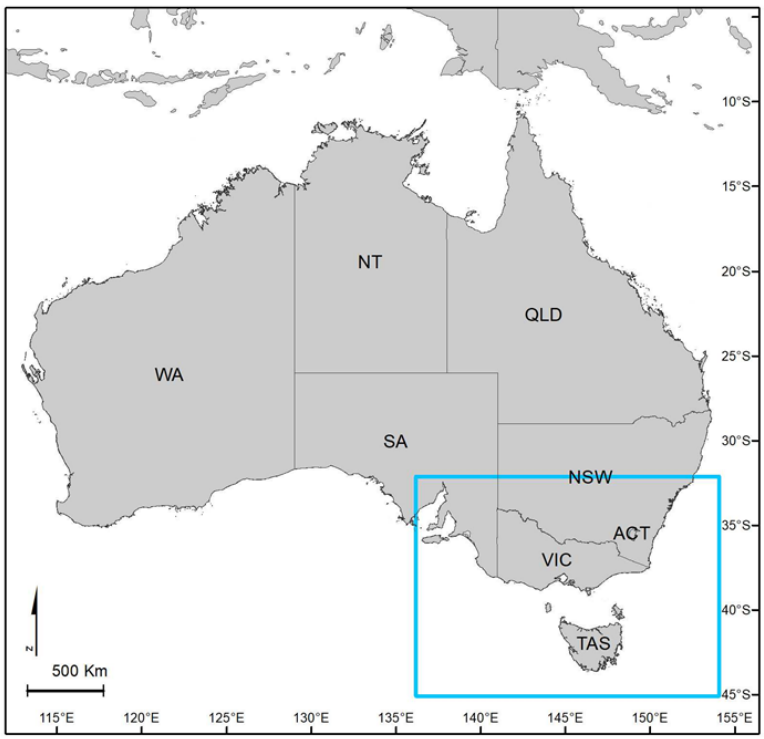

Figure 1.1: Map showing the thesis study area, south-eastern Australia waters. Maps in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

In this thesis I also use spatially explicit PVA to explore the impact of alternative commercial fisheries management strategies, integrating a range of movement distances for pink ling, *Genypterus blacodes* in south-east Australia (Fig. 1.1). Pink ling is a common species of south-east Australia, targeted in two important commercial fisheries sectors of Australia's commercial fishery (Patterson et al. 2019). Current fisheries management data provide the baseline scenario, while three alternative management scenarios were explored, a scenario where fishing mortality was reduced, another where the size of spatial closures was increased and a third scenario where the other two scenarios were combined. Adult movement patterns in pink ling are largely unknown, providing an ideal test-case for exploring how fisheries management decisions impact this species under different movement scenarios.

1.3 The importance of connectivity for marine ecology and conservation

Dispersal across the landscape is essential for most species to persist. It is a critical component in metapopulation dynamics in fragmented landscapes (Pulliam 1988, Hanski 1998). Most marine species disperse through the water along ocean currents, and population connectivity patterns emerge when this biological-physical dispersal process is combined with post-settlement processes ultimately contributing to the downstream population dynamics (Cowen and Sponaugle 2009). Larval dispersal patterns have a significant role in determining metapopulation-wide persistence by strongly influencing local-scale connectivity (Artzy-Randrup and Stone 2010). Species range expansion and persistence, core concepts in metapopulation theory, are strictly linked to larval dispersal, yet the methods and theory for explicitly including dispersal in the metapopulation framework for persistence represents a central question in ecology (Hastings and Botsford 2006). Quantifying and exploring connectivity to discover spatial dispersal pathways and critical 'stepping-stones' using a graph-theoretical approach has been effective in gaining a better understanding of larval connectivity patterns (e.g.,

Treml et al. 2008, Andrello et al. 2013, Thomas et al. 2014, Gamoyo et al. 2019). Within a graph-theoretical framework, connectivity can be visualised in form of a network, where nodes represent habitat patches and links represent the presence of ecological connections among patches (Urban and Keitt 2001). These network maps are useful in the design of marine protected areas and prioritising fisheries management actions (e.g., Beger et al. 2010, Andrello et al. 2013, Andrello et al. 2015, Krueck et al. 2017).

A critical component of seascape connectivity is the spatial context of these dispersal dynamics. In addition, the geographic distribution of habitat or populations is very important for spatially explicit population modelling and is essential when quantifying population viability and dynamics. Quantifying species-specific habitat characteristics and predicting the spatial distribution of populations requires significant prior knowledge and predictive capacity. Species distribution models (SDMs) are key tools in this context, and they are able to statistically relate species occurrence data with environmental characteristics to develop geographically comprehensive predictions of species presence/abundance (Elith and Leathwick 2009) suitable to use in a PVA. SDMs have been extensively used to study terrestrial, freshwater and marine species. Much research exists exploring how to improve the predictive performances of SDMs, how to choose appropriate methods for validation, and what the best practices are (Elith et al. 2006, Dormann et al. 2013, Guillera-Arroita et al. 2015, Roberts et al. 2017). Marine-based SDM models have been used for a variety of purposes such as understanding habitat shifts, designing conservation strategies and studying the impact of climate change on species distribution (Robinson et al. 2017).

Environmental parameters often included in SDMs represent environmental in-situ characteristics, but the spatial distribution of populations often also depends on habitat connectivity. There is growing interest on including connectivity into SDMs, largely aiming to explicitly integrate dispersal-related metrics within these models to augment their predictive performance (Cable et al. 2020, Monsimet et al. 2020). Landscape

connectivity is often described and quantified using network-based centrality measures to assign importance to habitat patches in a fragmented landscape (Estrada and Bodin 2008). This general approach emerged as a plausible and suitable pathway for integrating connectivity into SDMs (Foltête et al. 2012). However, few studies have attempted to include connectivity patterns among habitats or subpopulations into the set of environmental predictors commonly used in SDMs, and those that have are mainly focussed on terrestrial species (Foltête et al. 2012, Clauzel et al. 2013, Girardet et al. 2013, Tarabon et al. 2019). To date, no studies appear to exist which robustly incorporate network-based population connectivity patterns into marine-based SDMs.

In this thesis, I present a framework and case study on how to integrate seascape connectivity into marine-based SDMs. Different methods exist to quantify marine species connectivity and can be selected according to species-specific dispersal characteristics. I use least-cost path analysis and biophysical dispersal models, to quantify marine species movements for mobile fish and sedentary invertebrates, receptively. I apply this approach to two commonly found species in the study area of south-east Australia (Fig. 1.1), the Australasian snapper, *Chrysophrys auratus* (formerly known as *Pagrus auratus*) and the purple sea urchin, *Heliocidaris erythrogramma*. For these taxa, network-based centrality measures are calculated to characterise each patch contribution to habitat connectivity, and then I explore how these metrics influence the SDM predictions.

Quantifying dispersal and the ecological stability of metapopulations is critical to understand their persistence. Many studies have used network-based approaches to investigate the relationships between dispersal or connectivity and persistence using graph metrics (Figueira and Crowder 2006, Hastings and Botsford 2006, Artzy-Randrup and Stone 2010, Zamborain-Mason et al. 2017). An important finding was the relationship between the spatial patterns captured in the connectivity matrix, summarising dispersal dynamics, and metapopulation persistence (Artzy-Randrup and Stone 2010). However, most studies have focussed on a limited set of network metrics

describing connectivity, or apply these methods to only theoretical species and networks. In this thesis, real world metapopulations are used as case studies, to investigate the efficiency of matrix eigenanalysis and graph-based metrics to study metapopulation persistence and identify the most significant subpopulations in contributing to persistence. To explore this, larval dispersal is simulated for five species commonly found across the region (blacklip abalone *Haliotis rubra*, purple sea urchin *Heliocidaris erythrogramma*, long-spined sea urchin *Centrostephenus rodgersii*, Australasian snapper, *Chrysophrys auratus* and King George whiting, *Sillaginodes punctatus*). For each species, connectivity matrices summarising species-specific dispersal patterns are used to represent metapopulation networks. In this thesis, I use several network-level and node-level connectivity metrics to quantify metapopulation-level immigration and emigration in these metapopulation networks. Eigenanalysis is used to quantify the influence node-level network metrics have on metapopulation persistence and to identify the most significant habitat patches to persistence. Additionally, this thesis provides critical information on which dispersal-related life history traits might have the greatest influence on marine metapopulation persistence.

1.4 Thesis aims

The overarching goal of this research is to quantify the persistence of marine species living along the south-east Australian coast and investigate the combined effects of *i*) species-specific life history characteristics and habitat requirements, and *ii*) various fisheries management strategies. To achieve this aim, the sub-aims of this thesis are as follows:

1. Explore the potential benefit population viability analysis might have over traditional approaches in evaluating fisheries management strategies, using the blacklip abalone, *Haliotis rubra*, as a case study.

2. Investigate spatially explicit spatial approaches for quantifying the distribution and habitat use of two key species living on the south-east Australian coast, presenting a novel method integrating seascape connectivity into these models.
3. Characterize the influence of larval connectivity and network centrality on the metapopulation persistence of marine invertebrates and fishes, and to identify critical subpopulations and important early life history traits in this persistence.
4. Compare and contrast various fisheries management scenarios through population viability analysis, based on their predicted effects on the viability of the target species, exploring both conventional scenarios (e.g., restrictions on total biomass caught), but also recent spatially explicit approaches.

1.5 Thesis structure

In the following section I outline the structure of this thesis and the aims of the chapters contained within.

Chapter 1 - General introduction

This chapter has established the context for the research presented in this thesis, describing the use of spatially explicit models for marine species conservation and fisheries management. It has demonstrated the need for research improvements that can be made by the application of alternative models for assessing fisheries management strategies and the need for an improved understanding around marine connectivity.

Chapter 2 - Linking spatial heterogeneity of habitat and population viability analysis to evaluate fisheries management strategies

In Chapter 2, I compare three modelling approaches used to assess fisheries management strategies, using six performance criteria. The three approaches were: single species stock assessment, ecosystem-based models, and spatially explicit PVA.

A case study for blacklip abalone is provided to demonstrate the flexibility of the PVA approach and the importance of integrating spatial heterogeneity of the habitat in these models. In this chapter I demonstrate the potential of using PVA to evaluate the impact of fisheries management strategies on marine species (Aim 1).

Chapter 3 - Testing the influence of seascape connectivity on marine-based species distribution models

In this chapter, I illustrate a new approach to integrate seascape connectivity into SDMs and quantify the influence of connectivity on the predicted species distributions. To achieve this, marine-based species distribution models are developed for two common species of south-east Australian waters. In this chapter I investigate the contribution of connectivity in determining species spatial ranges and explore the ecological and applied significance (Aim 2).

Chapter 4 - Local connections and the larval competency strongly influence marine metapopulation persistence

In this chapter I use a marine connectivity model to simulate the larval connectivity for five species of south-east Australian waters. Eigenanalysis is used to help understand which network metrics (out of nine node-level metrics) is the most influential in ensuring metapopulation persistence. This chapter's findings are then used to understand which early life history traits might be the most important in determining metapopulation connectivity and persistence (Aim 3).

Chapter 5 – Individual movement behaviour determines the impact of management strategies for a commercially harvested fish

In this chapter I apply PVA to quantify metapopulation persistence for a commercial fisheries species of south-east Australia exploring alternative management strategies. In contrast to the review presented in Chapter 2, this chapter provides a more detailed case

study and explores several relevant management scenarios. Scenarios presented in this chapter were designed to investigate the effects of different movement behaviours on metapopulation dynamics, and the efficacy of contrasting fisheries management scenarios to better understand the effects of modifying fishing targets or spatial management tools and the combined effects of both strategies (Aim 4).

Chapter 6 - General discussion and conclusions

The final chapter provides a brief synthesis of the collective thesis results and discusses the limitations, implications, and applications of the analyses developed in this thesis.

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Chapter 2

Linking spatial habitat heterogeneity and population viability analysis to efficiently evaluate fisheries management strategies

Abstract

The focus of fisheries management has changed from considering just resource extraction to finding the balance between preserving biodiversity and ensuring fisheries yield. Traditional single species stock assessments are often inappropriate to ensure commercial fisheries sustainability because they can overestimate stock size and expose stocks to exploitation. Instead, new modelling tools such as ecosystem models that are then adopted within an ecosystem-based fisheries management (EBFM) framework, have been proposed to assess how harvest activity affects marine species. Whilst ecosystem models can successfully represent the whole ecosystem and promote regional sustainable fisheries, this framework is limited by its complexity. Population viability analysis (PVA) is an alternative tool that is extensively used in conservation biology as it allows for the comparison of alternative management scenarios and is suitable to assess fisheries impacts. PVAs are less complex than ecosystem-based models and, importantly, allow for traditional sensitivity analyses to investigate how variation in model results can be attributed to uncertainties in the input factors. First, we review how single species stock assessment, population viability analysis and ecosystem-based fisheries management approaches compare against six 'performance criteria' (life history, spatial heterogeneity, management strategies comparison, ecosystem structure, fisheries data and sensitivity analysis). This comparative analysis

highlights the suitability of PVA for fisheries management strategies evaluation. Second, we present a PVA case study to evaluate management strategies for blacklip abalone in south-east Australia proving the potential of this modelling tool. PVA has been demonstrated to be a reliable approach to evaluate alternative management strategies, accounting for spatial habitat heterogeneity and population dynamics, accurate to estimate future population size and structure.

2.1 Introduction

Tools that can assess the impact of fisheries management strategies on target species and their supporting ecosystems play a critical role in ensuring fishery sustainability. The development of suitable models and their application to management strategies evaluation (MSE) requires they be biologically robust and realistic, and readily facilitate scenario testing (Smith et al. 1999). We identified six key elements that need to be considered when choosing the best method to assess fisheries management strategies and build models that are effective, across both ecological and economic objectives, and realistic. First, a detailed knowledge of species' life history should form the foundation of these models (King and McFarlane 2003). Second, models that acknowledge spatial heterogeneity of habitat and population dynamics, such as connectivity, have a greater capacity to determine species persistence (Ying et al. 2011). Third, models have to efficiently allow the comparison of different fisheries management strategies (Akçakaya et al. 2004, Maunder et al. 2006, Marasco et al. 2007). Fourth, the inclusion of ecosystem structure increases the realism of scenarios and increases the capacity to detect emergent fishing impacts (Zhou et al. 2010). Fifth, consideration needs to be given to the availability of fisheries data, such as size, age, catch and occurrence, as data needs differ across modelling approaches (Akçakaya et al. 2004, Cotter et al. 2004, Plagányi 2007, Audzijonyte et al. 2019). And lastly, the ability to perform sensitivity analysis on parameters aids the detection of models' input uncertainty and is recommended when models are used for decision making (Steel et al. 2009). Commonly used fisheries models are often simplistic and not designed to include all these elements or they are complex, requiring detailed system understanding and high data needs. A method that has yet to receive extensive attention in fisheries management strategies assessment is spatially explicit population viability analysis (PVA). This tool has wide application in conservation science and can incorporate many of the above elements in a relatively simple framework.

Here, we initially review how traditional single species stock assessment, population viability analysis and ecosystem-based fisheries management models perform when assessed against our six key 'performance criteria' (life history, spatial heterogeneity, management strategies comparison, ecosystem structure, fisheries data and sensitivity analysis). We then present a case study, applying PVA to a coastal hand-capture fishery targeting blacklip abalone (*Haliotis rubra*) in south-east Australia to illustrate the flexibility of this tool in a real-world fisheries management context.

2.2 Model comparisons across six key elements

Effective mathematical and statistical models able to describe how populations respond to fishing pressure are needed to ensure the sustainable management of fisheries (Haddon 2010). Stock assessment has traditionally focussed on analysing abundance trends and other performance indicators such as fishing mortality, maximum sustainable yield and fishing quota in single stocks (Botsford et al. 2009). Advanced understanding of ecosystem processes, coupled with improved computing power, allowed these models to become increasingly complex (Bunnefeld et al. 2011). The resultant ecosystem-based fisheries management paradigm has emerged as a successful alternative to single species stock assessment with a strong focus on understanding the wider impact of fisheries on their supporting ecosystems (Smith et al. 2007). Population Viability Analysis (PVA) offers a complementary tool for assessing alternative fisheries management strategies. PVA has been extensively used in conservation biology and is often used to test effects of alternative spatially resolved management strategies on target species (Akçakaya 2000, Akçakaya et al. 2004).

Life history traits play a fundamental role in determining how populations respond to external impacts and are thus linked to population dynamics (King and McFarlane 2003). Consideration of life history strategies, such as size and age-dependent mortality and reproduction and growth, is critical when selecting an appropriate fisheries management strategy and for this reason is incorporated into existing fisheries management models

(King and McFarlane 2003). Importantly, these life history traits can vary through space and time. For example, changes in size, growth and reproductive investment might reflect environmental trends, such as spatial differences in water temperature (Baudron et al. 2014, Morrongiello and Thresher 2015, Claireaux et al. 2020). While best practice stock assessments regularly account for these features, in many fisheries management applications, life history traits are considered stationary (Table 2.1). This occurs despite increasing evidence that allowing for temporal and spatial variability of life history traits can not only improve model performance but also ensure that inappropriate decisions are not made (Booth 2000, Cadrin and Secor 2009, Whitten et al. 2013).

PVA models explicitly address a given population's structure by incorporating life history traits such as growth and survival and demographic stochasticity describing variations in population size, and growth and density dependence. PVA also accounts for spatial and temporal differences in life history parameters by explicitly incorporating environmental stochasticity, which in turn allows for greater model reality and a capacity to update them with new insight such as effects of genetics and dispersal (Table 2.1). Further, the expression of life history traits can be linked to the spatial distribution of suitable habitat or allowed to vary through time (Akçakaya et al. 2004). Ecosystem-based modelling tools also include key life history traits like mortality and growth for many species in an ecosystem (Table 2.1). Spatial structure of population dynamics is included in ecosystem models, such as the provision for environmentally dependent variations on mortality and recruitment, allowing the exploration of spatial management tools such as closures or protected areas. Temporal variations of these key traits are also implemented, reflecting in temporal variability in species abundance and trophic interactions (Plaganyi and Butterworth 2004).

The ability to include heterogenous habitat characteristics increases the reliability of models' predictions (Goethel et al. 2011). For example, incorporating spatial heterogeneity in the biophysical environment improves model reality because it allows

for the consideration of animal movements and spatial structure in management (Akçakaya et al. 2004, Carroll and Miquelle 2006). Whilst spatially explicit models become increasingly complex, predictions they generate are more robust to the impacts of change and thus any management decisions they help facilitate improved (Ying et al. 2011). For example, the impacts of climate change can negatively influence marine species persistence and spatial distributions by altering marine environmental conditions (Sanford and Kelly 2011, Ling et al. 2015). While modern stock assessment models and tools can accommodate the realistic spatial structure of populations (Punt 2019), their current management applications often adopt a much more simplistic structure, ignoring the spatial characteristics of habitat (Ying et al. 2011) (Table 2.1). Spatially explicit PVA models incorporate spatial heterogeneity of habitat suitability, abundance and management, and PVA outcomes can efficiently identify vulnerable and persistent populations (Table 2.1). These PVA characteristics provide an opportunity to formally describe temporal habitat changes, such as habitat loss (Akçakaya et al. 2004) which is a critical threat to marine ecosystems (Airoldi et al. 2008). Software implemented within the EBFM context, for example Ecospace (Pauly et al. 2000), are spatially explicit and readily account for variations in habitat factors (Christensen and Walters 2004). Allowing for spatial heterogeneity of habitat patches reflects the ability of fisheries management models to describe spatially-revolved differences in population dynamics, such as rates of connectivity, which represent critical process determining populations persistence (Hanski and Ovaskainen 2003).

A common characteristic of stock assessment, PVA and EBFM is the ability to quantify the impact of alternative management strategies on a fishery or fisheries, with the goal of selecting the most sustainable strategy (Table 2.1). Stock assessment performance indicators and management reference points (e.g. maximum sustainable yield MSY) evaluate current stock status and can be used to predict what will happen in the future and under different management strategies (Maunder et al. 2006). In comparison, PVA

adopts a risk assessment framework by evaluating the viability of target species (e.g. persistence through time or minimum abundance) under different management strategies. This approach integrates the spatial and temporal structure of harvesting (i.e., fishing) to assess their impact on the focal species' vulnerability to overexploitation (Akçakaya et al. 2004). EBFM also allows for the exploration of alternative management scenarios, including species' persistence and stock indicators together with the additional complexity of assessing harvest impacts on ecosystem trophic relationships (Christensen and Walters 2004). For example, Atlantis provides a data intense, complex, spatially explicit model of the interactions between environmental factors, marine species and humans which summarises the current knowledge of the ecosystem and allow users to explore alternative options for ecosystem-based fisheries management (Audzijonyte et al. 2019).

Modelling the true complexity of ecosystems allows for better designed management and enhanced environmental outcomes (Zhou et al. 2010). The benefits of incorporating ecosystem structure into models assessing fisheries management strategies includes the preservation of the broader ecosystem, including directly impacted species and ecologically dependent species, and the protection of species richness and genetic diversity (Zhou et al. 2010). However, these models require a lot of data to be informative, and several assumptions are required when data are unknown. Ecopath, with Ecosim and Ecospace (Christensen and Pauly 1992, Pauly et al. 2000, Christensen and Walters 2004) are used in EBFM to parameterise complex ecosystem relationships and assess fisheries management strategies, but necessitate the knowledge of the whole ecosystem structure, trophic relationships, spatial and temporal data and, most importantly, all the species-specific biomass parameters (Christensen & Walters, 2004). The time demand for building and running these models is significant. For instance, Atlantis (Audzijonyte et al. 2019) can be very informative and detailed, especially in the simulation of the management cycle and in the inclusion of several fishing effort characteristics (Fulton et

al. 2011), but the model necessitates information that is difficult to collect in a short time period (Audzijonyte et al. 2017). Stock assessment has generally been conducted on single species basis. PVA tools do not require extensive ecosystem-based data to be included, although multispecies applications for PVA exist (Root 2002, Pastorok et al. 2003, Kianirad et al. 2006). The application of these more complex PVAs is currently limited.

Models require different data types to account for fishing mortality (Table 2.1). Stock assessment and population viability analysis require relative detailed single-species fisheries data. In general, data used in these modelling approaches such as size, age, catches and harvest rates, can be easy to source. Specifically, stock assessment models use data from fisheries independent surveys and time series of landings (Cotter et al. 2004). Instead, PVAs represent harvest by applying constant or variable fishing mortality rates, or by gradually removing individuals according to the spatial distribution of fisheries activities (Akçakaya et al. 2004). Models' complexity increases in ecosystem models, making harder to fulfil all data requirements. In ecosystem models, data ranges from fixed fishing rate of a single functional group to spatially explicit harvest rates across multiple groups (Audzijonyte et al. 2019). Time series fisheries data can be included in whole ecosystem models to represent catch history, and may be coupled with spatial and temporal data on species biomass, trophic linkages and diet composition (Plagányi 2007).

Table 2.1: Summary of the six criteria used to review single species stock assessment, PVA and EBFM and how those criteria are implemented in each model.

	Stock assessment	**PVA**	**Ecosystem models**
Life history traits	Life history traits (age, growth, natural mortality, sexual maturity and reproduction) are included.	Life history traits (natural mortality, fecundity, growth, age) are included. Spatial and temporal variability of traits and populations is included.	Life history traits (natural mortality, growth, reproduction and survival) are included for multiple species or groups of species.

	Spatial and temporal variation of traits is included. These models can account for demographic stochasticity.	These models can account for demographic stochasticity.	Spatial and temporal variability is included.
Spatial heterogeneity	Spatial heterogeneity of the habitat can be included to modern stock assessment models. Models also account for environmental stochasticity.	Spatial heterogeneity of the habitat is included. Spatial characteristics can vary across time. Models also account for environmental stochasticity.	Spatial heterogeneity of the habitat is included. Spatial characteristics can vary across time but complex.
Management strategies comparison	Management strategies comparison allowed by varying performance indicators and predicting subsequent future biomass.	Management strategies comparison allowed by varying several characteristics of management (i.e. intensity, spatial distribution of effort, temporal characteristics of catches).	Management strategies comparison allowed by varying several characteristics (i.e. environmental, ecological, human interactions) of ecosystem-based management.
Multispecies (ecosystem-based approach)	Generally not allowed	Tools for multispecies models exist but not often used.	Implicit ecosystem-based structure.
Sensitivity analysis	Traditional sensitivity analysis allowed.	Traditional sensitivity analysis allowed.	Traditional sensitivity analysis not allowed.
Fisheries data	Time series of landings and fishery independent survey data. Catch per unit of effort (CPUE), data from landing records, size and distribution of catches are commonly used in these models.	Fisheries harvest can be modelled as constant fishing mortality rate or by removing individuals according to harvest data, based on spatial distribution of fishing effort and spatial closures.	Time series of fisheries data for all or most important species. Data range from a constant fishing rate on a single functional group to spatially explicit harvest rates for many fisheries.

Sensitivity analysis is a critical part of best practices to assess if a model can be suitable to inform decisions, despite its parameters' uncertainties (Mateus and Franz 2015). Sensitivity analysis addresses how sensitive the model is to changes in individual parameter values, and which parameters have more influence on the results (Mateus and Franz 2015). It is common to provide measures of uncertainty in the output of stock assessments, such as those derived from sensitivity analysis, bootstrapping to produce distributions or Bayesian posterior distributions (Hilborn 2003). Spatially explicit PVA allows users to perform sensitivity analysis (McCarthy et al. 1995, Naujokaitis-Lewis et al. 2009). Traditional sensitivity analyses are frequently not possible with complex ecosystem-based models such as Atlantis. Instead, parameter uncertainty can be assessed using other approaches such as "bounded parameterisation" (Audzijonyte et al. 2017, Audzijonyte et al. 2019).

2.3 Case study: PVA application to blacklip abalone

2.3.1 Methods

Blacklip abalone, *Haliotis rubra*, is one of the most valuable fisheries species in Australia's commercial fishery sector (Savage 2015). Industry involvement in abalone fisheries management is significant and fishery management strategies are evaluated annually by fishery-dependent performance criteria such as yield and biomass (Bedford et al. 2013). Abalone stocks are spatially discrete and due to their sedentary nature, are prone to local depletion (McShane 1995). Assessment tools that incorporate spatial resolution and local-scale demography are thus beneficial due to the variability in processes affecting local populations (McShane 1995). Despite the relative health of Victoria's abalone fishery, the loss of key kelp habitat caused by urchin grazing, and concurrent competition with urchins for remaining food are risks to the fishery's long-term viability (Strain et al. 2013, Ling et al. 2015). Furthermore, blacklip abalone persistence has been impacted by the spread of abalone viral ganglioneuritis (AVG) which had

caused dramatic increases in mortality (Hooper et al. 2007, Hooper et al. 2012, Corbeil et al. 2016).

Victoria's coastline is divided into three management zones, Western Zone, Central Zone and Eastern Zone (Fig. 2.1), each with specific catch limits for commercial and recreational fisheries based on results of annual stock assessments (The State of Victoria Department of Economic Development Jobs Transport and Resources 2015). On a zone-by-zone basis assessment completed by the Victorian Fisheries Authority, only the Western Zone is considered "sustainable", while Central and Eastern zones are classified as "transitional depleting", indicating that stock biomass has been overfished. The impact of fisheries on Victorian abalone stock is assessed using time series catch, effort and size. (Victorian Fisheries Authority 2017). Management measures such as zone-specific reductions on harvest rates have been implemented and these stocks are recovering (Victorian Fisheries Authority 2017). By combining the available information on blacklip abalone fisheries management with a PVA model it is possible to predict the future trend in species abundance under current fisheries management scenarios and identify which zones are expected to be at risk of depletion. Here, PVA provides information that can be critical to implement effective spatial management strategies such as understanding where the current catch quota levels are appropriate or need to change to ensure the sustainability of abalone fishery.

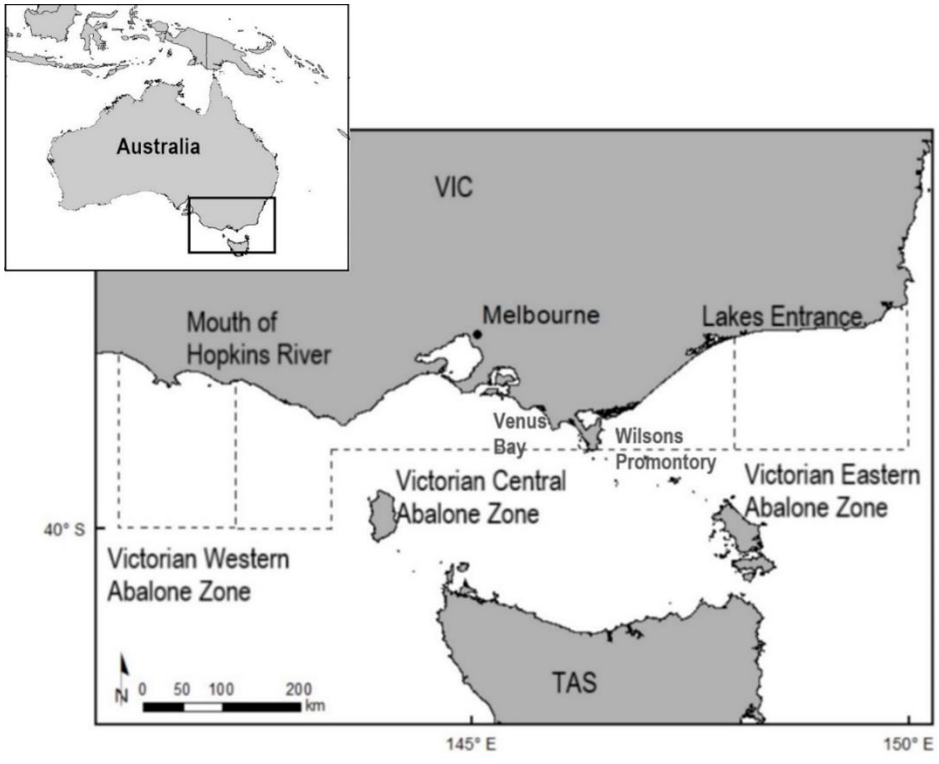

Figure 2.1: Commercial zones for blacklip abalone fishery, as defined in the "Victorian Wild Harvest Abalone Fishery Management Plan" 2015. Victorian map in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

We addressed four of the six key criteria used earlier to compare management scenarios in fisheries models. Key life histotry traits were included in the models through parameters describing survival and reproduction within the stage matrix, matrix stochasticity and density-dependent controls on population growth (Hart and Gorfine 1997, Bardos et al. 2006, Fordham et al. 2013). A stage-structured approach was used to model population growth according to the abalone seven-stage matrix available from the COMADRE database (Fordham et al. 2013, Salguero-Gómez et al., 2016). A stochasticity matrix was also defined to describe the uncertainty around stage matrix parameters. Initial abundance of abalone was quantified using stable state stage distributions multiplied by the carrying capacity of the system, estimated by fishery-independent survey data (Hart and Gorfine 1997). We applied competition as a density-dependent mechanism only to adult stages, since these individuals likely compete for substrate and food (Akçakaya et al. 2004, Fordham et al. 2013).

We focused on increasing model realism by allowing for spatially variable environmental conditions and habitat fragmentation, as well as incorporating spatial variability to life history traits. Habitat suitability and quality largely determined different local population size and dynamics through alterations to patch carrying capacity (Bardos et al. 2006). Environmental stochasticity accounted for uncertainty about environmental fluctuations in our system. While PVA models can also accommodate dispersal dynamics, we did not include it here as abalone larvae have a relatively short pelagic larval duration, and, despite some disagreement, abalone populations may be considered substantially closed at this spatial extent and model resolution and reliant on local retention to persist (Bardos et al. 2006).

Assessing the spatial variation in model parameters was a key focus of our simulations. In general, variability of habitat influences the number of individuals within a habitat patch which influences our ability to understand the spatial structure of a given stock. The spatial distribution of abalone populations across the whole study area was mapped using the predictions of a generalised additive model fitted to observed occurrence and environemntal data (see Appendix 1). We also explored the importance of temporal habitat change on abalone abundance, assessing the impact of a gradual loss of habitat caused by increased sea urchin prevalence (Worthington and Blount 2003, Ling et al. 2015). See below for further description.

The addition of zone-specific abalone commercial catch quota within our PVAs, representative of annual catches (Victorian Fisheries Authority 2019), developed a zone-specific fisheries management context that was useful to compare the impact of different managament scenarios. For each cell of suitable habitat, a fixed number of abalone was removed at each timestep. Fishing depletion was equally distributed within each zone because the spatial distribution of fishing is unknown (Victorian Fisheries Authority 2019). Populations within protected areas such as marine parks, marine protected areas and marine reserves were excluded from the fishery, together with populations within

areas where commercial fishery is not permitted (Victorian Fisheries Authority 2019, UNEP-WCMC and IUCN 2020).

Our PVAs focussed solely on blacklip abalone persistence so we could easily compare our results with past stock assessment reports. Therefore, we used tools suitable to perform single species PVA without further exploration of emerging multispecies PVA modelling tools (Root 2002). To evaluate abalone predicted abundance, we investigated the presence of populations below a fixed local extinction threshold of abundance, representing the minimum viable population (Catton et al. 2016). Finally, we analysed and tested our abalone abundance results for sensitivity to model parameter uncertainty by performing one-at-time sensitivity analysis. The analysis was achieved by sequentially increasing and reducing by 10% several PVA parameters (carrying capacity, fishing catches, habitat suitability, stage matrix parameters, habitat loss rate for eastern Victoria and AVG mortality rate for western Victoria). Then we compared each new model's results to the baseline model, visualising the different abundance trends in both directions and estimating an average coefficient of variation of abundance from baseline model. These comparisons provide a valuable insight into our understanding of a given fishery and help inform fisheries scientists and managers on where extra data collection is needed and where model structure improvements can be made.

The future abundance of blacklip abalone was simulated for the three Victorian management zones, as a function of three different scenarios. These PVAs were developed to illustrate the flexibility of PVA modelling tools. Our first scenario was a baseline and included just central Victoria current fisheries management. Our second scenario focussed on habitat loss in Eastern Victoria caused by the increasingly abundant sea urchins. A coefficient of habitat loss of 0.1 (see Appendix 1 for details) was applied to gradually reduce habitat suitability in each cell of the model domain, at each timestep. Our third scenario investigated the impact of disease-dependent mortality in Western Victoria using as disease case study abalone viral ganglioneuritis (AVG). The

impact of a disease outbreak was simulated by applying an additional mortality rate of 0.8 to abalone populations based on past published models (Gorfine et al. 2008). Future long-term abundance of abalone populations was predicted over 30 annual timesteps, and each timestep should be interpret as one year. For each zone, we included three PVA replicates to account for environmental stochasticity and results were averaged across the three replicates. Blacklip abalone population dynamics and fisheries harvest were simulated using R v3.6.2 (R Core Team 2019) and the STEPS package (Visintin et al. 2020). For further details on the PVA methods see Appendix 1.

2.3.2 Results and Discussion

Abalone populations in the Central Zone persisted across all timesteps, however, total abalone abundance initially grew until reaching an abundance peak then it dramatically declined (Fig 2.2a). Thereafter, Central Zone abundance remained steady for the remainder of time steps. This trend did not appear to be related to fishing pressure and is likely dependent on the ceiling-type density-dependence (Bardos et al. 2006) applied to the simulations. Abalone populations inside protected areas, such as those distributed along Wilsons Promontory and Venus Bay, had the highest abundance at the beginning and at the end of the simulations (Fig 2.3). Very few populations had abundance below the extinction threshold at the beginning of the simulations, corresponding to 0.02% of the domain, and were generally dispersed across whole central Victoria coast (aside from Port Phillip Bay). Some of these populations were able to increase their abundance by the end of the simulations as fisheries pressure is generally low in this zone and thus allows for potential recovery in vulnerable areas (Fig. 2.3a). Exploring the spatial distribution of blacklip abalone showed how habitat distribution strongly influenced our abundance results (Fig. 2.3a) and indicates that managers might benefit from more accurate knowledge of habitat characteristics. More generally, habitat variability determines cues for settlement and larval metamorphosis (Huggett et al. 2005), and

different abalone genotypes have been associated with different habitat features (Miller et al. 2019).

We performed sensitivity analysis to test the impact of parameter uncertainty on model predictions. Sensitivity analysis results showed that Central Zone abalone abundance at the final timestep was not influenced by variations in the abalone catch quotas or from uncertainty in demographic parameters such as mortality and fecundity. Focussing on the final timestep, habitat appeared to play a critical role, with predictions largely influenced by environmentally-driven changes in carrying capacity. The other models (modified carrying capacity, stage matrix and fishing quota) predicted about the same final abundance as the baseline model. Overall, habitat suitability (especially its 10% reduction) explained an average of 25% of variation rate in model output. All population abundance curves follow the same trend of the baseline simulations scenario (Fig. 2.2a).

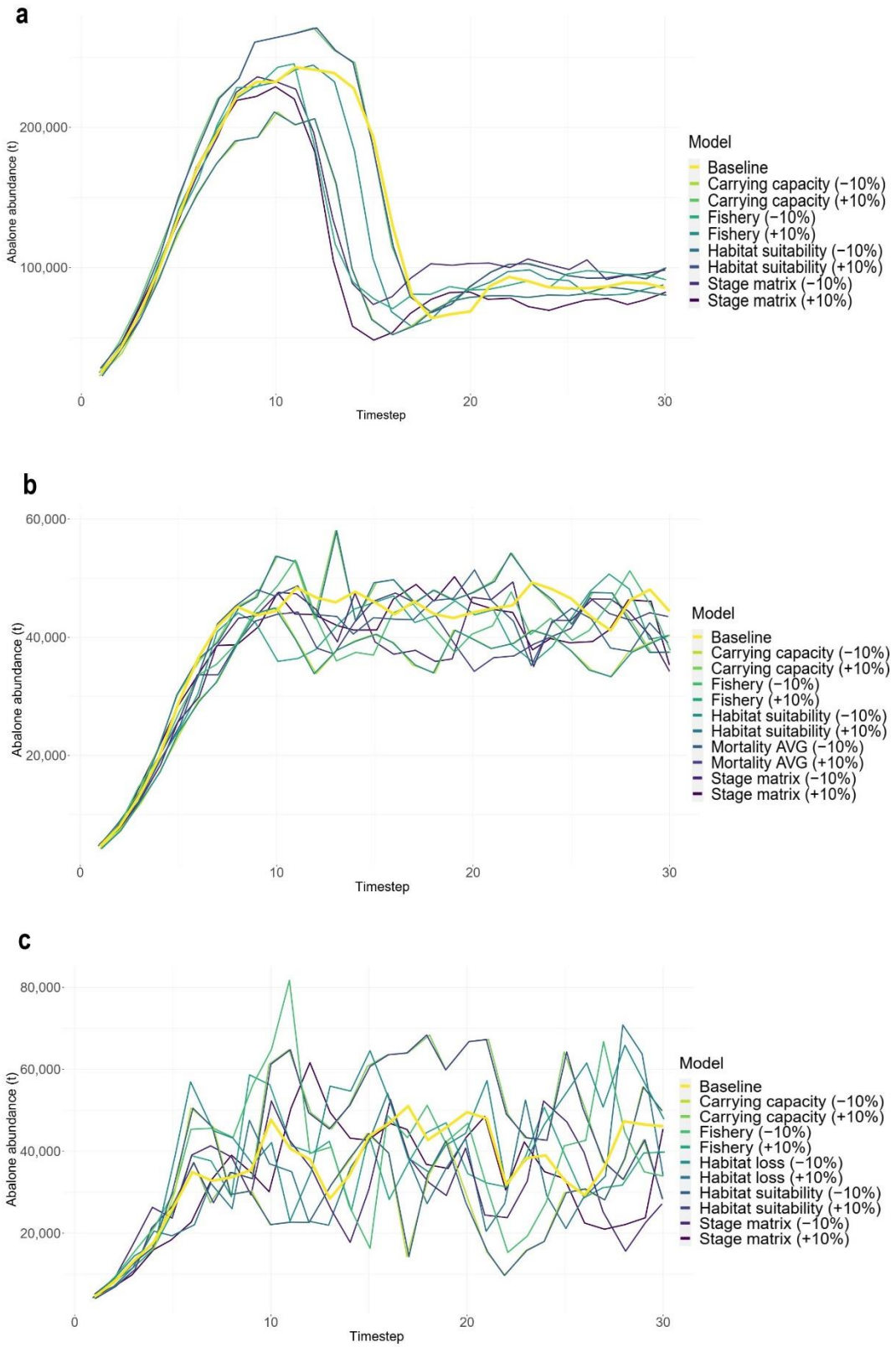

Figure 2.2: Abalone total abundance for Central (a), Western (b), and Eastern (c), management zones. Results were averaged over all replicates. Yellow line shows the baseline scenario, representing the current management. Other lines show the results of one-at-time sensibility analysis. In each model we modified by ±10% the values of carrying capacity, fishing catches, habitat suitability, stage matrix parameters, disease dependent mortality ("Mortality AVG") (b) and habitat loss rate ("Habitat loss") for Eastern zone (c).

In western Victoria commercial fishery activity was coupled with an AVG outbreak in the early 2000s that resulted in abundance to plummet (Corbeil et al. 2016). Current management of the Western Zone abalone fishery is focussed on the recovery of these populations (Gorfine et al. 2008). Overall, in our PVA populations were persistent through time and even predict potential increases in the abundance of individuals entering (i.e. recruiting) to the fishery. The Western Zone abundance curve rapidly grew in the first stages of the simulations and reached a peak, corresponding to timestep 11, whereafter it remained constant until the end of the experiment (Fig. 2.2b). This rapid expansion can be related to the large availability of vacant habitat due to recent population acute mortality and reduced fishing pressure. Populations near the coast were predicted to be the most abundant, while populations further from the coastline had lower abundance at the initial stage of the simulations. Shallower habitats are generally associated to kelp forests, providing the most suitable habitat for blacklip abalone (Daume et al. 2000). However, all these populations improved across the simulation time and no population fell below the minimum viable abundance threshold at the last simulation timestep (Fig. 2.3b). Results from sensitivity analysis showed that the models' predictions were similar for all models tested until reaching timestep 10, after which predictions diverged. The curves showed that changes in either natural mortality (varying stage matrix parameters), increases in fishing mortality or disease-dependent mortality led to the lowest abundance. Positive changes in carrying capacity and habitat suitability contribute to the highest abundance peak (Fig. 2.2b). Negative changes (-10%) in habitat suitability instead contribute to an average decline of 14% in abalone abundance.

A major innovation in our PVA models was the simulation of habitat loss together with fisheries pressure. This aspect was simulated for the abalone Eastern Victoria Management Zone. Overall, the simulations suggest that abundance could initially increase and then reaching a state characterised by large fluctuations compared to the other management zones when no other unpredicted factors occur (Fig. 2.2c). Temporal

fluctuations are generally considered indicators of stock vulnerability. For instance, large temporal variations in larval supply lead to recruitment variability, which contributes to detrimental effects on long-term persistence. Managers might aim to increase stability by reducing temporal fluctuations in abundance and reducing catches (Harrison et al. 2020). Along eastern Victoria, populations closer to the coasts showed the highest abundance. These populations were distributed heterogeneously throughout the region reflecting the underlying spatial complexity of available rocky reef and macroalgal composition of abalone habitat (Huggett et al. 2005). Less than 1% of the total area was occupied by populations below the local extinction threshold (Fig. 2.3c).

Habitat parameters seem to be the main driver of the predicted abundance fluctuations in eastern Victoria as these were not present in the west, which was exposed to an elevated mortality rate. Especially, it appears that a low rate of habitat loss resulted in the greatest abundance fluctuations. Sensitivity analysis identified that an increase of 10% in habitat loss resulted in an average 10% decrease in abalone abundance, while a 10% reduction of habitat loss rate resulted in abalone abundance increasing of 20%.

Habitat suitability was another key driver of abalone abundance trend in the Eastern Zone. A 10% increase and decrease in suitability led, respectively, to 20% increase and 15% decrease of total abalone abundance. These results demonstrate the importance of understanding habitat characteristics in order to obtain more realistic predictions. The Eastern Zone model was more stable to variation in other parameters, such as increasing fishing quota, despite lower abundance of abalone at the final simulation timestep (Fig. 2.2c). Managers would benefit from including spatial data of abalone abundance with realistic habitat data, particularly in vulnerable coastal areas (e. g., proximity of abalone populations to coastal areas exposed to urchin outbreaks) to identify important monitoring sites to assess key populations in these areas. Maps showing population abundance across the three zones and all timestep are available in Appendix 1 (Figures A1.3-A1.4-A1.5).

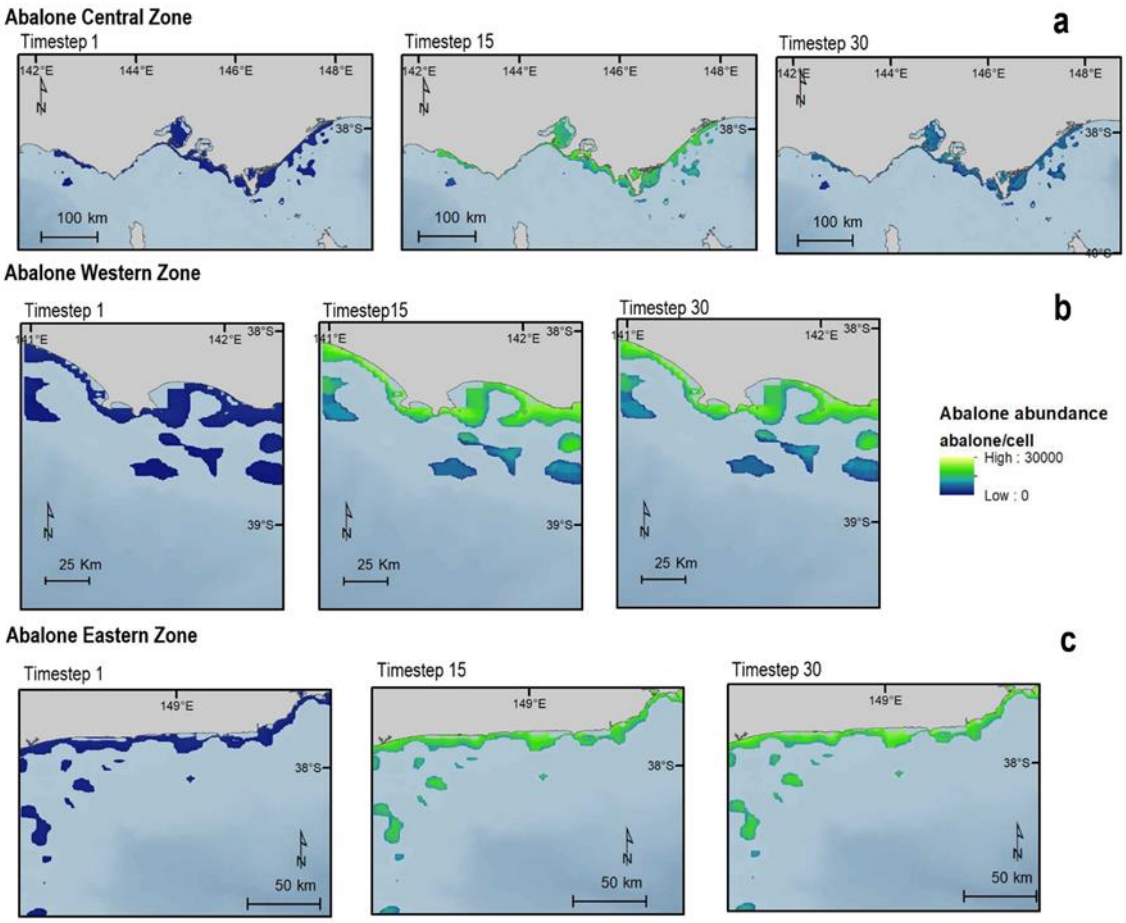

Figure 2.3: Abundance of abalone (recruitment stage) for timestep 0-15-30, averaged over 3 replicates, for baseline scenario for Abalone Central (a), Western (b) and Eastern (c) management zones. Values show abalone for cell. Maps in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

Our PVAs predicted that current abalone management could reflect in a rise in abalone abundance, especially for Eastern and Western Zone, and that modelled harvest only had a limited impact on forecast abundance. These results corroborate the findings of the most recent stock assessment where abalone stocks are listed as recovering after being overexploited (Victorian Fisheries Authority 2017). The role of habitat emerged as key in this framework and sensitivity analysis showed how variations of habitat suitability, habitat loss rate and carrying capacity (which here was assumed proportional to habitat suitability) strongly influenced persistence results. Previous ecological studies already highlighted the detrimental effect of habitat loss on blacklip abalone (Strain et al. 2013, Ling et al. 2015), but more generally few fisheries models have incorporated habitat change when assessing management strategies (but see Fordham et al. 2013).

Knowledge of spatial heterogeneity of habitat characteristics, critical to build robust models and obtaining reliable predictions, reflects on the importance of developing appropriate spatially resolved management tools. Much work has been done to develop indicators for effectiveness of spatial management tools such as Marine Protected Areas (MPAs). MPAs can be fully closed or allow multiple uses, but generally aim to protect critical habitats and life stages of marine species from the fishing impacts (Breen et al. 2015). MPAs can deliver positive outcomes for fisheries management and conservation challenges, ensuring the restoration of the marine populations and promoting sustainable and local based fisheries practices (Di Franco et al. 2016). Adopted measures such as MPAs and other marine parks and reserves appeared to preserve large abalone populations which corresponded to protected areas (e.g. Wilsons Promontory in the Central region).

Sensitivity analysis revealed that fisheries pressure has limited influence on abalone persistence. Specifically, predictions of abalone abundance increased by only 1-13% across all zones when we decreased each zone maximum allowable catch (respectively 5% for the Western Zone, 1% for the Eastern Zone and 13% for the Central Zone). This might be related to the recent implementation of a more sustainable management of abalone fisheries, which gradually reduced the total amount of abalone allowed to catch, after experiencing a large stock depletion during the past decades (Victorian Fisheries Authority 2017).

2.4 Summary

Fisheries models play a critical role in increasing our understanding of the impact of fisheries management on marine species and thus help contribute to the identification of sustainable fisheries practices. As a range of modelling approaches are available to fisheries scientists, it is important to appreciate their benefits and limitations. Population viability analysis is a flexible tool to explore the impact of fisheries management on marine species, efficiently including additional elements such as habitat changes, that

are infrequently accounted for in other modelling approaches. Spatial heterogeneity in species' distribution and abundance influences their viability (Ying et al. 2011), indicating that spatially explicit models can better inform managers on which areas are the most vulnerable or the most productive and which areas will be most responsive to management intervention. Introducing habitat loss into our analysis was very informative, revealing that this environmental change could strongly influence abalone persistence. Such insight indicates that managers need better knowledge of spatial and temporal habitat heterogeneity if they want to accurately forecast future stock size.

The population viability analysis presented here has the advantage of being able to not only account for demographic and environmental stochasticity, but also for variations of habitat characteristics through time, such as habitat loss (Visintin et al 2020). Similar to other commonly used models, our PVA framework is flexible and can be readily expanded to include a range of environmental, demographic, biological parameters relevant to specific management scenarios. All the elements incorporated into a PVA can either be added as a fixed value or allowed to temporally change according to a function (Visintin et al. 2020). Spatio-temporal variability in parameters allows PVA models to more realistically represent interannual variability of local habitat characteristics and population size and dynamics. Whilst not presented thoroughly here, due to species specific limited dispersal characteristics of abalone, PVA also allows for the incorporation of connectivity which is fundamental in determining marine population dynamics (Cowen et al. 2006).

Species and individual movements (dispersal) can be specified using kernel-based dispersal that is stage or proportion-dependent when this information is known or critical for the species studied (Akçakaya et al. 2004). Assisted species movements (i.e. translocations, culling or reintroductions) can also readily be parameterised (Visintin et al. 2020). PVA results are easy to interpret and communicate, not only informing managers on trends of total biomass across time but also identifying locally vulnerable

regions that may need additional management intervention. The relative simplicity of PVA provides an ideal tool for initial analysis and to understand which strategy can be the more appropriate to focus on, reducing scientists and managers effort (Akçakaya et al. 2004).

The ability to perform sensitivity analysis is another key element for assessing the impact of fisheries activity on marine species. It allows users to quantitatively assess model performance and parameters influence which are critical steps when developing complex models. Performing one-at-a-time sensitivity analyses can be computationally demanding, so grouping parameters and being changed in different scenarios offers a more pragmatic analysis approach (Mateus and Franz 2015). Sensitivity analysis can be accommodated in fisheries management strategies evaluation models and its results should be used by managers to improve model precision and provide more detailed model outputs (Steel et al 2009).

Spatially explicit population viability models do have limitations that must be considered when applying this method. As with many models, the ability to produce accurate results relies on the quality of the data available (Coulson et al. 2001), and often, data are missing or not available. However, species subject to commercial and recreational fisheries are usually well studied and data to analyse their viability, such as growth, mortality, fishing catches and population dynamics, are available to fisheries scientists. Appropriate targeted data collection can be helpful to increase the quality of data and improve the reliability of models results. Multiple species PVA (Root 2002, Pastorok et al. 2003, Kianirad et al. 2006) will likely be beneficial to fisheries scientists in developing multispecies or ecosystem-based management strategy evaluation

Knowing the persistence of marine species subject to fisheries harvest can inform managers and scientists on planning more sustainable fisheries management strategies. Focusing on the spatial heterogeneity of distributional, demographic and fishing parameters provides important information that can assist in designing spatial

management tools such as protected areas or managing fishing. Our case study using blacklip abalone presents an approach that will be directly transferable to many benthic fisheries. We proved how for species like abalone, fisheries managers would benefit from using spatially explicit population models to assess fisheries management strategies impact on species persistence.

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Chapter 3

Testing the influence of seascape connectivity on marine-based species distribution models

Abstract

Species distribution models (SDMs) are commonly used in ecology to predict species occurrence probability and how species are geographically distributed. Here, we propose a method to efficiently integrate information on connectivity into SDMs, a key element of population dynamics strongly influencing how species are distributed across land/seascapes. We also quantify the influence of various connectivity estimates on the marine-based SDMs outcomes. Seascape connectivity was modelled for two common marine species occurring in southeast Australian waters, using two different modelling approaches to accommodate species-specific dispersal characteristics. We used network-based centrality metrics to compute patch-level importance values and include these metrics in the group of predictors of correlative SDMs. We employ boosted regression trees (BRT) to fit our models, calculating the predictive performance, comparing spatial predictions and evaluating the relative influence of connectivity-based metrics among other predictors. Network-based metrics provide a flexible tool to quantify seascape connectivity that can be efficiently incorporated into SDMs. Connectivity was found to have an important contribution to SDMs predictions and model performance was not negatively influenced from including these connectivity measures. Degree centrality, quantifying incoming and outgoing connections of habitat patches, was the most influential centrality metric. Pairwise interactions between predictors revealed that the species was predominantly found around hubs of connectivity and in warm, high-oxygenated, shallow waters. Further research is needed to quantify the complex role that

marine habitat network structure and dynamics may have on SDMs spatial predictions and explanatory power.

3.1 Introduction

Conservation of biodiversity is a priority in management plans for conservation scientists and managers. The presence and absences, as well as the distribution of species, is central to conservation planning and as a result, understanding species' spatial distribution patterns is critical to identify important habitats and improve management strategies (Monk et al. 2010, Foltête et al. 2012). Classic strategies used in conservation to manage species include the establishment of protected areas and reserves around key habitat. Today, connectivity is considered essential, and plays a fundamental role in characterising the importance of protected areas within a broader network of habitat patches (Agardy 1994). The movement of individuals among habitat patches, or connectivity, ensures species persistence and is critical to determine population dynamics, particularly when species are distributed across fragmented habitat patches (Hanski 1998). Managers now routinely include connectivity, along with species occurrences data, in conservation planning using decision support tools like Marxan and Zonation, which identify priority areas for conserving biodiversity, minimising fragmentation as well as overall costs (Delavenne et al. 2012, Daigle et al. 2020).

Species distribution models (SDMs) represent a key tool for the prediction of species distributions, driven by environmental parameters. SDMs have been applied to marine, freshwater and terrestrial species and demonstrated to perform quite well in predicting the geographic distribution of species in a variety of contexts (Elith and Leathwick 2009). Distribution modelling techniques have developed using presence/absence or abundance data, but recent research has focussed on proposing methods which perform well when presence-only data are available (i.e., the lack of absence and abundance data) (Elith et al. 2006). Though it can be hard to detect model errors and uncertainties in these cases, best practises are necessary to ensure that SDMs have strong predictive capability (Robinson et al. 2017). Correlative SDMs correlate species occurrence data with environmental characteristics to quantify the suitable habitat niche and predict

distribution across a land/seascape. This approach is quite valuable and broadly applicable across diverse fields such as ecology, evolutionary biology and conservation biology (Pearson 2007). In addition, hundreds of papers used species distribution modelling approaches to address different marine-related research goals (Robinson et al. 2017), for instance describing essential fish habitat (Monk et al. 2010), assessing the impact of climate change (Jones and Cheung 2015), understanding habitat distribution shifts (Gormley et al. 2015), studying the spread of invasive species (Báez et al. 2010) or better designing conservation strategies (Adams et al. 2016). Yet, applying SDMs to marine species can be particularly challenging. Challenges in understanding how species are distributed across space arise when comprehensive sampling is not possible, for example for species with high degree of niche specialization, and/or restricted range (Araujo and Guisan 2006). Several issues are somewhat unique of the marine environment. For example, a strong spatial bias in data collection, since different effort is required to collect data in shallow waters compared to deep waters, and the widespread spatial-temporal bias in global satellite-derived ocean measurements, due to unpredicted or unusual atmospheric properties affecting the algorithm interpretation, and the lack of *in situ* data to use for tuning (Robinson et al. 2011, Robinson et al. 2017).

Appropriate environmental parameters are crucial for the robust development and realistic predictions of SDMs, but global marine environmental datasets are often of coarse spatial resolution and coastal data are often missing or inaccurate. However, extensive work has been done to make data more reliable and available to researchers for marine species distribution modelling, such as Bio-ORACLE global environmental dataset (Tyberghein et al. 2012). Environmental parameters used in SDMs most often represent static in-situ characteristics (e.g., annual mean temperature). But, the spatial distribution of populations is often equally as dependent on the dynamics or variability in these parameters (e.g., changes in weekly maximum temperature). For example, in marine systems, larval dispersal is a critical component in population dynamics (i.e.,

population connectivity), fundamental for persistence of metapopulations inhabiting fragmented landscapes (Hanski 1998) and in source-sink dynamics (Pulliam 1988). This connectivity, in particular, is governed by dynamic ocean currents and other dynamic environmental variables (Cowen and Sponaugle 2009). As a result, when modelling the spatial distribution of populations, it is important to consider dispersal and habitat connectivity (Foltête et al. 2012). Even though habitats might be suitable for their intrinsic environmental characteristics and potential value to the metapopulation, they might be difficult to reach and therefore not effectively contribute to the population. However, SDMs rarely directly consider dispersal of species (Robinson et al. 2011), effectively ignoring this potentially important process. Clearly, including dispersal dynamics and population connectivity into the study of species distributions is critical.

A recent improvement in SDM techniques has been the inclusion of data around population dynamics. This new brand of SDMs may be incredibly helpful in conservation and management planning efforts (Lawler et al. 2011). These data may include indices related to habitat patch reachability, primarily focussed on neighbourhood characteristics, but this approach assumes movement is based on distance alone, and ignores direction (Franklin 2010). More indices have been used to capture anisotropic landscape properties for species where directionality in movement across the landscape is important. Initially, indices such as the proximity index were based on Euclidean distance (Gustafson and Parker 1994), advanced through the index of functional patch connectivity (IFPC) using least-cost path algorithms (Richard and Armstrong 2010). Incorporating these indices in SDMs has proved to be valuable, and the integration of connectivity metrics in SDMs has catalysed further research around landscape connectivity analysis and ecological network modelling (Foltête et al. 2012).

The fluid marine environment allows several ways to disperse, for some species, movements can be limited to early life stages (Cowen and Sponaugle 2009), while fish species or crustaceans can move across the seascape, throughout the whole lifespan.

Habitat destruction and natural habitat decline can impact species distributions, as well as connectivity. For example, the decline in seagrass cover due to human impacts (Bell et al. 2001) and the loss of coral reefs due to bleaching (Bellwood et al. 2006) have a negative impact on population persistence and habitat connectivity due to the loss of these habitat patches. Smaller or more distant patches will be less functionally connected with surrounding habitats, increasing the isolation and vulnerability to extinction (O'Hara 2002). In these isolated habitat patches, marine populations are often demographically closed, and species' persistence depends on replacement through local retention of larvae, whereby larvae are released and settled back to the natal habitat patch (Burgess et al. 2014).

Seascape connectivity, representing the functional connectedness of marine habitat patches, combines environmental attributes and the geographic configuration of the seascape with information on the ability of the species to move (Weeks 2017). Seascape connectivity is particularly critical in metapopulation dynamics and persistence (Engelhard et al. 2017). Quantifying seascape connectivity is challenging and several methods have evolved. Empirical methods for quantifying connectivity include both direct and indirect methods. Direct methods include traditional mark-recapture techniques, chemical-based analysis for small or cryptic organisms and recent advancements use radar technology, cameras and environmental sensors and satellite archival tags (Kool et al. 2013). Indirect methods rely on population genetic analysis using genetic markers and parentage analysis (Kool et al. 2013). However, it is often impossible to sample at the broad spatial and temporal extent required, and researchers have therefore developed numerical models of connectivity to augment these direct and indirect methods. Early approaches to assessing connectivity used dispersal kernels to estimate the effective distance on connectivity, assuming symmetric dispersal and no effect of habitat structure (Kool et al. 2013). Other methods used habitat reachability estimates in terms of intra-patch and inter-patch connectivity, such as the Probability of Connectivity

(PC, Saura and Pascual-Hortal 2007). More recent estimates of seascape connectivity use scores based on area-weighted proximity between juvenile and adult habitat patches, which may be particularly appropriate for data-poor context (Weeks 2017). An alternative method quantifies connectivity as the probability of connectivity based on fish species-specific home ranges and distance thresholds (Engelhard et al. 2017). Few studies assess connectivity taking advantage of terrestrial examples; this method utilizes a cost-surface incorporating the influence of ocean currents on marine species movements, such as currents magnitude and directionality, to determine least-cost paths connecting marine habitats of the same type (Fischer et al. 2011, Caldwell and Gergel 2013). An increasingly popular approach to quantify seascape connectivity is based on biophysical models used to determine connectivity in marine systems, coupled with graph theory to study structure and properties of connectivity networks. Spatial predictions of population connectivity across the seascape are created based on habitat characteristics, ocean currents' velocity and species-specific biological parameters (Treml et al. 2008). Despite the importance of seascape connectivity, it has not been extensively included into spatial prioritization process to design Marine Protected Areas, MPAs, due to challenges that scientists face when defining connectivity for marine species (Weeks 2017).

A well-known and appropriate framework to represent and analyse connectivity takes advantage of graph-theory. Habitat connectivity, and all of its complexities, can be summarised as a network, where habitat patches are nodes and the presence and strength of connections between patches are represented by links or edges in the network (Urban and Keitt 2001). In landscape and seascape ecology, network algorithms have been used in understanding and managing habitat fragmentation, reserve design and conservation planning (Urban and Keitt 2001, Bodin and Norberg 2007, Minor and Urban 2007, Estrada and Bodin 2008, Grober-Dunsmore et al. 2009). Few studies in landscape ecology effectively integrated graph-based metrics into SDMs to summarise

landscape connectivity, although these studies have been limited to terrestrial systems and simplified connectivity, including connectivity estimates improved the predictive performance of the SDMs (Foltête et al. 2012). These approaches have been used for terrestrial species impacted by urban development (Tarabon et al. 2019) and by linear infrastructures such as roads and railways (Clauzel et al. 2013, Girardet et al. 2013). Throughout much of this work, network-based centrality measures have received much attention for summarising patch-level connectivity attributes and determining patch-level contributions and metapopulation importance. Among these centrality metrics, betweenness centrality (BC) (Freeman 1978) has often been used in the context of habitat prioritization and species conservation to identify stepping-stones habitats (Estrada and Bodin 2008, Bodin and Saura 2010, Carroll et al. 2012). BC is defined as the number of shortest paths within an entire habitat network that pass through a given node and may indicate common or important stepping-stones important for maintaining network-wide connectivity. Eigenvector centrality (Bonacich 1987), a similar network-wide measure of the most 'influential' nodes in a network has also been used to identify important habitat patches in connected landscape networks (Estrada and Bodin 2008). A local centrality measure, degree centrality, quantifies the number of incoming and/or outgoing connections and determines which habitat patches may act as local highly-connected hubs of connectivity. These centrality measures may be ideal proxies for a habitat's connectivity importance and offer a useful pathway for integrating the connectivity process into SDMs (Foltête et al. 2012).

The main aims of this study are *i*) to illustrate how centrality metrics, suitable proxies for seascape connectivity, can be incorporated in traditional marine-based SDMs and *ii*) to test whether including connectivity in these models influences SDM predictions. This is the first study that uses a connectivity-enhance SDM approach in the marine environment to evaluate where, and to what degree, connectivity influences model predictions. We aim to integrate graph-based network metrics into SDMs for two types

of marine species, a benthic invertebrate and a pelagic fish. Here, we focussed on two widely distributed marine species living across the south-east coast of Australia. This region consists of a mosaic of habitats and home to a broad group of species. We focussed on the Australasian snapper *Chrysophrys auratus*, a species of fish, characterised by the ability to move across the region through the whole lifespan, and on a marine invertebrate, purple sea urchin *Heliocidaris erythrogramma*, where dispersal is limited to the larval stage. We quantify patch-level metrics using graph theory algorithms, defining centrality metrics for each habitat patch, and we integrate these metrics into our marine-based SDMs. We perform SDMs, comparing models' results and evaluating the contribution of seascape connectivity to models' performance. We assess the relative influence of centrality measures among other predictive variables identifying which metrics mostly influence SDMs. We investigate differences in the predicted geographic ranges of distribution, understanding whether these differences corresponded to critical areas for connectivity.

3.2 Methods

3.2.1 Study area

The spatial domain extends across the south-eastern coast of Australia (Fig. 3.1), from the south coast of New South Wales, including Tasmania and Victoria waters, and as far west as Kangaroo island in South Australia. This region consists of a mosaic of habitat, from hard to soft bottom habitat, populated by a range of diverse species. It spans from warm temperate waters in the north to cooler waters around Tasmania and contains one of the most diverse marine floral assemblage of the world's marine environments. This region is also important in terms of conservation values, including both protected species and protected areas, such as MPAs and marine reserves. (Bax and Williams 2000, Commonwealth of Australia 2015).

3.2.2 Study species

For this study we selected two representative species of the south-eastern Australian coast, the Australasian snapper, *Chrysophrys auratus* formerly known as *Pagrus auratus*, and the purple sea urchin, *Heliocidaris erythrogramma*. These species are widely distributed across south-east Australia waters. Snapper represents an important resource for commercial and recreational fisheries (Hamer et al. 2011). Purple sea urchin is well-known because of its role in altering coastal habitat towards a dominated urchin barren seascape (Ling et al. 2015). These species are usually associated with rocky reefs habitats (Vanderklift and Kendrick 2004, Pederson and Johnson 2006, Ling et al. 2010, Harasti et al. 2015, Terres et al. 2015).

We identified habitat patches using data available through Seamap Australia National Benthic Habitat Classification Scheme (Butler et al. 2017). Data from this dataset were downloaded at state-resolution then we merged data for South Australia (SA), Victoria (VIC), Tasmania (TAS) and New South Wales (NSW). The extent of the study domain is 1990 km x 1850 km. We performed a search through the Seamap Australia National Benthic Habitat Classification Scheme entire dataset to select only habitats that are classified as rocky reefs contained in the domain area, and we aggregated habitat patches that showed a very limited size (of order of less of 1 km^2) into a single patch, were possible. We defined 236 rocky reefs patches across the whole region.

3.2.3 Seascape connectivity for snapper (C. auratus)

To model adult snapper movements across the seascape and quantify habitat connectivity, we 1) built a cost surface layer based on magnitude and direction of oceanic currents, and 2) completed a least-cost path analysis to quantify seascape connectivity. The cost surface, required for the least cost path analysis (LCP), assumed fish movement was influenced by the magnitude and the direction of currents, with least cost following the direction of currents. Magnitude and direction of currents were derived from a global ocean circulation model (HYCOM, https://www.hycom.org) using the Marine

Geospatial Ecology Toolbox, MGET (Roberts et al. 2010) in ArcGIS® 10.5.1 (ESRI 2017). Data were aggregated into single annual cumulative cost layers, representative of currents magnitude and currents direction for the entire region. Following examples from terrestrial habitat, first we created two cost surfaces, one for currents' magnitude and one currents' direction, quantifying the increasing relative cost of moving across the seascape. Generally, due to the dominant eastward flow of currents, the cost of moving in this direction was less than that travelling westwards (Caldwell and Gergel 2013). We reclassified both layers and assigned a relative score representing the cost of travelling (Rayfield et al. 2010), ranging from 1 to 10, with a score of 1 representing the least cost, while 10 represented the greatest cost of travel, ten times more costly compared to cells with a value of 1. Finally, we combined the currents magnitude and currents direction cost surfaces, calculating the weighted mean and defining one cumulative movement cost surface among all study area, assuming parameters have equal weight. See Appendix 2 for further details.

We performed LCP analysis using Linkage Mapper 2.0.0 (McRae and Kavanagh 2011) a toolbox freely available for ArcGIS® 10.5.1 (ESRI 2017). To add realism to the model, we applied a maximum threshold of 100 km of travelled distance, based on maximum swimming linear distances recorded from acoustic tagging of snapper in South-east Australia (Fowler et al. 2017). We modelled only ecologically meaningful corridors among all habitat patches within the swimming range of snappers. Our LCP analysis resulted in maps representing seascape connectivity for adult snapper, with routes showing the least costly paths among all habitat patches (nodes). This LCP network was used to further quantify the structure of seascape connectivity (see Network analysis and spatial generalization of centrality measures, below, and more details on LCPs in Appendix 2).

3.2.4 Seascape connectivity for purple sea urchin (H. erythrogramma)

For marine invertebrates such as *H. erythrogramma*, movements across the seascape are largely determined by the larval dispersal phase. Connectivity for species like the

purple sea urchin is often quantified by modelling larval dispersal through the ocean and subsequent settlement into suitable downstream rocky reef habitat. We modelled larval connectivity using an existing spatially explicit biophysical marine connectivity model (Treml et al. 2012). In this model, we used 1) a map defining suitable rocky reef habitat patches, same data as above for snapper, where all the habitat patches are source and destination sites for larvae, 2) data describing the ocean currents (HYCOM) and 3) species-specific life history traits for *H. erythrogramma* (Appendix 2 Table A2.1), obtained from the literature (Okubo 1971, Williams and Anderson 1975, Rumrill 1990, Lamare and Barker 1999, Huggett et al. 2008, Swanson et al. 2012).

We simulated larval dispersal from 1992-2012 at a 3-hourly time-step, using all the available data for all spawning times. Clouds of larvae were released from source reef patches and the likelihood of larval settlement to all destination patches was estimated based on species-specific biological parameters and ocean characteristics. The model output was a dispersal matrix, recording the cumulative quantity of larvae released from each source patch that survived and settled to each destination patch, summarising across all modelled dispersal events and years, and scaled by the size of the available habitat area. The dispersal matrices were converted to migration matrices, **M**, representing the proportion of settled larvae arriving at each destination, *j* (column), that came from each source patch, *i* (row). The migration matrix was used to build a network of seascape connectivity, where rocky reef patches correspond to graph nodes and presence of larval connectivity was represented as graph edges. More details on model data, structure and outputs are available in Appendix 2.

3.2.5 Network analysis and spatial generalization of centrality measures

The species-specific connectivity data (the LCP output graph for snapper and the larval dispersal migration matrix for purple sea urchin) were used to quantify patch-level metrics representing patch importance, a common spatial ecology approach (Estrada and Bodin 2008, Bodin and Saura 2010, Carroll et al. 2012). All metrics were calculated

in R (R Core Team 2019 https://www.R-project.org/) with the 'igraph' package (Csardi and Nepusz 2006). For all patches, we calculated degree centrality, betweenness centrality and eigenvector centrality. Degree centrality quantifies the number of outgoing (out-degree) and/or incoming (in-degree) linkages to a subpopulation or node (Minor and Urban 2007), identifying local hubs of connectivity. Betweenness centrality defines the number of shortest paths that use a focal node (Newman 2005) and identifies critical habitat stepping-stones within the networks (Urban and Keitt 2001, Bodin and Norberg 2007, Bode et al. 2008, Estrada and Bodin 2008). Eigenvector centrality is a node-level metric which quantifies the overall importance based on connectivity with all other sites (Bonacich 1987) and identifies 'influential' nodes and have been shown to strongly correlate with metapopulation persistence (Watson et al. 2011).

SDMs require continuous explanatory variables, therefore we interpolated our centrality estimates across the seascape domain. The interpolation technique and distance used was dependent on each species' capacity to move throughout the seascape. In the case of the purple sea urchin, with its limited ability to move great distances following settlement, centrality values were interpolated locally only and assigned to all habitat cells in the focal rocky reef patch. For the snapper we assigned the corresponding centrality value to each patch cell, and due to the likelihood of movement at greater distances, we extrapolated the centrality measure into the neighbouring seascape using a negative exponential function with respect to distance. Consistent with the 100 km threshold used in the LCP analysis (Fowler et al. 2017), a maximum dispersal distance of 100 km corresponds to a probability of presence of $p = 0.05$ (Urban and Keitt 2001, Foltête et al. 2012). We multiplied this probability by the centrality value of the habitat patch. Where values from two or more patches intersect, the mean centrality value was used in these intervening areas. The result is a continuous centrality surfaces which can then be appropriately integrate into SDMs.

3.2.6 Species distribution modelling and comparison of models' performance

We developed SDMs for both species, one model including the species-specific centrality surfaces, and a second SDM without connectivity variables. Species occurrences data were derived from the Atlas of Living Australia, (Atlas of Living Australia, ALA, https://www.ala.org.au), and contained reliable occurrence data for species around Australia. For these species data, we included only species occurrences recorded inside our spatial domain. Environmental parameters were extracted from Bio-ORACLE (Tyberghein et al. 2012) using the Bio-Oracle package in R, which contains many marine data layers for ecological modelling. We selected a group of ecologically important parameters which were believed to contribute to the distribution of urchins and snapper. The environmental parameters used were mean bathymetry, mean sea water temperature, mean currents velocity, dissolved oxygen concentration, salinity, chlorophyll A concentration, primary production (measured as net primary productivity of carbon) and pH. Temperature, chlorophyll A concentration, primary production, currents velocity, dissolved oxygen data were summarised by the long-term monthly mean, pH, bathymetry, and salinity were downloaded from models or summarised in-situ measurements (more information on the environmental data are available in Appendix 2). In addition to these environmental data, we included the seascape connectivity layers of betweenness centrality, degree centrality and eigenvector centrality. Collinearity among predictors was quantitatively checked, and those with a Pearson correlation threshold of 0.7 or greater were identified and one was eliminated leaving the most ecologically meaningful parameter in the model. Collinearity among predictors is a known source of uncertainty, and when collinearity increases, the efficiency and statistical power of the model decrease (De Marco and Nóbrega 2018). Environmental and connectivity predictors used in the SDMs are mapped in Figure 3.1.

Among the many SDMs algorithms available, we used a popular machine learning method, Boosted Regression Trees, BRT (Elith et al. 2008). BRT is a form of logistical regression using decision trees and a boosting algorithm, an optimization technique that reduces predictive deviance by combining numerous trees into a single model. BRT has a powerful predictive performance and it has features such as, handling different type of predictors, missing data, moderate collinearity, and complex non-linear relationships (Elith et al. 2008, Cimino et al. 2020). We selected this approach because it also performs well for presence-only data (Elith et al. 2006). To model presence-only data with machine learning methods, a random sample of the background landscape is taken to represent unavailable 'absence' data. We followed the protocol for fitting BTR established within the 'dismo' package (Hijmans et al. 2017) in R, to understand which was the best predictive model and compare the significance of including seascape connectivity in the models. We built a training dataset and a test dataset by resampling presence and background data, allocating them to cross validation (cv) folds, applying a 5-folds cross validation procedure using the 'caret' R package (Kuhn 2008). We used cross-validation to evaluate the predictive power of the models and assessed performance using AUC-ROC, or area under the curve - receiver operating characteristics curve approaches. Then, we quantified the relative influence of seascape connectivity metrics with respect to all other environmental variables to assess their contribution in predicting species distributions. We also quantified pairwise interactions between environmental and connectivity variables, which is useful to define the most suitable environment for the species (Elith et al. 2008). To minimise overfitting and maximise predictive performance (Duan et al. 2014), we selected the single centrality metric with the largest relative influence in the model to remain in the model during fitting. These additional models help to understand the role of connectivity and whether the SDM predictions were influenced by the number of connectivity parameters included in the model.

Finally, we mapped the spatial distribution of species across the study area to visualize and quantify differences in spatial predictions. To evaluate if there is a statistical relationship between centrality measures and models' predictions, we tested them for correlation. Spatial indicators were used to quantify the differences in predicted habitat suitability from integrating connectivity or excluding connectivity. An overlay analysis was performed to identify areas within the SDM predictions that corresponded to critical connectivity areas, such as important habitat stepping-stones or hubs of local connectivity revealed in the network analysis.

3.3 Results

3.3.1 Seascape connectivity

We estimated seascape connectivity for both species and no consistent spatial trend existed between species, revealing different connectivity structures across the seascape, according to species-specific dispersal characteristics. All centrality measures showed some spatial consistency within species. Degree centrality, betweenness centrality and eigenvector centrality identified similar areas of high and low values, revealing that hubs of connectivity (high degree centrality), populations stepping-stones (high betweenness centrality) and critical nodes (high eigenvector centrality) largely matched and were clustered in similar locations. Purple sea urchin showed well-connected areas, high eigenvector centrality and degree centrality, across north and east Tasmania, eastern Victoria, and New South Wales coast, while South Australia nodes had weak connections with the rest of the domain (Fig.3.1). Purple sea urchin stepping-stone habitats are clustered in central and eastern Victoria. Snapper connectivity revealed high values of centrality for patches along north of Tasmania and central Victoria coasts, while areas on the eastern and western boundaries of the domain, along South Australia and New South Wales coasts, showed less connectivity (Fig 3.1).

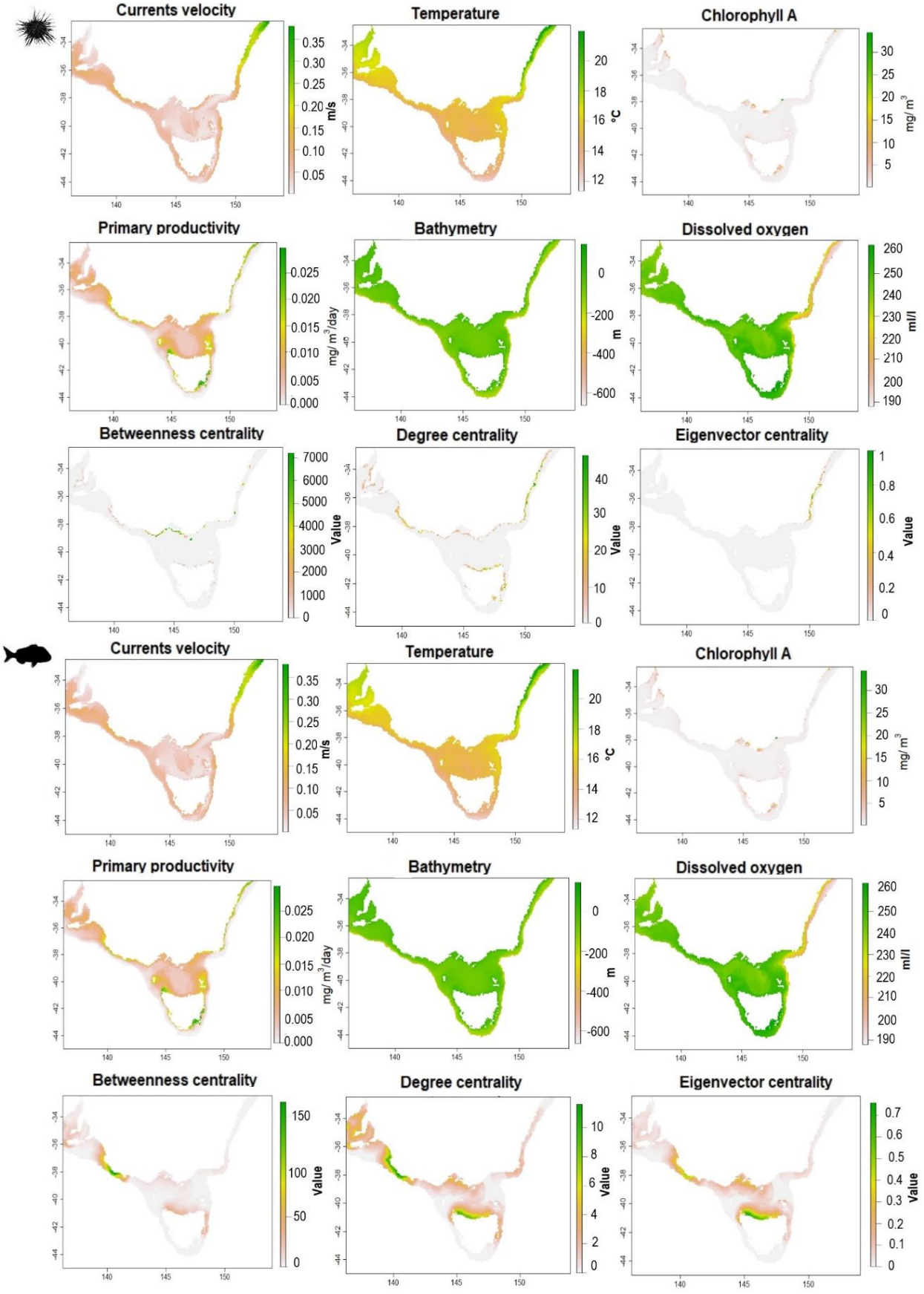

Figure 3.1: Maps of environmental and connectivity predictors used in the SDMs for purple sea urchin, *H. erythrogramma* (top), and snapper, *C. auratus* (bottom). All Maps in WGS84.

Seascape connectivity maps for both species are available in Appendix 2 Figure A2.2 and A2.3, while maps summarising node-level centrality metrics for betweenness centrality, degree centrality, eigenvector centrality can be found among SDMs predictors map (Fig. 3.1), in Figure 3.3a-3.3c or Appendix 2 Figure A2.9.

3.3.2 Species distribution modelling and comparison of models' performance

The final SDMs included centrality measures, and the environmental variables of mean sea water temperature, chlorophyll A concentration, primary production, bathymetry, dissolved oxygen concentration, currents velocity (more details on Bio-ORACLE dataset are available in Appendix 2 Table A2.3). Salinity and pH were removed for both species, due to strong correlation with other environmental variables. Note that centrality measures displayed low correlation with the environmental variables included in the models, although they displayed greater correlation between connectivity metrics, especially for snapper (Appendix 2 Figure A2.4-A2.5).

For both species, SDMs used a tree complexity of 5, a learning rate of 0.005, bag fraction of 0.75, 5 folds for tuning and a maximum of 10,000 trees. These settings were selected according to the recommendations in the literature (see Elith et al., 2008). The selected settings (i.e. learning rate and tree complexity) directly affect the number of optimal trees. As a result, by keeping the learning rate and tree complexity constant, we can optimise the number of trees to fit a good model. The settings were selected to aim for a model with a high number of trees (e.g. a few thousand), so the model can reliably estimate our response (Elith et al. 2008). The optimal model for sea urchin used 4300 trees for the model integrating connectivity and 5700 for the model without seascape connectivity. Both models showed good predictive performance with mean AUC score (0.95 ± 0.01) for both models, with and without connectivity. The optimal model for snapper used 4000 trees for the model integrating connectivity metrics and 3200 trees when seascape

connectivity was excluded. The mean AUC score was 0.91 ± 0.03 for the model with connectivity and 0.90 ± 0.03 without connectivity.

Centrality measures had some influence across both species with degree centrality revealed as the most important centrality measure. For the purple sea urchin SDM, connectivity contributed to a total of 18.6% to the final model, with degree centrality having the largest relative influence (8.2%), followed by betweenness centrality (7.2%) and eigenvector centrality (3.2%) (Fig. 3.2a). Degree centrality was more influential than current velocities (7.3%) and similar to chlorophyll A concentration (9.2%). Centrality measures showed pairwise interactions with several of the environmental variables. Eigenvector centrality had the strongest interactions with currents velocity and primary production, degree centrality had interactions with primary production and bathymetry, while betweenness centrality interacted with temperature and bathymetry. For snapper, all centrality measures have a lower relative influence than the environmental parameters, and contributed at most 17% to SDM predictions. Degree centrality was the most influential among the connectivity metrics, with a relative influence of 6.9%, followed by eigenvector centrality (6.4%) and betweenness centrality (3.6%) (Fig. 3.2C). Centrality measures interacted with environmental variables, and the strongest interactions were with temperature for degree centrality and eigenvector centrality, and bathymetry for betweenness centrality. For additional information, the pairwise interactions are plotted in Appendix 2 Figure A2.6.

We selected only the network-based metric with the largest influence to reduce the number of predictive variables and increase the predictive power. Degree centrality was selected for both species and we therefore compared the SDM results between model with and without degree connectivity included. The optimal sea urchin model used tree complexity of 5 and learning rate of 0.005 and 4700 trees for the model including connectivity. The mean AUC score was 0.95 ± 0.01, equal to the mean AUC of the model without connectivity. In this model the relative influence of degree centrality increased,

with 11.5% relative influence, more than currents velocity and similar to chlorophyll A concentration, primary production and dissolved oxygen (respectively 11.6%, 12.7% and 13.3%) (Fig. 3.2b). Degree centrality had some interactions with all the environmental parameters, but the strongest interactions were with bathymetry and high dissolved oxygen (Appendix 2 Figure A2.6). For snapper, when selecting degree centrality only, the optimal model used tree complexity of 5 and a learning rate of 0.005 and 3300 trees. The mean AUC score was 0.91 ± 0.03 when including degree centrality and 0.90 ± 0.03 without degree centrality. The relative influence of degree centrality increased in this model up to 9.5%. In this model degree centrality had more influence than primary productivity (7.8%) and bathymetry (7.6%), and comparable to dissolved oxygen concentration (9.7%) (Fig. 3.2d). Degree centrality interacted with all environmental variables, particularly with warm temperature and high bathymetry (Appendix 2 Figure A2.6).

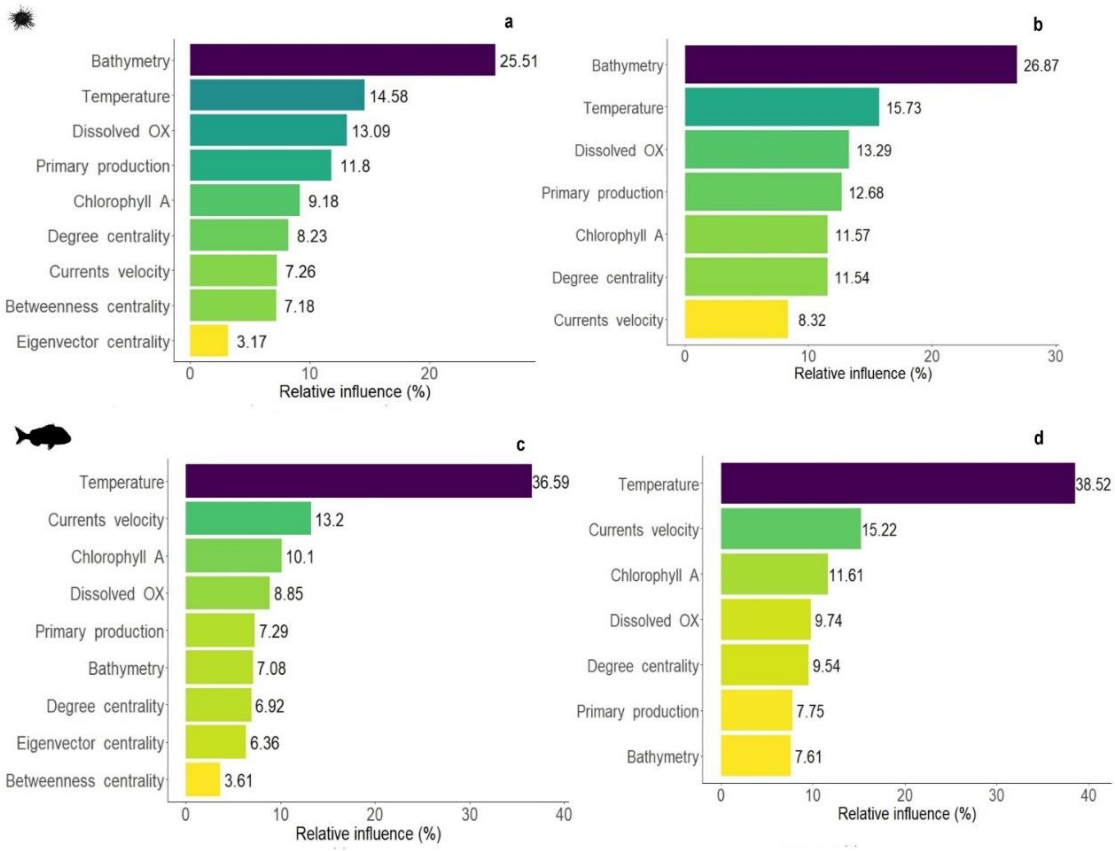

Figure 3.2: Relative influence of environmental parameters and connectivity metrics on SDM results for sea urchin *H. erythrogramma* (top) and snapper, *C. auratus* (bottom). Fitting BRT including all centrality measures (plots a and c) or selecting only the most influential variable degree centrality (plots b, d). Relative influence expressed in percentage (i.e., total influence sums up to 100%).

We predicted species distribution and habitat suitability and we compared maps of habitat suitability, highlighting differences in species range (see Appendix 2 Figure A2.7 for habitat suitability spatial predictions for the models with and without all connectivity metrics). Despite these models predicted somewhat different species distribution range, when tested for pairwise correlation, the differences in spatial distribution showed low correlation with the seascape connectivity metrics. Pairwise correlation of the differences in habitat suitability between the two models (with and without connectivity) and each centrality metric is low for purple sea urchin (correlation coefficient of differences in spatial distribution and betweenness centrality r = 0.2, degree centrality r = 0.3, eigenvector centrality r = 0.2, for the degree centrality only model r = 0.3), and it was small for snapper (correlation coefficient of differences in spatial distribution and

betweenness centrality r = 0.1, degree centrality r = 0.2, eigenvector centrality r = 0.2). Results of pairwise correlation can be found in Appendix Figure A2.8.

The impact of including (or not) connectivity in the SDM predictions revealed geographic structure in terms of the increase or decrease in modelled habitat suitability Fig. 3.3). Mapped differences in habitat suitability between models with and without including degree centrality for connectivity showed species-specific differences. For the purple sea urchin, most areas showed a decrease in habitat suitability when connectivity was included (i.e., these areas became less suitable in the model), particularly for Port Phillip Bay in Victoria and Spencer Gulf in South Australia and areas far from the coastline (Fig. 3.3). Areas of increased habitat suitability were smaller and focused around 'central' rocky reefs (Fig. 3.3b). located primarily around high degree centrality sites in central and western Victoria, north and east Tasmania and New South Wales (Fig. 3.3a). Rocky reef patches with high betweenness centrality and eigenvector centrality did not corresponded to key zones revealed from SDMs results (Appendix 2 Figure A2.9). Snapper habitat suitability predictions decreased for models including connectivity, especially for areas far from the coast. Areas associated to high degree centrality largely corresponded to higher suitability, particularly along north Tasmania, central Victoria and on the border between Victoria and New south Wales and South Australia habitats (Fig. 3.3d). Areas of high eigenvector centrality in central Victoria and north Tasmania also correspond to high degree centrality, while no consistent spatial trend for betweenness centrality (Appendix Figure A2.9).

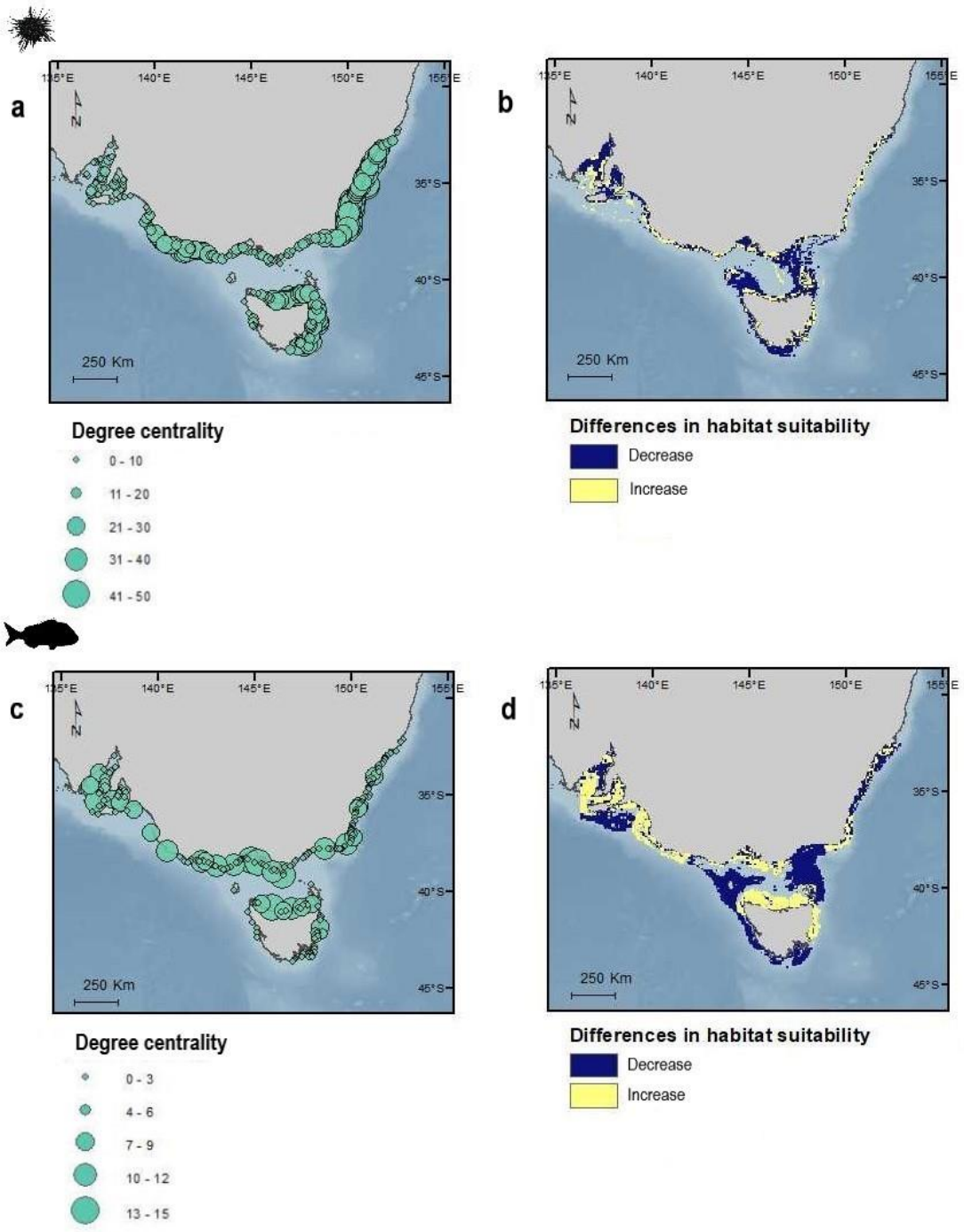

Figure 3.3: Maps showing the geographic distribution of degree centrality (a and c) and differences in spatial predictions of habitat suitability (b and d) for sea urchin *H. erythrogramma* (top) and snapper, *C. auratus* (bottom). Degree centrality (a and c) is shown as dots corresponding to the habitat patches centroids. Values of habitat suitability are classified as 'Increase' when predicted habitat suitability is larger for SDM incorporating connectivity compared to the SDM without connectivity. Values are classified as 'Decrease' when predicted habitat suitability is lower for SDM incorporating connectivity compared to the SDM without connectivity. Maps in WGS84.

3.4 Discussion

Seascape connectivity is essential for ensuring long term species persistence and considered significant in determining the distribution of species, and as a result is expected to have a significant influence on predicting species distribution with SDMs. Graph-based connectivity metrics moderately influence SDMs and degree centrality appeared to be the most important metric among the centrality measures.

Machine learning methods such as BRT offer the advantage of exploring not only model performance but also the extent of each variable's relative influence. If predictors have no contribution, the model algorithm calculates the relative variable influence as zero or near zero. In our species distribution models, connectivity was an important predictor, yet the influence on predictions was not as strong as several environmental variables, such as temperature, currents and chlorophyll. As a result, if connectivity metrics were omitted, the resultant models would have resulted in different habitat suitability predictions, especially affecting their spatial range. When we included the most influential connectivity metric, degree centrality, the influence of connectivity on SDMs predictions increased. In both species the area under the curve (AUC-ROC) of the models was close to one, indicating that the model performance and predictions were very good (Jiménez-Valverde 2012). AUC scores were similar for models with and without connectivity, suggesting no differences in the models' predictive performance, however the spatial range of habitat suitability predictions differed among the models, indicating that differences between the models exist. This apparent contradiction may be explained by the high accuracy typical of machine-learning algorithms (Bucklin et al. 2014). Independent to connectivity, the main influential environmental drivers were bathymetry and temperature for purple sea urchin, and temperature and currents velocity for snapper (Fig. 3.2), commonly found to have the largest influence across marine-focused SDMs (Reiss et al. 2011, Tyberghein et al. 2012).

Degree centrality was the most significant among the centrality measures included in the model. Degree centrality quantifies the incoming and outgoing connections of a node, identifying hubs of connectivity, and it is critically important for benthic species dispersing only during the larval stage, representing the quantity of downstream larval connectivity, identifying important sources and destinations of larvae (Treml et al. 2015, Zamborain-Mason et al. 2017). Hotspots of connectivity ensure persistence in marine metapopulations (Zamborain-Mason et al. 2017, Cecino and Treml, in press), and in this work resulted also significant in defining the species spatial distribution, showing that highly central nodes identified areas of greater habitat suitability. Connectivity variables had interactions with the environmental parameters revealing that the most suitable habitat also corresponded to critical habitats for connectivity. Quantifying interactions among variables helps to define more clearly which is the most suitable habitat for the species (Elith et al. 2008), showing how the effect of one environmental predictor on a species changes according to the levels of other predictors. Recognizing these environmental interactions is critical to assess changing environmental conditions, and integrating environmental and ecological interactions produces more robust SDMs and improved understanding of causes of species' distributions (Guisan et al. 2006). The results for degree centrality indicate that the sea urchin is predicted to occur in shallow waters, around high oxygen concentrations and in hubs of connectivity (degree centrality values between 10 and 20 ecological linkages). Snapper, in contrast, is predicted to be found around hubs of connectivity (degree centrality of value 4 and 8), and in in warm shallow waters.

When incorporating connectivity in SDM's spatial predictions revealed reduced suitability primarily for deep waters, defining a more restricted geographic range for snapper and sea urchins, limiting the distributions to shallow coastal waters. In addition, the inclusion of connectivity in the SDMs increase the suitability around hubs of connectivity. Hubs of connectivity, habitat with high degree centrality, were identified in central Victoria, in

proximity of Wilson Promontory particularly for snapper population, key habitats for metapopulation persistence across species and corresponding to marine protected areas and reserves (Cecino and Treml, in press). This region significance is well known and includes several ecological features, which define the structure of the coastal communities. For example, Eastern Victoria was identified as potential biogeographic break for many taxa often associated with limits in species' ranges and changes in community assemblages (Colton and Swearer 2012). Habitat patches in northern Tasmania may also be essential for ensuring connectivity between Tasmania and Victoria coasts. Eastern Tasmanian hotspots have also been identified as a key ecological feature in the South-east Marine Regional Profile (Dambacher et al. 2012). This oceanographic mixing zone where subantarctic water masses, driven by westerly winds, interact with eddies from the East Australian current and lead to enhanced productivity, phytoplankton blooms and mass aggregations of coastal temperate taxa (Hosack and Dambacher 2012, Commonwealth of Australia 2015). The hubs of connectivity we identified for snapper in South Australia are also consistent with key habitat sites for the snapper fishery and for spawning grounds (Fowler and Jennings 2003).

Both study species used for this work have somewhat limited dispersal ability, especially in relationship to the extent of the model domain. This choice was made due to high computational requirements necessary when modelling species with longer larval dispersal duration or a much more extended swimming capacity. However, further research effort may focus on species where dispersal can potentially be more critical, and more influential in determining species' distributions, particularly for species with larger home ranges, swimming capacity, or extended larval dispersal periods.

Collecting data on the presence of marine species is challenging and expensive, and this may have created artifacts with influence our results. Species occurrence data and environmental parameters were not necessarily collected for the same temporal extents,

which often did not correspond to the temporal extent of connectivity models. Occurrence data collected from the Atlas of Living Australia include data from early 1900s, while environmental data were based on information collected from 2000 (full details on temporal extent of environmental parameters can be found in the Appendix 2) and the connectivity models used ocean current data for the period 1992-2012. This might result in an underestimation of the importance of connectivity and its influence on model predictions. The lack of true absence data may be another limitation when developing SDMs, especially for marine species, where presence data sampling is biased towards coastal waters and areas near ports (Robinson et al. 2011). Though we addressed this limitation to some degree by choosing BRT methods, an appropriate procedure when working with species presence and pseudo-absence data (Cerasoli et al. 2017). BRTs outperform other approaches like generalized linear and additive models, as well as combine many decision trees to improve model's accuracy, include stochasticity, reducing variance and improving predicting performance (Cimino et al. 2020). That said, BRTs are often criticised for their tendency to overfit models. Other limitations common to SDMs include changes in habitat conditions due to climate change and human impacts, and attempting to predict species around range shifts. For exploited taxa like snapper, the distribution of fishing effort likely influences species distribution and presence/absence data. Our models could potentially be improved by including data on fishing pressure and environmental changes to producing more realistic and reliable spatial predictions.

In comparing two different marine taxa, centrality measures proved to be appropriate and flexible proxies to describe seascape connectivity and can effectively identify hotspots and stepping-stones of connectivity. Using these patch-level metrics to describe seascape connectivity is an efficient way to incorporate connectivity information into marine-based SDMs. Centrality metrics proved to have a significant contribution in determining the spatial distribution patterns and the most suitable habitat patches.

Connectivity is fundamentally important for marine species and should be included in models of species distribution or abundance. Our new methods chart a pathway forward for efficiently incorporating connectivity into marine-based SDMs and open the door for exploring the broader influence of dispersal and movement on species distributions in general.

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Chapter 4

Local connections and the larval competency strongly influence marine metapopulation persistence

Abstract

The relationship between metapopulation stability and connectivity has long been investigated in ecology, however, most of these studies are focussed on theoretical species and habitat networks, having limited ability to capture the complexity of real-world metapopulations. Network analysis became more important in modelling connectivity, but it is still uncertain which networks metrics are reliable predictors of persistence. Here we quantify the impact of connectivity and larval life history on marine metapopulation persistence across the complex seascape of southeast Australia. Our work coupled network-based approaches and eigenanalysis to efficiently estimate metapopulation-wide persistence and the subpopulation contributions. Larval dispersal models were used to quantify species-specific metapopulation connectivity for five important fisheries species, each summarised as a migration matrix. Eigenanalysis helped to reveal metapopulation persistence and determine the importance of node-level network properties. Across metapopulations, the number of local outgoing connections was found to have the largest impact on metapopulation persistence, implying these hub subpopulations may be the most influential in real-world metapopulations. Results also suggest the length of the pre-competency period may be the most influential parameter on metapopulation persistence. Finally, we identified two major hotspots of local connectivity in southeast Australia, each contributing strongly to multi-species persistence. Managers and ecologists would benefit by employing similar approaches in making more efficient and more

ecologically informed decisions and focusing more on local connectivity patterns and larval competency characteristics to better understand and protect real-world metapopulation persistence. Practically this could mean developing more marine protected areas at shorter distances and supporting collaborative research into the early life histories of the species of interest.

4.1 Introduction

Many terrestrial and marine populations can be viewed as metapopulations due to their fragmented distribution, as a result of natural habitat characteristics or because of anthropogenic landscape changes (Hanski 1998). Understanding metapopulation persistence in these patchy landscapes is critical for conservation planning where the identification of vulnerable, as well as the most influential, subpopulations is fundamental in the development of cost-effective and ecologically meaningful management decisions (Hanski and Ovaskainen 2000, Hanski and Ovaskainen 2003). Conservation biologists and wildlife managers can estimate population persistence and viability through mathematical models to quantify the effectiveness among a suite of alternative management options (Fieberg and Ellner 2001). In metapopulation theory, metapopulations can persist when there is stability between the loss of subpopulations and the establishment of new subpopulations in unoccupied areas (Hanski 1998). In spatially structured metapopulations, patch size and the rate of movements among patches, or connectivity, are fundamental to determining persistence in fragmented landscapes (Hanski 1998, Sale et al. 2006). In this context, metapopulation persistence largely depends on the dispersal dynamics between each pair of patches or subpopulations (Adler and Nuernberger 1994, Figueira and Crowder 2006).

Metapopulation persistence can be estimated through various numerical approaches, such as the metapopulation mean lifetime (Frank and Wissel 1998, Kininmonth et al. 2010) or estimating local extinction and colonization rates (Etienne and Heesterbeek 2001). Another common approach estimates the metapopulation growth rate through a matrix population model (Caswell 2001). The dominant eigenvalue, or spectral radius (λ), of the Leslie matrix represents the persistence condition, where growing (i.e., persisting) populations have values greater than one (Hanski and Ovaskainen 2000, Hanski and Gaggiotti 2004). This metapopulation growth rate estimate has been regularly used to quantify persistence in many aquatic (Mari et al. 2014, Bertuzzo et al. 2015), terrestrial (Saikkonen et al. 2002, Touloumis and Stamou 2009), and marine (Armsworth 2002, Williams and Hastings 2013) systems.

In many cases, persistence estimates for age-structured metapopulations rely on models where subpopulation viability was based on the intrinsic growth rate of the individual patches alone (Hastings and Botsford 2006a). Yet, to develop a more realistic estimate of subpopulation persistence in complex landscapes, the implications of immigration and emigration dynamics on persistence must also be considered. As a result, more recent work in metapopulation dynamics has evolved to include realistic dispersal and migration estimates between subpopulations explicitly (Hanski and Ovaskainen 2003, Figueira and Crowder 2006, Sale et al. 2006, Figueira 2009, Shima et al. 2010, Puckett and Eggleston 2016). Metapopulation models, now including local and non-local dispersal dynamics can be summarised in an appropriately structured migration matrix, representing the proportion of individuals that successfully settle to a patch that came from each source patch (Artzy-Randrup and Stone 2010). In this dispersal-dominated context, persistence is controlled by the magnitude of the dominant eigenvalue (λ) of the connectivity matrix, when this represents a strongly connected network (Artzy-Randrup and Stone 2010).

The continuous marine environment provides the potential for long-distance dispersal among marine populations, yet the intensity of realised dispersal and the spatial scale of connectivity is often more local and highly context dependent (Cowen et al. 2000, Mora and Sale 2002, Bode et al. 2019). For many coastal species, the larval stage dominates the dispersal dynamics, determining the connections among patches. As a result, understanding the early life history characteristics is essential for determining the dynamics of population connectivity. Here, we explicitly refer to connectivity as the movement of individuals as larvae, among habitat patches or subpopulations (Cowen and Sponaugle 2009), a critical process contributing to subpopulation growth or decline and metapopulation persistence.

Many biological and physical processes drive larval dispersal patterns (Cowen and Sponaugle 2009, Shanks 2009, Treml et al. 2015a). In marine systems, larval dispersal outcomes are strongly influenced by the extent of pelagic larval duration (PLD) and competency window (Baums et al. 2006, Levin 2006, Shanks 2009). In addition, larval mortality, and post-

settlement mortality is critical as it causes significant fluctuations in settlement and recruitment (Houde 1989, White et al. 2014). Experimental and laboratory work has also shown that behaviour during the larval stage may alter dispersal trajectories, depending on the local seascape setting and larval traits (Paris et al. 2007). Yet larval biology alone is not enough to understand realised dispersal patterns in marine environments, as ocean currents act on the larvae and can greatly influence outcomes (Largier 2003).

Numerous approaches exist to quantify and summarise larval connectivity for real world metapopulation networks (Botsford et al. 2009, Burgess et al. 2014, Holstein et al. 2014, Samsing et al. 2017); among them, graph theory was used to analyse and visualize the network-based connectivity (Treml et al. 2008, Thomas et al. 2014). Graph theory is an appropriate framework to use to quantify the spatial and temporal patterns in larval connectivity because it can efficiently accommodate complex real-world networks (Urban and Keitt 2001, Treml et al. 2008). Metapopulation connectivity summarised in the migration matrix can be visualised and analysed through these network-based algorithms. An important insight from the study of metapopulations is that the dominant eigenvalue of this matrix estimates metapopulation persistence (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). The relationship between the metapopulation network structure and metapopulation persistence has been extensively investigated to understand the ecological significance of network metrics. For example, asymmetry is a network characteristic that quantifies the probability that two nodes in a network are equally connected in both directions (Shtilerman and Stone 2015). Real-world metapopulations are frequently asymmetric, especially in marine systems, where dispersal is driven by directional current, with asymmetric metapopulations being more vulnerable to extinction (Bode et al. 2008, Vuilleumier et al. 2010, Kleinhans and Jonsson 2011, Shtilerman and Stone 2015). Directed networks are often heterogenous where the rate of immigration and emigration to/from a habitat patch is not equal. Heterogeneity has been shown to have mixed effects on metapopulation persistence (White et al. 2010, Shtilerman and Stone 2015). Similarly, network cycles have been shown to influence

metapopulation persistence, where loops of connections provide multigenerational (and multi-patch) pathways of recruitment back to the origin patch (Artzy-Randrup and Stone 2010). Various centrality measures have also been explored to quantify patch-level importance in metapopulation dynamics (Bodin and Norberg 2007, Bode et al. 2008, Estrada and Bodin 2008, Watson et al. 2011). Self-seeding has a fundamental role in local metapopulation dynamics (Hastings and Botsford 2006a, b), and network metrics accounting for self-connections are better predictors of metapopulation persistence for real-world networks (Pascual-Hortal and Saura 2006, Zamborain-Mason et al. 2017).

Much of this previous work was based on theoretical models, however real-world applications are required to help us understand real system dynamics and how to best inform marine conservation and management decisions. Here, we used network models to represent connectivity of several complex real-world marine metapopulations, where a mosaic of habitat patches, defined as nodes or vertices, are connected through dispersal linkages, called edges (Urban et al. 2009). The dispersal linkages are determined by the presence of ecologically-significant larval dispersal and settlement. As a result, our realistic and geographically-referenced metapopulation networks were characterised by directional dispersal linkages, each connection with a dispersal strength. These resultant marine metapopulation networks are broadly representative of many other real-world networks in marine environments where the movements of larvae are strongly influenced by biological traits and ocean currents (Bode et al. 2008, Mitarai et al. 2009, Berglund et al. 2012).

The primary aim of this study is to understand the link between metapopulation persistence and connectivity, from patch-level properties to network-wide metrics. In addition, we identify the relative importance of subpopulations or patches which contribute the most to metapopulation persistence within the seascape of Southeast Australia. Finally, we also explore the influence of species-specific life history traits on the network measures and metapopulation persistence. We illustrate a powerful and straight-forward approach to evaluating patch contribution to metapopulation persistence for five real-world marine

metapopulations. We combined network-based and matrix-based approaches for quantifying metapopulation persistence and identifying species-specific habitat patches critical to this persistence. These priority sites, as well as the multi-species geographic hotspots can help inform marine management efforts throughout this complex seascape.

4.2 Methods

4.2.1 Study area

The South-east Marine Region of Australia is one of the six marine managed regions in Commonwealth waters around Australia. This region extends from the south of New South Wales (NSW) through the coast of Victoria (VIC) and Tasmania (TAS) to Kangaroo Island in South Australia (SA). It consists of a mosaic of habitat, from hard to soft bottom habitat, populated by a range of diverse species, and includes the biodiversity hotspot of Wilsons Promontory marine park. (Bax and Williams 2000, Commonwealth of Australia 2015). The spatial domain for this study (Fig. 4.1) was defined by buffering this Marine Region along South Australia and New South Wales coasts by 200 km to include subpopulations beyond our focal seascape to avoid edge effects in the analysis and results.

4.2.2 Study species

For this study, we selected five representative and economically important species of the south-eastern Australian coast, also representing a broad range of dispersal capacities. We selected species across a wide range of life history characteristics to build a broad understanding of the relationship between network characteristics and metapopulation persistence, yet focus on locally important taxa to maximise local relevance. The blacklip abalone, *Haliotis rubra*, long-spined sea urchin, *Centrostephanus rodgersii*, and purple sea urchin, *Heliocidaris erythrogramma*, are three important marine invertebrates inhabiting rocky reefs, characterised by differences in larval traits and spawning seasons traits, and are widely distributed throughout the region. *H. rubra* also represents one of the most important species for Australian commercial fisheries, producing 2578 tons of abalone for export, for a value of 174 million dollars each year (Savage 2015). Both *C. rodgersii* and *H. erythrogramma* are

extensively studied for their role as ecosystem engineers in the nearshore rocky reef kelp systems throughout Australia (Pederson 2003, Pecorino 2012). They also represent two growing fishery species in this area (King et al. 1994, Blount and Worthington 2002). We also modelled two species of fish, the snapper, Chrysophrys auratus formerly known as *Pagrus auratus*, and the King George whiting, *Sillaginodes punctatus*; the former fish species with somewhat limited larval dispersal, the latter with greater dispersal capability. C. auratus and S. punctatus are widely distributed across the South-East Marine Region of Australia, where both are important taxa in commercial and recreational fisheries (Hamer et al. 2011, Jenkins et al. 2016).

4.2.3 Quantifying marine metapopulations connectivity

A series of 1441 larval dispersal simulations, for a total of 788 habitat patches, were completed for the study species. We used an existing spatially explicit biophysical model (Treml et al. 2012) to simulate larval dispersal for all species using the University of Melbourne high performance computing cluster, Spartan (Lafayette et al. 2016). The data requirements of this model are 1) a map of habitat patches or subpopulations; 2) data describing the ocean currents; and 3) information on species demographic parameters and dispersal strategies (e.g., spawning timing, larval competency and mortality rates). Each of these are described in detail, below.

4.2.3.1 Habitat patches

Spatial information on the distribution of the metapopulation within the seascape is necessary to define the habitat patches where each subpopulation resides within the model (Treml et al. 2012). Habitat data for this study were developed using ArcGIS® 10.5.1 software (ESRI 2017) and environmental data from various sources (see below). The extent of the area is 1990 km x 1850 km using 5 x 5 km cell size, consistent with the resolution of best-available hydrodynamic data.

Species distribution models (SDMs) were used to estimate habitat suitability for *H. rubra*, *H. erythrogramma* and *C. rodgersii* and to identify unique habitat patches. We built the habitat

suitability maps using species presence data from the Atlas of Living Australia occurrence (Atlas of Living Australia, ALA, https://www.ala.org.au). Environmental parameters for the SDMs consisted of bathymetry (General Bathymetric Chart of the Oceans, GEBCO, https://www.gebco.net), chlorophyll concentration, monthly average sea surface temperature, and the magnitude of currents, all freely available from AODN portal (https://portal.aodn.org.au, specifically Beggs et al. 2010, Johnson et al. 2013, http://imos.aodn.org.au/oceancurrent). Other habitat data used to build the SDMs were seabed gravel and sand content, available from data.gov.au for the entire Australian Exclusive Economic Zone (Jin Li et al. 2010, 2011).

We modelled *C. auratus* and *S. punctatus* habitat patches by mapping the species-specific location of spawning and settlement (Fowler et al. 2000, Jenkins et al. 2000, Fowler and Jennings 2003, Hamer et al. 2011, Hamer and Conron 2016, Jenkins et al. 2016). Despite the wide distribution in adult stages, snapper's spawning and settlement locations are concentrated in the Spencer Gulf region for South Australia and Victorian estuaries and bays, available from the Estuary Watch Victoria database, (Estuary Watch Victoria, http://www.estuarywatch.org.au).The identification of source patches for the King George whiting was derived from published spawning areas (Fowler et al. 2000, Jenkins et al. 2000, Jenkins et al. 2016), while destinations patches were identified based on settlement habitat preferences and mapped using data on presence of seagrass beds, available through Seamap Australia National Benthic Habitat Classification Scheme (https://seamapaustralia.org, Butler et al. 2017). Further details on habitat patches maps and SDMs can be found in Appendix 3.

4.2.3.2 Oceanographic model

We modelled the larval movements between patches using ocean current data derived from a global circulation model (HYCOM, https://www.hycom.org). Data are available from 1992-2012 at a 3-hourly time-step, and all available data were used in this study. We simulated the dispersal of each species' spawning season for all years of data. In the model, clouds of larvae

were released from source patches and the likelihood of larval settlement to all destination patches was estimated based on the species' biological parameters (below). Further details on the larval dispersal model can be found in Appendix 3.

4.2.3.3 Species' parameters

The biological parameters included in the biophysical larval dispersal model were maximum PLD, the larval competency window, larval mortality, the species' spawning period based on previously published data (Williams and Anderson 1975, Prince et al. 1987, Laegdsgaard et al. 1991, Francis 1994, Jenkins and May 1994, McShane 1995, Fowler et al. 1999, Fowler and Jennings 2003, Litaay and De Silva 2003, Huggett et al. 2005, Huggett et al. 2008, Swanson et al. 2012, Hamer and Conron 2016), larval settlement rates, and other biophysical parameters such as sub-scale turbulence (Table 4.1). Other parameters were held constant across species due to unknown or unjustifiable differences such as homing behaviors and vertical migration strategies. For a review of sensitivities and further modelling details, see (Treml et al. 2012).

Table 4.1: Demographic species-specific parameters included into the marine connectivity model.

Parameter	***Haliotis rubra* (blacklip abalone)**	***Heliocidaris erythrogramma* (purple sea urchin)**	***Centrostephanus rodgersii* (long spined sea urchin)**	***Chrysophrys auratus* (Australasian snapper)**	***Sillaginodes punctatus* (King George whiting)**
Depth	0-10m[1]	0-35m[5]	0-30m[9]	0-50m[12]	0-200m[16]
Max PLD	12 d[2]	5 d[6]	155 d[10]	32 d[13]	170 d[17]
Competency period	6.5 to 12 d[3]	3 to 5 days[7]	105 to 155 d[10]	27 to 32 d[14]	75 to 170 d[17]
Pre-competency period (Length)	2.5 to 6.5 d (4 d)[3]	1.5 to 3 d (1.5 d)[6]	77 to 105 d (28 d)[7]	18 to 27 d (9 d)[14]	45 to 75 d (30 d)[17]
Spawning period	August to January[4]	December and March [8]	June to September[11]	November to February[15]	March to May[18]
Diffusivity	100 m^2s^{-1} [19]	100 m^2s^{-1} [19]	100 m^2s^{-1} [19]	100 m^2s^{-1} [19]	50 m^2s^{-1} [19]
Larval settlement likelihood	90%	90%	98%	90%	98%
Larval mortality	5% per day[20]	16% per day[20]	16% per day[20]	26% per day[21]	25% per day[21]

References: 1. Morgan and Sheperd 2006; 2. McShane 1995; 3. Prince et al. 1987; 4. Litaay and De Silva 2003 5. Huggett et al. 2008; 6. Williams and Anderson 1975; 7. Swanson et al. 2012; 8. Williams and Anderson 1975, Laegdsgaard et al. 1991; 9. Pecorino 2012; 10. Huggett et al. 2005; 11. King et al. 1994, Byrne et al. 1998, Huggett et al. 2005; 12. Kailola et al. 1993, Froese and Pauly 2000 http://www.fishbase.org; 13. Francis 1994; 14. Fowler and Jennings 2003; 15. Hamer and Conron 2016; 16. Jenkins et al. 2016; 17. Jenkins and May 1994; 18. Fowler et al. 1999; 19. Okubo 1971; 20. Rumrill 1990, Lamare and Barker 1999; 21. Houde 1989.

Larval production within habitat patches was scaled by available habitat area, where the patch size was the explicit proxy for reproductive output from the subpopulation (Bunn et al. 2000, Urban and Keitt 2001, Treml et al. 2012). Larval mortality was incorporated into the model as a Weibull function, capable of representing variants on the exponential decay function, believed to be common in many species (Connolly and Baird 2010), and informed by previous studies on similar taxa (Houde 1989, Rumrill 1990, Lamare and Barker 1999).

4.2.4 Connectivity matrices and metapopulation persistence

The output of the marine connectivity model for each species was a dispersal matrix, recording the cumulative quantity of larvae released from each source patch that survive and settled to each destination patch, summarising across all modelled dispersal events and years. The dispersal matrices were converted to migration matrices, **M**, entries of which represent the proportion of settled larvae arriving at each destination, *j* (column), that came from each source patch, *i* (row) and the diagonal of the matrix represents self-recruitment. Matrices diagonals were included in the analysis. A threshold of 0.001 was applied to the migration matrices, setting any value below this threshold to zero. This focuses the analysis on only ecologically meaningful connections which contribute more than 0.1% of total settlement of larvae to a destination, a level consistent with values found for a range of fisheries stock-recruitment dynamics studies (Myers et al. 1999). We used these migration matrices to visualise and analyse the network structure of the metapopulations in relation to persistence, which was summarised by the matrices' dominant eigenvalue (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). We quantified metapopulation persistence at the component level (or fully connected sub-graph), a condition required to satisfy the Perron-Frobenius

Theory (Li and Schneider 2002). The approach used in Artzy-Randrup and Stone, 2010 defines metapopulation persistence as the product of the largest eigenvalue and the reproductive output, using a symmetric adjacency matrix to describe connectivity. We modified this approach and maintained the asymmetries to preserve directions in connectivity, yet convert the strong ecological migration matrices into binary adjacency matrices as per Artzy-Randrup and Stone (Artzy-Randrup and Stone 2010), thereby focussing the analysis on the topology or structure of the ecological metapopulation networks. The elements in the adjacency matrix are one when the nodes are strongly connected and zero in the absence of an ecologically-significant connection (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). With this assumption we omitted the strength of connectivity, represented by the edge weight, but we maintained edges directions. As a result, our migration matrices focus exclusively on strong ecologically-significant connectivity to and from all patches in the system. With this required generalization our matrices were non column-stochastics, resulting in informative dominant eigenvalues, often greater than 1, allowing the species' migration matrix eigenvalues to be quantitatively compared.

4.2.5 Network analysis

To identify the most critical subpopulations influencing metapopulation persistence we performed network analysis in R version 3.6.2 (R Core Team 2019 https://www.R-project.org/) and the 'igraph' package (Csardi and Nepusz 2006). We built graphs from these matrices, where nodes in our networks represented the habitat patches and linkages quantified the dispersal likelihood between all sources and destinations. We used a suite of node-level and network-level metrics to quantify the influence of patches on metapopulation persistence (Appendix 3 Table A3.1). We calculated a variety of centrality measures. Degree centrality quantifies the number of outgoing (out-degree) and/or incoming (in-degree) linkages to a subpopulation or node, extended to weighted in-degree and weighted out-degree for analysing weighted networks. Betweenness centrality a measure based on the number of shortest paths going through a node (Newman 2005) which identifies critical habitat stepping-stones within

the networks (Urban and Keitt 2001, Bodin and Norberg 2007, Bode et al. 2008, Estrada and Bodin 2008). Closeness centrality, quantified as the reciprocal of the sum of the shortest paths between all nodes and all other nodes (Freeman 1978), was used to identify core or central subpopulations (Gonzalez et al. 2010, Cabral et al. 2016). Eigenvector centrality (Bonacich 1987) which identifies centrally important nodes, assigning relative scores based on the connections with other high-scoring node, and has been shown to strongly correlate with metapopulation persistence in a benthic boundary current system (Watson et al. 2011). Alpha-centrality as an eigenvector-like measure of centrality for asymmetric networks (Bonacich and Lloyd 2001) was also calculated.

We also quantified network-level metrics such as network asymmetry using asymmetry gamma, γ, an index of the pair-wise difference in directionality among each pair of subpopulations defined as the ratio of symmetric connections among all connections (Kleinhans and Jonsson 2011). We estimated network heterogeneity as the coefficient of variation of degree (Zamborain-Mason et al. 2017) measuring the unbalance between incoming vs outgoing connections to/from a patch. Finally, we quantified the number of cycles (of length 3) in the networks counting the cycle occurrence in each graph (Fischer et al. 2015) to help evaluate the influence of these feedback loops on metapopulation persistence (Artzy-Randrup and Stone, 2010). For additional details on network-level and node-level metrics see Appendix 3, Table A3.1.

To explicitly quantify the influence of these network-based proxies on metapopulation persistence, we removed the top 5%, 10% and 20% of the most important nodes as determined by patch area and by each node-level metric and recalculated metapopulation persistence (largest eigenvalue). We explored the effect of habitat loss by gradually removing the largest habitat patches. The impact of important subpopulations (e.g., those with high degree or high eigenvector centrality) in terms of the decrease in metapopulation persistence was summarised as the ratio between the largest eigenvalue of the adjacency matrix after and before removing the top 5%, 10%, 20% of these key nodes. This ratio should be interpreted

as the magnitude of decline in metapopulation persistence resulting from the removal of these focal subpopulations.

An additional node removal exercise was performed to quantify the patch-level influence on metapopulation persistence. All nodes were removed iteratively (with replacement), and the matrix eigenvalue was recalculated to quantify the magnitude in the decrease in metapopulation persistence. This method allows nodes to be ranked, thereby assisting managers in identifying important habitat patches that may represent conservation priorities or opportunities for management actions.

Finally, we investigated the role life history traits may have on metapopulation persistence through changes in the network structure and emergent properties. Clearly, species-specific traits such as larval duration influence the dispersal potential among subpopulations and therefore contribute significantly to metapopulation dynamics and persistence. Yet, this functional link between life history and persistence may be through emergent network properties which also integrate system-wide habitat characteristics and spawning patterns. To explore this potential link, we summarised the species-specific network properties and node-level results, and the correlation between persistence and life history parameters. In this exploratory analysis, we included habitat size (a proxy for reproductive output), number of sources patches, extent of the spawning season, length of pre-competency window (the period of time before larvae are capable of settlement), and larval mortality (see online Appendix 3 for further details). This analysis has the potential to highlight the life history traits which influence network-level metapopulation persistence.

4.3 Results

After completing 1441 dispersal simulations across five species and all years, we mapped the species-specific metapopulation networks. Mapping connectivity allowed us to visualise and investigate the geographic structure of the dispersal pathways, and provided the seascape context for network analysis. Note that the total area of habitat, the area of individual patches,

and the total number of patches varied among species due the species-specific habitat requirements. Metapopulation network maps (Fig. 4.1) show presence and strength of dispersal connections among source and destination subpopulations, as defined by the migration matrices. Networks varied in the number of dispersal connections (graph size), dependent on the species-specific attributes: 2205 dispersal links for *H. rubra*, 2086 for *H. erythrogramma*, 861 for *S. punctatus*, 542 for *C. auratus* and 8736 for *C. rodgersii*.

4.3.1 Network-level metrics

Network-level metrics calculated for all species are listed in Table 4.2. The *S. punctatus* network was fully asymmetric, with a degree of asymmetry of 0, *C. rodgersii* was strongly asymmetric; while the other species' networks (*H. rubra, C. auratus, H. erythrogramma*) revealed a low level of asymmetry (Table 4.2) with gamma indices close to 1, due to a nearly symmetric exchange of larvae among habitat patches.

A heterogeneity index was calculated from each node's in-degree and out-degree connections, and is based on the coefficient of variation of degree per matrix (Table 4.2). These indices allowed us to compare heterogeneity across species, where values between 0 and 1 indicate that the in-degree or out-degree are under-dispersed, values larger than 1 indicate high variability or heterogeneity. In species with limited dispersal capacity (e.g., *H. rubra, C. auratus, H. erythrogramma*), the heterogeneity in in-degree and out-degree was similar. There were differences between in-degree and out-degree heterogeneity for two species; a small difference for *C. rodgersii* (in-degree heterogeneity of 0.25 and out-degree of 0.65) and a strong difference for *S. punctatus* (in-degree of 0.31 and out-degree index of 8.74).

In all species we found many 3-node cycles (Table 4.2), with the only exception of *S. punctatus*, which was an acyclic network. Though the number of cycles appears large, these values are far from the maximum possible number of cycles in theoretical networks (Arman and Tsaturian 2019, Gerbner et al. 2018) that might contribute to increased metapopulation persistence and stability (Artzy-Randrup and Stone 2010).

Table 4.2: Result for network-level metrics: asymmetry index(γ), heterogeneity index and the number of cycles.

Species	Asymmetry Index γ	Heterogeneity Index				Cycles (3 connections)
		In-degree edges	Out-degree edges	Weighted in-degree edges	Weighted out-degree edges	
H. rubra	0.65	0.42	0.45	0.39	0.45	4674
H. erythrogramma	0.74	0.29	0.31	0.45	0.39	3346
C. rodgersii	0.35	0.25	0.65	0.32	0.51	37609
C. auratus	0. 86	0.09	0.1	0.12	0.14	1583
S. punctatus	0	0.31	8.74	0.41	9.77	0

4.3.2 Node-level metrics

Each species' node-level properties and network metrics (Appendix 3 Table A3.2), and degree distribution (Appendix 3 Figure A3.1) were quite variable due to species-specific characteristics and habitat requirements (Minor and Urban 2008). For species with somewhat restricted dispersal capabilities (*H. rubra*, *H. erythrogramma* and *C. auratus*), areas of the seascape with large in-degree and out-degree were largely aligned. The metapopulation network for *H. rubra*, highlighting patterns of in-degree, is shown in Fig. 4.1a. High degree nodes for *H. rubra* are clustered on the eastern coast of Victoria and New South Wales while more isolated nodes are concentrated along the Tasmanian coast. In *H. erythrogramma* (Fig.4.1b) we found hubs of connectivity in Victorian and New South Wales subpopulations but also across north-east Tasmania. In *C. auratus* (Fig. 4.1c) central Victoria had a large concentration of well-connected nodes. For species with a greater dispersal capacity, areas of strong local connectivity (in- and out-degree) were much more variable. *C. rodgersii* showed high in-degree in eastern Tasmanian coast subpopulations while habitat patches across the northwest coast of Tasmania were strong sources (high out-degree). *S. punctatus* had different spawning and settlement areas, and degree data denoted that South Australian spawning grounds can reach more settlement areas (higher out-degree) than Victorian and Tasmanian grounds, due to the potential of larvae generated in South Australia to reach

patches in the whole model domain. Other centrality measures such as betweenness centrality, closeness centrality, eigenvector centrality and alpha centrality, were calculated at a component level for disconnected graphs for three species, *H. rubra, H. erythrogramma and C. auratus*, (see Appendix 3 Table A3.2 for species and component-level data).

Metapopulation stepping-stones were identified by patches with a high betweenness centrality. The most central and most influential subpopulations were identified by those with high values of closeness, eigenvector and alpha centrality. Mapping these network-level centrality measures across all species, revealed no strong geographic trends with each species displaying different key stepping-stone patches and central nodes.

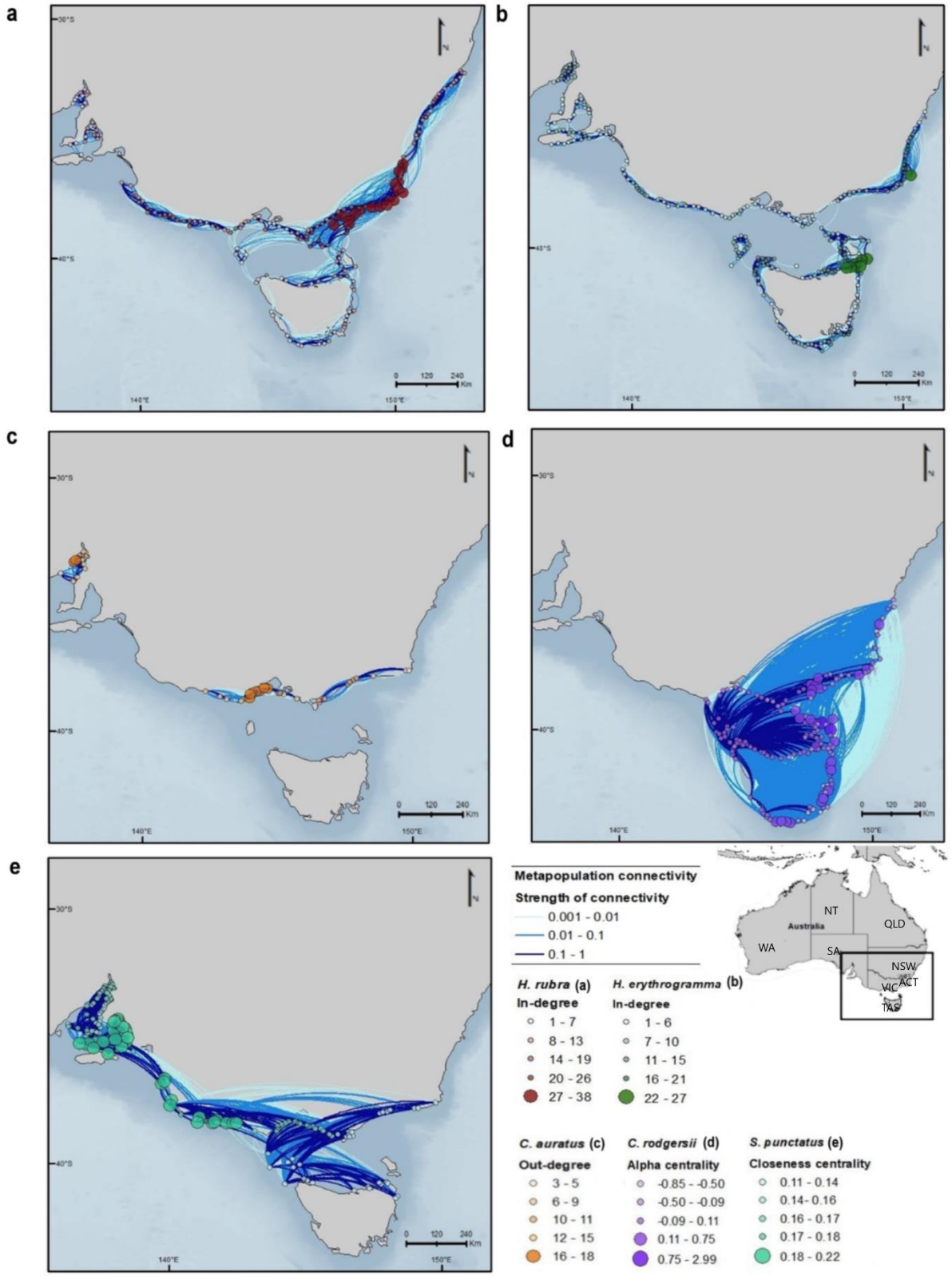

Figure 4.1: Spatial distribution of metapopulation connectivity and a variety of node-level metrics across study area. The weight of the connections is indicative of the strength of dispersal and the directionality is implied by following the arcs in a clockwise direction. The study area of South-east Marine Region of Australia including waters off Victoria (VIC), southern New South Wales (NSW), Tasmania (TAS) and eastern South Australia (SA). All maps in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

We found geographic consistency between alpha centrality (Fig. 4.1d) and degree centrality for *C. rodgersii*, *C. auratus* and *H. rubra*. In *S. punctatus,* closeness centrality is shown in Fig.4.1e, with largest values along the western Victorian coast and St Vincent Gulf. In *C. auratus* the distribution in betweenness centrality was opposite to closeness centrality, nodes with large closeness centrality were found in the South Australian component, while betweenness centrality identified most of species' stepping-stones around Victoria.

Network structure, as well as the spatial pattern in node-level metrics appeared to be influenced by species-specific life history traits (see traits in in Table 4.1). In general, species characterised by greater dispersal capacities and longer competency periods tended to have higher mean in-degree and out-degree, as well as a greater range across in-degree and out-degree nodes. Mean centrality statistics did not show a clear pattern with respect to species' traits. For detailed species-specific summary statistics across networks, see Appendix 3 Table A3.2, and the supporting data contained in Appendix 4 (supplementary material for all node-level metrics results).

4.3.3 Eigenanalysis and network-based metrics influence on persistence

All species satisfied the condition of persistence with eigenvalues and persistence conditions larger than the persistence threshold of 1 (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). Across species, persistence was most impacted by removing subpopulation 'hubs' of connectivity (Fig. 4.2 and further details in Appendix 3 Figure A3.2), or those with the largest out-degree (13% drop in persistence when removing 5% of top out-degree nodes, 29% drop in persistence for 10% node removed and 43% in persistence for 20% of nodes removed). Other common centrality measures appeared to have a more limited impact on metapopulation persistence. Patch area also had an important role, with an overall impact on persistence lower than the degree metrics, but above all other centrality metrics, as the loss of available habitat (and therefore lower population sizes and reproductive output) has a direct negative impact on metapopulation persistence. All other node-level network metrics revealed variable impacts on system-wide metapopulation persistence across species. For each

species, we also progressively removed all nodes to identify species-specific estimates of metapopulation resilience. *C. rodgersii* emerged as the most resilient species where the metapopulation started to be significantly affected only after more than 25% of the most important subpopulations were removed, after which it suffered a severe decline in persistence. *S. punctatus*, on the other hand, was the most vulnerable species, where a precipitous decline in persistence was immediately revealed with only 5% of important nodes removed (Appendix 3 Figure A3.3).

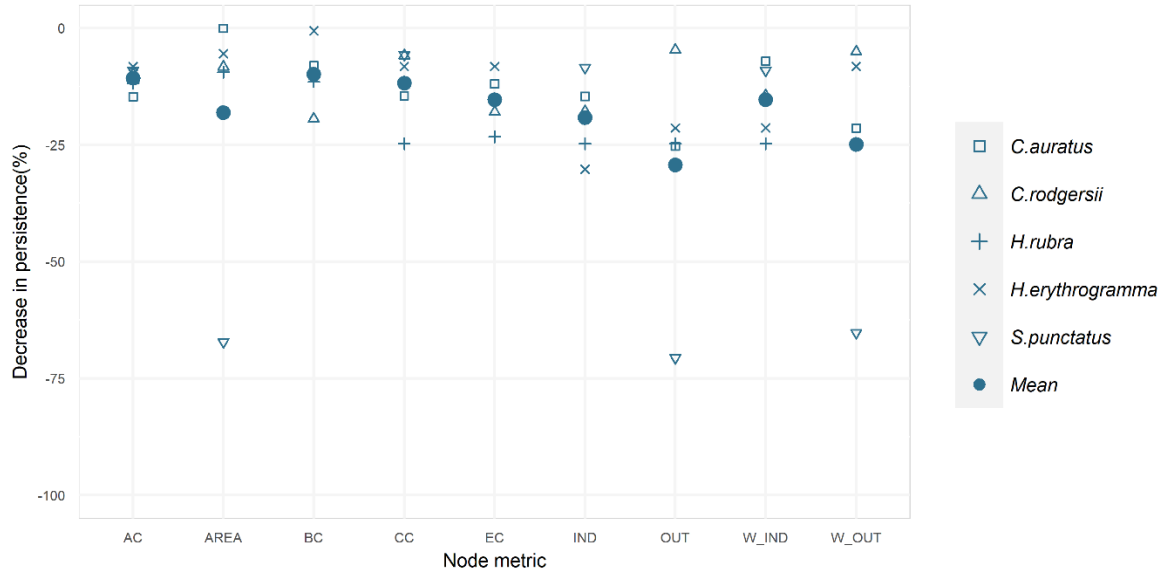

Figure 4.2: Decrease in metapopulation persistence by network metric. Decrease in metapopulation persistence (%) when removing top 10% of nodes determined by each node-level network metric for each species and mean across species. Metrics used to select nodes to remove from the graphs include AC (alpha centrality), Area, BC (betweenness centrality), CC (closeness centrality), EC (eigenvector centrality), IND (in-degree), OUT (out-degree), W_IND (weighted in-degree) and W_OUT (weighted out-degree).

We mapped the out-degree metric, the most influential metric, across all species to reveal geographically consistent hotspots of important nodes identified by this network metric proxy (Fig 4.3). After intersecting all species and using a moving window to summarise the density of linkages, the north-west coast of Tasmania was revealed as a critical multi-species hotspot where many species have important subpopulation hubs. Secondary hotspots appear along the north-east coast of Tasmania, as well as in eastern Victoria. Each node's influence on metapopulation persistence was individually quantified for each species and mapped across

the study area (Appendix 3 Figure A3.4). Species-specific spatial patterns are largely consistent with the multi-species geographic hotspot found by out-degree, although revealing species-specific clusters of critical nodes, broadly distributed across the north coast of Tasmania and east coast of Victoria.

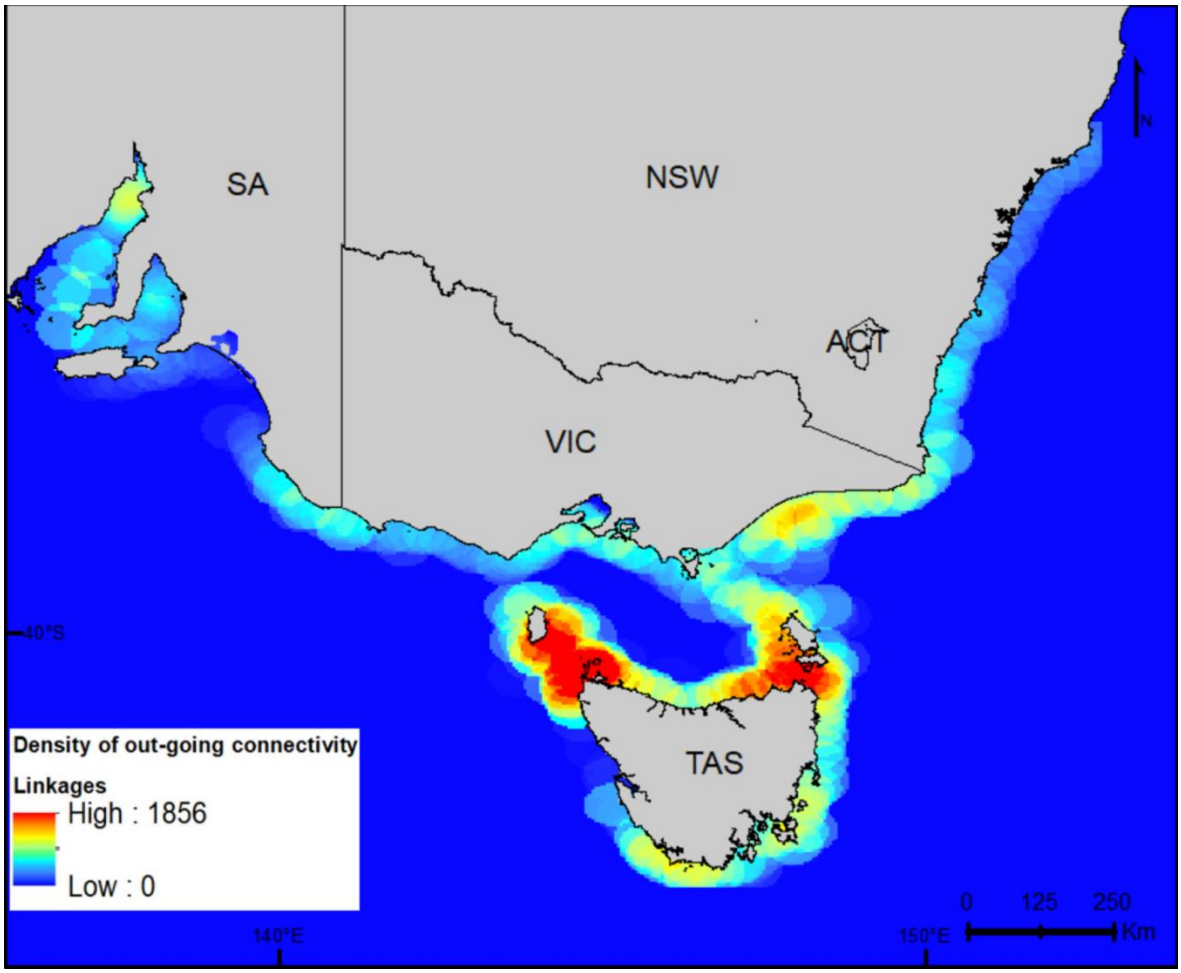

Figure 4.3: Local connectivity hotspot map. Map showing the density of out-going connections across all species modelled. Densities are displayed using a linear stretch within the upper and lower limit defined by the 3rd standard deviation value. Map is in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

Finally, the investigation of the relationship between early life history characteristics and habitat on metapopulation persistence revealed mixed results. Habitat quality parameters, such as source habitat area and number of habitat sources, did not show consistent trends in metapopulation decline or impacts. In contrast, traits such as the length of the competency window, and particularly the duration of the pre-competency larval stage (Fig. 4.4), displayed a negative relationship with metapopulation impact (see online Appendix 3 Figure A3.5 for

further details). As the pre-competency period gets larger, metapopulation persistence appears to drop quickly with the removal of habitat, particularly at levels of 20 – 25% nodes removed.

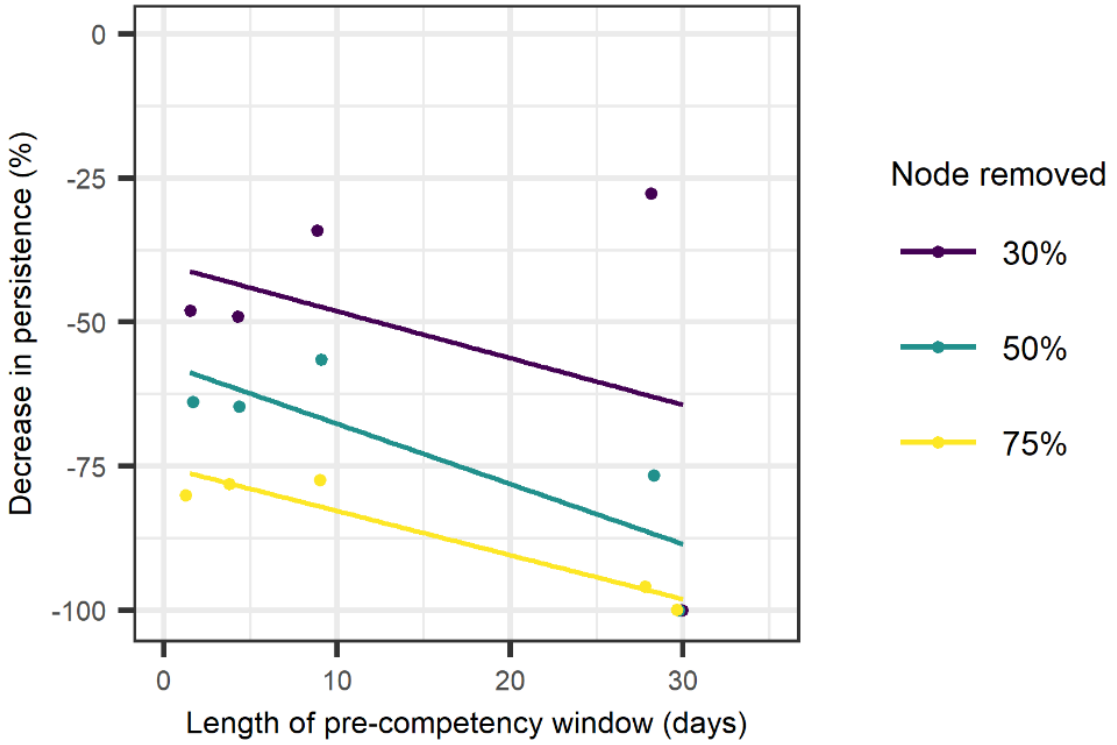

Figure 4.4: Length of pre-competency window and decrease in persistence correlation. Relationship between length of pre-competency window (days) and change in persistence. Respectively at 30%, 50%, 75% change in persistence R = -0.39, n = 5, p = 0.52; R = -0.83, n = 5, p =0.08; R = -0.96, n = 5, p = 0.01.

4.4 Discussion

Degree centrality, measured by out-degree, proved to be the most informative node-level metric when quantifying the impact on metapopulation persistence (Fig. 4.2). Other centrality measures common in the literature (e.g., eigenvector centrality, betweenness centrality) showed a limited influence on metapopulation persistence through this analysis. Out-degree was observed to be the most important network metric with the strongest impact on metapopulation persistence (more than 10% decline in persistence after removing the top 5% of these hubs), although the size of habitat patches was also important for persistence. Habitat patches with large out-degree are important sources of larvae to many neighbouring

subpopulations, creating local hubs sustaining the population. Source habitats with great dispersal capacity are critical to ensure persistence of metapopulations since these habitats have an important role in ensuring successful reproduction and increasing the gene pool size, dispersing across a wide area. The network analysis suggested protecting hubs of local-scale connectivity as an important strategy in ensuring long-term persistence.

Knowing how node-level characteristics, such as size and degree centrality, impact persistence helps us identify which subpopulations or patches are vital to metapopulation persistence. This site-specific information is important for conservation scientists, as it provides an effective and ecologically-meaningful way to value and prioritise areas for management or conservation efforts. Although prioritising hubs of connectivity in conservation is not new (e.g., Kininmonth et al. 2011), the methods and results presented here reinforce the importance of these hubs, and put this in context with other common (and less effective) connectivity measures.

Multi-species hubs of important connectivity (out-degree) are clustered across the coast of Tasmania, particularly in the northwest and northeast (Fig. 4.3). Among the species modelled here, marine invertebrates showed similar distribution of high out-degree hubs, mostly located across northern Tasmania. It appears these habitat patches in northern Tasmania may be essential for ensuring connectivity between Tasmania and Victoria coasts. Eastern Tasmanian hotspots have also been identified as a key ecological feature in the South-east Marine Regional Profile (Dambacher et al. 2012). In this area subantarctic water masses driven by westerly winds interact with eddies from the East Australian current. This oceanographic mixing zone enhances productivity and experiences phytoplankton blooms and mass aggregations of coastal temperate taxa (Hosack and Dambacher 2012, Commonwealth of Australia 2015). These areas are also recognised as significant for their conservation value, critical habitats in northern and eastern Tasmania are classified by the Tasmanian government as Conservation Areas, which mostly protect the coastal zone as regulated under the Nature Conservation Act 2002. We also found that some connectivity hubs correspond to Australian

Marine Parks of the South-east Network, such as Freycinet Marine Park in the southeast and Boags Marine Park in northwest Tasmania. Other important hubs of multi-species connectivity appear to exist in eastern Victoria. Several sites in this region have also been previously identified as associated with biogeographic breaks for many taxa (Colton and Swearer 2012). Breaks have been located in some cases at Wilsons Promontory (O'Hara and Poore 2000) or in the vicinity of Ninety Miles Beach (Hidas et al. 2007, Gomon et al. 2008). These biogeographic breaks are often associated with changes in species range and assemblages (e.g., due to temperature gradients or local of habitat), and can potentially limit broad-scale dispersal connections (Colton and Swearer 2012). Waters surrounding Wilsons Promontory correspond to Protected areas, such as the Beagle Marine Park, part of the South-east Network of the Australian Marine Parks, and the Wilsons Promontory Marine Park and Wilsons Promontory Marine Reserve.

Network-based approaches can be a powerful tool to help understand metapopulation structure, particularly when studying species where dispersal dominates metapopulation dynamics, like many marine taxa. Connectivity has recently been shown to be an important criterion to better design protected area networks, possibly more important or efficient than habitat quality or quantity alone (Berglund et al. 2012). Network-level metrics can also help managers understand the overall geographic structure of a metapopulation, efficiently identifying where hubs and barriers exist. These metrics store information on network symmetry or heterogeneity, where a very asymmetric (Vuilleumier and Possingham 2006) or heterogeneous network can be an indicator of a vulnerable metapopulation (Shtilerman and Stone 2015). Similarly, node-level metrics help identify core areas important for building optimal management strategies (Kininmonth et al. 2011, Watson et al. 2011, Berglund et al. 2012). Broad scale spatial management often involves many diverse agencies, often leading to programmatic challenges in funding and implementation (Cowan et al. 2012, Garavelli et al. 2018). This can be alleviated to a degree by identifying local-scale areas of interest, such as multi-species connectivity hubs or consistent biogeographic zones, thereby aligning

management with these ecologically-meaningful scales. In other circumstances, managers may benefit from disconnecting hubs of connectivity to optimizing invasive species management (Perry et al. 2017, Samsing et al. 2017). This can be an option for *C. rodgersii* and *H. erythrogramma* management, which are spreading across the South-east Marine Region of Australia causing dramatic habitat alterations (Ling et al. 2015).

Identifying node-level metrics that strongly influence metapopulation persistence, provides opportunities to more directly investigate the influence of life histories and location on persistence (Dallas et al. 2019). Network structure and node metrics were influenced by species-specific differences, associated to species-specific life history traits, and were mostly evident for in-degree and out-degree results. Identifying key life history traits and the associated species, may help quickly redirect funds and research to these vulnerable species and locations. From our preliminary analysis of species-specific life-history traits, we found the pre-competency period to be the most influential parameter (Fig.4.4), where metapopulation persistence declines with an increase in the pre-competency period; the relationship is driven by the species with the longest pre-competency period. However, a significant relationship with the pre-competency period is only found when 75% of the important nodes are removed. Extended pre-competency periods may be associated with greater dispersal ability downstream (Heyward and Negri 2010), lower local retention (Treml et al. 2015b), and may make larvae more vulnerable to mortality and starvation (Jenkins and May 1994). Further research is required to investigate the potential relationship between life history traits and metapopulation persistence and to identify vulnerable species and habitat patches and locations.

Despite this approach is flexible and applicable to many species and habitat, the model presented here has several limitations. Our analysis on persistence was based on averaged data across years, and temporal variability was not considered, but it might be important to explore the consistency of node importance through time, and whether the network structure itself changes through time. In addition, our model assumes the habitat quality is

homogeneous (i.e., quality/density is the same per suitable habitat cell) and habitat patches vary only in individual patch sizes and locations. Ignoring spatial heterogeneity will impact predictions of connectivity, particularly where the relationship between patch size and reproductive output does not hold, and therefore might change results. Finally, there is limited availability of empirical data on the early life history of most coastal species (e.g., swimming, sensing, and mortality), and virtually no data describing how these parameters might vary across the seascape. Improving our understanding with field and laboratory-based research is critical to produce more accurate predictions around metapopulation connectivity and persistence.

In conclusion, larval dispersal modelling and network analysis provides an efficient approach in studying real-world marine metapopulation persistence. Degree centrality, identifying hubs of out-going connections, was shown to be a major predictor of persistence. Multi-species hubs of connectivity highlight important hotspots for management and conservation consideration. In this seascape, these connectivity hotspots occur where tropical and temperate currents merge and in regions surrounding known biogeographic breaks. Finally, a preliminary analysis suggests that the length of the pre-competency phase may be a predictor of local-scale connectivity (i.e., out-degree) and have a strong influence on metapopulation persistence. Together, these species-level attributes and important hotspots in southeast Australia can assist managers in making more efficient and more ecologically informed decisions regarding priorities to ensure persistent metapopulation of fished and/or threatened species.

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Chapter 5

Individual movement behaviour determines the impact of management strategies for a commercially harvested fish

Abstract

Many studies describe the importance and the consequences of ignoring individual movement and spatial structure in fisheries management. These omissions can contribute to bias in estimating biomass, subsequent overfishing and even stock collapse. Spatially explicit management strategies can have variable impact because fish move through the marine environment and are thus exposed to differential probability of capture. We used spatially explicit population viability analyses to simulate the future persistence of pink ling (*Genypterus blacodes*) in south-east Australia under a range of fish movement and management scenarios. Little is known of pink ling movement behaviour, so we explored the impact of four different movement distance types on biomass of adult pink ling. We simulated the current fisheries management scenario for the Commonwealth Trawl Sector, which uses total allowable catch (TAC) limits, as a baseline. We then explored the impact of three alternative fisheries management scenarios: 1) reducing fishing mortality; 2) increasing the extent of spatial closures; and 3) combining both reduced mortality and increased closures. We performed a sensitivity analysis to understand whether model projections are influenced by differences in individual movement behaviour, habitat suitability, carrying capacity, or differences in survival and reproduction parameters. Our simulations revealed that pink ling persistence across its range was highly variable but showed an overall decline over time regardless of movement type and management scenario, suggesting that current fisheries management might be

inappropriate to ensure stability in pink ling abundance and further restrictions to catch limits are needed. Spatially explicit population models allow us to identify the most vulnerable and the most persistent populations within a species' range: the eastern stock of pink ling was the most persistent under all the scenarios even though it is exposed to the highest fishing effort. Dispersal distance was a key determinant of population abundance trends and short distance movements were associated with variable abundance, suggesting that fisheries scientists and managers would benefit from better knowledge of pink ling movements. Our approach highlighted a concerning declining trend for this species, suggesting that more sustainable fisheries management strategies are needed to reduce the vulnerability of pink ling stock to fishing depletion.

5.1 Introduction

A key goal of fishery science is to understand the status of fish stocks and ensure their future persistence (Bonfil 2005). To do this, fisheries scientists examine how populations compensate in response to fishing depletion, and quantify stock persistence in response to different fisheries management strategies (Rose et al. 2001, Breen et al. 2015). There is global acknowledgement that many fisheries are in serious decline but also signs that active fisheries management can help reverse this trend (Hilborn et al. 2020). The limited understanding of biology and ecology for many marine species remains an impediment to the development, assessment and application of alternate fisheries management strategies (Hutchinson 2008, Ying et al. 2011).

Movement behaviour is a key biological parameter that affects how individuals interact with their environment and fishery (Eikeset et al. 2013, Erisman et al. 2017) but it remains under-described for many marine fishes, especially those inhabiting the logistically difficult to study continental shelf and slope (Afonso et al. 2014). Models predicting fisheries management consequences have limited value if our understanding of the general characteristics of the spatial dynamics of marine species is incomplete, and there is large uncertainty around movements rates (Botsford et al. 2009). Spatially explicit population viability analyses, that incorporate population dynamics, demographic stochasticity, connectivity, environmental stochasticity and spatial management tools, provide a flexible approach to effectively compare management strategies to evaluate long term populations persistence (Akçakaya et al. 2004).

Stock assessment relies on a variety of data, including historical catch and demographic parameters such as natural mortality and growth rates, to estimate stocks status and set management targets for sustainable fisheries management (Dick and MacCall 2011). Several methods have been implemented to assess stock status, often comparing reference points such as the fishing mortality coefficient, *F*, or biomass at maximum sustainable yield, B_{MSY} (Jiao et al. 2005) to ensure future stock persistence (Carruthers et al. 2012). Single species stock assessment has evolved towards a holistic management approach, called ecosystem-

based fisheries management (Pikitch et al. 2004). Common ecosystem-based tools used in fisheries management are Ecopath with Ecosim and Ecospace (Christensen and Pauly 1992, Pauly et al. 2000, Christensen and Walters 2004) or Atlantis marine ecosystem model (Audzijonyte et al. 2019). However, these approaches have limitations, due to the large amount of data required to efficiently assess fisheries management strategies, and technical limitations such as complexities in validating, assessing, reproducing these models and communicating their results (Peterman 2004, Cowan et al. 2012, Trochta et al. 2018). It is critical that fisheries scientists and managers use effective tools to better understand stock status and provide reliable predictions of persistence in light of uncertainty in our understanding of species biology and ecology (Beverton 1990).

Population viability analysis (PVA) is efficient and rigorous modelling approach for management strategy evaluation but is not extensively used in fisheries science (Cecino et al. in review). PVA is a risk-assessment method successfully used in conservation biology for diverse terrestrial (Lahaye et al. 1994, Menges 2000, Haines et al. 2006, Menges et al. 2006, Aiello-Lammens et al. 2011), freshwater (Jarić et al. 2010) and marine species (Ellner and Fieberg 2003, Sweka and Wainwright 2014). PVA describes species' vulnerability to extinction and performs well in comparing alternative management strategies (Boyce 1992, Akçakaya et al. 2004). PVA approaches can effectively accommodate the spatial and temporal structure of fishing and can assess sub-population extinction vulnerability, and identify the minimum viable population in the context of the focal species' regional persistence (Akçakaya et al. 2004). PVA results are suitable to inform spatial prioritization, recovery planning, and to help in understanding the influence of movements between populations on persistence and the impact of climate change (Lahaye et al. 1994, Burkhart and Slooten 2003, Akçakaya et al. 2004, Jarić et al. 2010, Fordham et al. 2013, Sweka and Wainwright 2014).

Australia has the world's third largest Exclusive Economic Zone (EEZ) covering an area over 800 million km^2. In south-east Australia, fishing has caused changes to species abundance, composition and size of target and non-target species (Fulton et al. 2007). However, much is

still unknown about the marine ecosystem and the fishery target species of south-east Australia. For instance, uncertainty around movement types, larval processes and nursery habitats, as well as trophic relationships, remain undetermined for many species (Bruce et al. 2002). Additionally, the complexity of southern Australia's marine habitat has been linked to high spatial and temporal variability in species distribution and size of catches (Bruce et al. 2002).

The Southern and Eastern Scalefish and Shark Fishery (SESSF) is a multi-sector, multi-species fishery. The fishing methods used within the SESSF are demersal otter trawl and Danish-seine, and occasionally midwater trawls (Patterson et al. 2019). In this region spatial closures are in place to help manage the impacts of fisheries on vulnerable species such as marine mammals and sharks (AFMA 2018). The biological status of target species is monitored and included in annual fishery reports, and each species is classified as "not subject to overfishing", "subject to overfishing" or "uncertain". Despite the negative impact of trawling on many benthic species (Foster et al. 2015), recent implementation of fisheries management strategies and fishing techniques have helped lead to abundance recoveries for many species (Patterson et al. 2019).

Pink ling, *Genypterus blacodes*, is a significant contingent of the SESSF. Spatial differences in catch-rate trends, and size and age between eastern and western areas of south-east Australia region has led to these areas being managed as separate stocks (Patterson et al. 2019). These biological differences between the two stocks make them an ideal candidate for the application of spatially structured management strategies assessment. A spatially explicit population viability analysis provides an effective approach to understand spatial heterogeneity of pink ling populations and identifying areas vulnerable to over-exploitation.

Here, we investigate persistence of pink ling through time and evaluate how these changes under current and three alternate fisheries management scenarios. Current management involves separate catch limits for eastern and western stocks. Our first alternate scenario is based on reducing the current fishing mortality, the second scenario examines the effect of

increasing the extent of current spatial closures, and a third scenario combines both variations. Pink ling is believed to be sedentary (Ward et al. 2001, Punt et al. 2016), but no studies exist formally describing this species' lateral movement behaviour (see Mitchell 1984 for evidence of vertical movement associated with feeding). We therefore implemented four different types of movement into our model: complete sedentary behaviour (no movements), limited individual movements (up to 10 km), medium individual movements (50 km) and large individual movements (up to 100 km). We quantified pink ling abundance in simulations that were run over 30 years, and identified regions vulnerable to fishing depletion by assessing how abundance changes according to each movement type and fisheries management scenario. We tested model sensitivity to parameter uncertainties by performing a multi-factor sensitivity analysis. We demonstrated that population viability analysis is an efficient and simple approach to compare alternative fisheries management strategies, helping to inform managers on predicting future abundance of the stocks and identify the location of vulnerable and persistent populations. Additionally, we showed that better knowledge around movements of pink ling is needed, due to the sensitivity of persistence to different fish capacity to move through the south-east Australian marine habitat.

5.2 Methods

5.2.1 Study area

We simulated population growth and analysed abundance for eastern and western pink ling populations of south-east Australia in response to fishing pressure. The spatial domain of this model consisted of the management area defined for the Commonwealth Trawl Sector, using a spatial grid at 5x5 km cell size (Fig. 5.1). This area stretches from Sydney southwards around Tasmania to Cape Jervis in South Australia, where it is adjacent to the Great Australian Bight Trawl Sector.

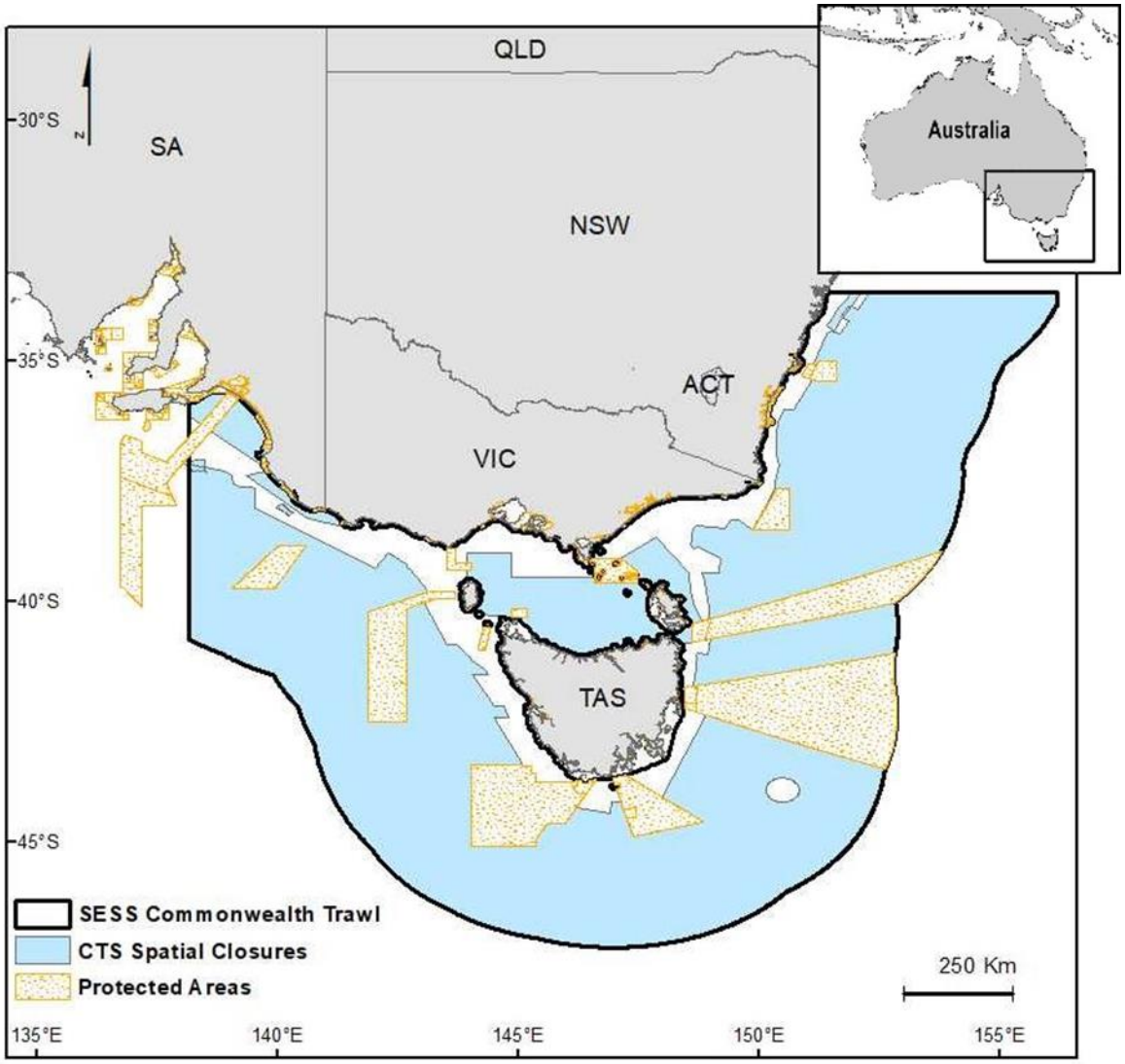

Figure 5.1: Map showing the study area of this study, the Commonwealth Trawl Sector region and current fisheries management spatial closures and protected areas. Map in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

5.2.2 Study species

Pink ling, *Genypterus blacodes*, is a demersal species caught by trawlers on the continental slope around southern Australia. The Eastern and Western pink ling stocks are defined as being east and west of longitude 147° E (Patterson et al. 2019). Although pink ling catches are combined and managed under a single quota, management arrangements are in place to constrain catches of the eastern stock (Patterson et al. 2019). Current management uses projections of how the stock would respond to different level of catch, and aims to rebuild the eastern stock and pursue the reference targets for the western stock (Patterson et al. 2019).

The 2018 stock assessment classified the combined stock as not overfished, with the western stock above the biomass target, and the eastern stock showing signs of recovery (biomass between the limit and target reference points; Cordue 2018). A reliable stock assessment is challenging due to short time series data available for pink ling and limited availability of fishery-independent data. Spatial closures are also in place to protect the spawning stock and reduce local fishing mortality.

5.2.3 Population viability analysis

We modelled pink ling's spatial distribution across South-eastern Australia using a species distribution model (SDM) bounded by its observed depth distribution (22 to 1000 metres),presence data from the Atlas of Living Australia, ALA (https://www.ala.org.au) and pseudo-absence locations generated within a delimited distance from reference points. Environmental parameters used in the SDM were bathymetry and long-term averages of current velocity at the seafloor, dissolved oxygen concentration, bottom temperature, salinity, pH and chlorophyll concentration. These parameters were downloaded from Bio-ORACLE, a global dataset of environmental data specific for species distribution models (Tyberghein et al. 2012). Collinearity among predictors was quantitatively checked, and those with a Pearson correlation threshold of 0.7 or greater (Dormann et al. 2013) were identified and we retained the most ecologically meaningful parameter in the model. Collinearity among predictors is a known source of uncertainty, and when collinearity increases, the efficiency and statistical power of the model decrease (De Marco and Nóbrega 2018). Our pink ling SDM was built using Boosted Regression Trees (TREE), following the protocol within 'dismo' package (Hijmans et al. 2017) in R v3.6.2 (R Core Team 2019). The optimal model used a learning rate of 0.001 and a total of 5650 trees with AUC score 0.97 for training data. The environmental predictors included in the optimal model were mean water temperature, dissolved oxygen, pH, velocity of currents and chlorophyll A concentration. SDM spatial predictions were used as input of our PVAs to define the spatial structure of pink ling populations (more details on SDMs are available in Appendix 5).

The STEPS R package (Visintin et al. 2020) was used to simulate population growth through time and space. We used an age-structured approach to model populations with stages defined according to the five stage matrix available from COMADRE database (Salguero-Gómez et al. 2016). Pink ling populations are structured with the following stages: (1) 3 year-old recruits; (2) 4 year-old juveniles; (3) 5 year-old juveniles; (4) 6 year-old juveniles; (5) 7–14-year-old adults (González-Olivares et al. 2009). We used a stochasticity matrix describing the uncertainty around the stage matrix transition probabilities (as standard deviations) to simulate environmental stochasticity, where zeros indicate no uncertainty about environmental fluctuations in our system. We applied a growth rate (R_{max}) of 1.08 (González-Olivares et al. 2009) to the life-stage transition matrix to define how population growth occurs at each timestep. Then, we included carrying capacity (*k)* of the populations in the model to control growth, reflecting the maximum number of individuals contained in each cell. Here, *k* was predicted as a function of each cell habitat suitability and B_{MSY}, a proxy for biomass in fishery science (Maunder 2008). Ceiling-type density was assumed to affect only adult stages, as is common for invertebrates and fish populations (Akçakaya et al. 2004). The initial abundance of pink ling for each stage was obtained using stable state age distributions multiplied by the carrying capacity of the seascape, and then drawn from a multinomial distribution to return whole integers (Visintin et al. 2020). Four different scenarios of individual-based movements were implemented (sedentary, 10 km, 50km and 100 km). Only adult pink ling could move freely through the seascape when suitable habitat is available, according to the maximum distance applied to each movement scenarios. A cellular automata dispersal function was applied, simulating movements of individuals using rule-based cell movements depending on the permeability of the seascape and interrupted on reaching cell carrying capacity (Visintin et al. 2020).

We modelled pink ling for 30 annual timesteps and performed ten replicates for each simulation to account for environmental stochasticity. We averaged the 10 replicate annual estimates of adult pink ling abundance within each scenario. Greater replication can be of

value but was not implemented due to the computational effort of increasing the number of replications for all scenarios. Our annual timestep duration corresponds to the temporal resolution of available fisheries data and the stage matrix data, where transitions among stages occur yearly. We performed a multi-factor sensitivity analysis to test the sensitivity of our model over different parameters combinations. We used a fractional factorial design, selecting to test for sensitivity only some key parameters due to the large number of model parameters and the high computational requirements to perform a full factorial sensitivity analysis. The first factor investigated was differences among the four movement types (sedentary, limited, medium, long distance). We tested model sensitivity to parameter uncertainty by applying ±10% variations in the stage matrix parameters describing pink ling survival and fecundity, carrying capacity and habitat suitability within all four movement strategies. Paired comparisons of pink ling abundance time series were used to assess and visualise the impact of simulated variables under nominal and perturbated scenarios (Devenish et al. 2012, Paton et al. 2013, Pianosi et al. 2016).

5.2.4 Fisheries management scenarios

We simulated long-term pink ling stock growth under the current management for the fishery (baseline scenario), and under different fisheries management scenarios (Table 5.1). We used recent stock assessment data for the 2018-2019 fishing season to describe the current management regime (Patterson et al. 2019). Fishing mortality was quantified based on the estimated median biomass depletion of areas subject to fishery, which was $0.35B_0$ for eastern stock and $0.84B_0$ for western stock (Patterson et al. 2019). We excluded marine protected areas (MPAs) and marine reserves from being exposed to fishing in our PVA, with data on their spatial extent available through the World Database on Protected Areas (UNEP-WCMC and IUCN 2020). We also excluded current fishing closures areas (AFMA 2018) from the area available to fishery.

We measured long-term abundance of pink ling to evaluate the impact of alternative fisheries management strategies. We modelled three alternative fisheries management scenarios.

First, we evaluated the impact of changes in fishing mortality by reducing the current fishing mortality by 10%. A decrease in fishing rates of 10% can be interpreted as a modification in total catches from 852 tonnes to 742.5 tonnes (Patterson et al. 2019). The second scenario involved extending current spatial closures, marine reserves and MPAs by a 10 km buffer. This scenario resulted in a 50% reduction in the overall available fishing area. However, buffering the entire fishing area of 10 km primarily excludes areas where fishing intensity is very low or almost absent (for example in the proximity of the Bass Strait or near Sydney and South Tasmania). Closure of high fishing effort zones was limited. The last scenario consisted of a combination of the fisheries and spatial closures scenarios, in order to investigate if a combined approach could amplify positive effects on stock abundance.

The impact of management and movement scenarios on long term persistence of pink ling was calculated as tonnes of adults for each timestep, but results were also mapped to understand spatial heterogeneity in pink ling abundance, identifying productive and vulnerable areas and examining whether these areas changed through time.

Table 5.1: Summary and description of the 16 scenarios simulated for pink ling PVA.

Movements	**Management Scenario**	**Description**
Sedentary	Baseline scenario	Current management of pink ling fishery in south-east Australia for the CTS fishery.
	Fishery scenario	Reduced fishing pressure.
	Closure scenario	Increased spatial closures size.
	Fishery and closure scenario	Combination of reduced fishery and spatial closures size.
10 km movements	Baseline scenario	Current management of pink ling fishery in south-east Australia for the CTS fishery.
	Fishery scenario	Reduced fishing pressure.
	Closure scenario	Increased spatial closures size.

	Fishery and closure scenario	Combination of reduced fishery and spatial closures size.
50 km movements	Baseline scenario	Current management of pink ling fishery in south-east Australia for the CTS fishery.
	Fishery scenario	Reduced fishing pressure.
	Closure scenario	Increased spatial closures size.
	Fishery and closure scenario	Combination of reduced fishery and spatial closures size.
100 km movements	Baseline scenario	Current management of pink ling fishery in south-east Australia for the CTS fishery.
	Fishery scenario	Reduced fishing pressure.
	Closure scenario	Increased spatial closures size.
	Fishery and closure scenario	Combination of reduced fishery and spatial closures size.

5.3 Results

5.3.1 Population viability analysis - baseline scenarios

Averaged abundance in base case scenarios across all movement types was temporally variable but nonetheless revealed an overall declining trend (purple lines; Fig. 5.2, and Table 5.2 for coefficients of variation, CV, for each model). Total abundance declined by 23% in the no movement scenario, with a simulated low abundance of 892 tonnes at timestep 22 followed by some recovery to 955 tonnes by timestep 30 (Fig. 5.2). Simulations of population abundance assuming limited movements (10km) showed more robust estimates of abundance. This scenario had the highest peaks across simulations (1112 tonnes at timestep 8, 1063 tonnes at timestep 22) and a final abundance of 1044 tonnes. Abundance declined of 20% during the simulation timesteps. When movement distance was increased, medium (50km) and long distance (100km) movements had a similar trend in fluctuations and abundance results were similar, largely decreasing until timestep 10 and fluctuating between

1000 and 1040 tonnes for each timestep between 10 and 30. For simulations where movements increased to 50 km and 100 km, we observed an increase of 4% in final pink ling abundance compared to the absence of movements (Fig. 5.2, purple line).

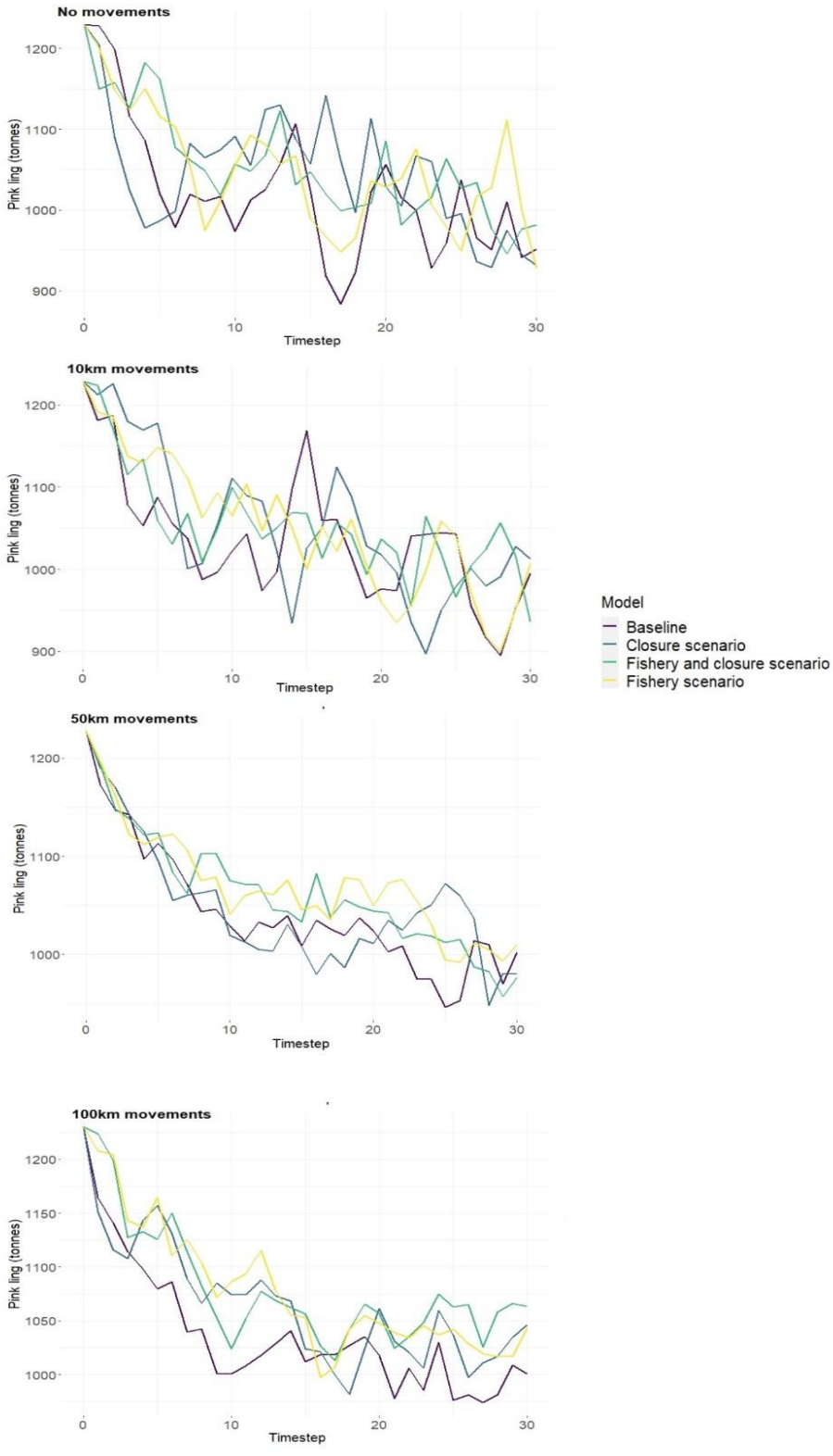

Figure 5.2: Adult pink ling abundance (tonnes) for 30 future annual timesteps. Each plot represents a different movement type (sedentary, 10 km movements, 50 km movements, 100 km movements). The purple line shows the baseline scenario, representative of the current fisheries management, the blue line shows the persistence under a "closure" scenario (spatial closures were modified by increasing their extent for 10 km); the yellow line shows the "fishery" scenario where it was simulated a reduction of 10% of fishing mortality; and the green line shows the combination of both within the "fishery and closure" scenario.

For all movement strategies, stage matrix parameters had a larger influence in determining abundance compared to habitat suitability and carrying capacity (Fig. 5.3). Modifications to stage matrix values caused the largest variability, with much variability in abundance across simulation timesteps compared to the baseline scenario. This difference was more evident for the sedentary scenario, which showed the largest increase in abundance (445 extra tonnes) compared to the baseline model. Variation in habitat suitability and carrying capacity had less impact on model results and temporal trends showed more stability (Fig. 5.3). Differences in model results were less marked when movements were modelled. For all alternative management scenarios, the longer distance movements resulted in the less differences in abundance, compared to the current management (baseline scenario). This trend is more evident for stage matrix variations compared to the models investigating the sensitivity of PVA to carrying capacity and habitat suitability (Fig. 5.3).

Table 5.2: Coefficients of variations (CV) for each modelled management scenario and movement behaviour.

Management scenario	**Movement behaviour**	**CV**
Baseline	Sedentary	0.082
Fishery	Sedentary	0.070
Spatial Closure	Sedentary	0.071
Fishery and Spatial Closure	Sedentary	0.064
Baseline	10 km movements	0.074
Fishery	10 km movements	0.078
Spatial Closure	10 km movements	0.083
Fishery and Spatial Closure	10 km movements	0.062
Baseline	50 km movements	0.061
Fishery	50 km movements	0.052
Spatial Closure	50 km movements	0.061
Fishery and Spatial Closure	50 km movements	0.057
Baseline	100 km movements	0.057
Fishery	100 km movements	0.056
Spatial Closure	100 km movements	0.052
Fishery and Spatial Closure	100 km movements	0.052

Whilst different scenarios of movement, demographic parameters, and spatial heterogeneity influenced temporal patterns of abundance, the spatial distribution of populations remained similar across all simulations. Analysis of the spatial distribution of pink ling across timesteps for the average of all replicates, revealed that the eastern stock was more abundant than the western stock. Fishing targets areas of predicted high population abundance. High abundance areas were located between eastern Victoria and New South Wales followed by areas in eastern Tasmania (Fig. 5.4). The Bass Strait area was covered by spatial closures implemented to protect School and Gummy Shark habitat, as defined in the Southern and Eastern Scalefish and Shark Fishery and Small Pelagic Fishery Closures Direction 2016 (AFMA 2018). Though Bass Strait is currently closed to the trawl fishery, this location appeared less suitable for pink ling with low predicted abundance even though no fishing mortality was applied (Fig. 5.4). Maps displaying the spatial distribution for each timestep and for all scenarios can be found in Appendix 5.

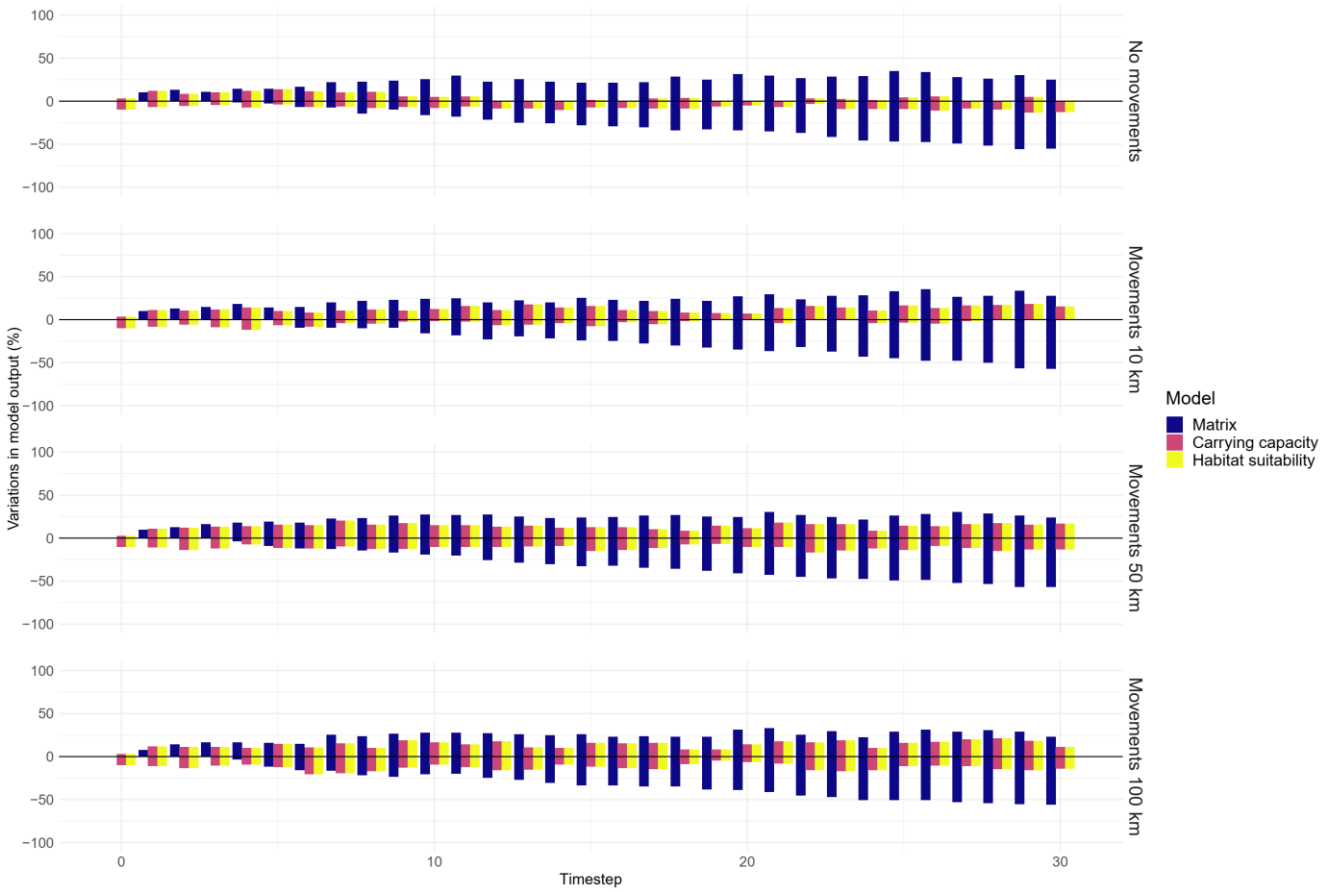

Figure 5.3: Variations in models' results showing the sensitivity of the models to perturbations of stage matrix parameters ("Matrix" in blue), carrying capacity (pink bars) and habitat suitability (yellow bars). Variations in models' outputs are shown for each simulated movement scenario. The bars show the percentage of variation in pink ling total abundance when the model is perturbated by a factor of ±10% for each timestep.

5.3.2 Fisheries management scenarios

We modelled the future abundance of adult pink ling under three alternative fisheries management scenarios for 30 annual timesteps and compared these to the baseline scenario. In all scenarios, ling abundance displayed temporal fluctuations around an overall declining trend. Abundances declined considerably over the first 10 timesteps and tended to stabilise thereafter (Fig. 5.2). When movements are absent or limited, we found high variability in total adult pink ling abundance (Fig. 5.2 and Table 5.1 for CV).

Overall, variation in how pink ling abundance responded to different management strategies was sensitive to the selected movement behaviour. No single fisheries management scenario emerged as consistently the most suitable to ensure population persistence across movement

types (Fig. 5.2). All management scenarios resulted in less fluctuations in population abundance compared to the baseline model (Fig. 5.2 and Table 5.1). Despite a 50% reduction of areas available to fishing in the 'Closure' scenario, the abundance benefits of this strategy were limited. The final timestep of abundance was larger than the baseline model scenario only when ling were allowed to make large movements (Fig 5.2). Reducing fishing mortality ensured final pink ling abundance was larger than the baseline scenario in all management scenarios when movement distance was 10km or greater (Fig. 5.2).

The spatial distribution of abundance was relatively invariant to management scenarios. The eastern stock consistently had a larger abundance than the western stock (Fig. 5.4). Pink ling populations distribution was similar for all fisheries management scenarios and movement behaviours, with limited differences in total abundance of pink ling per cell. Within the western stock area, larger populations were found to correspond to high fishing effort areas. Limited temporal variation was found in the spatial distribution of pink ling for all managements and movement scenarios. All maps displaying the spatial distribution for each timestep and for all the fisheries management scenarios simulated can be found in Appendix 5.

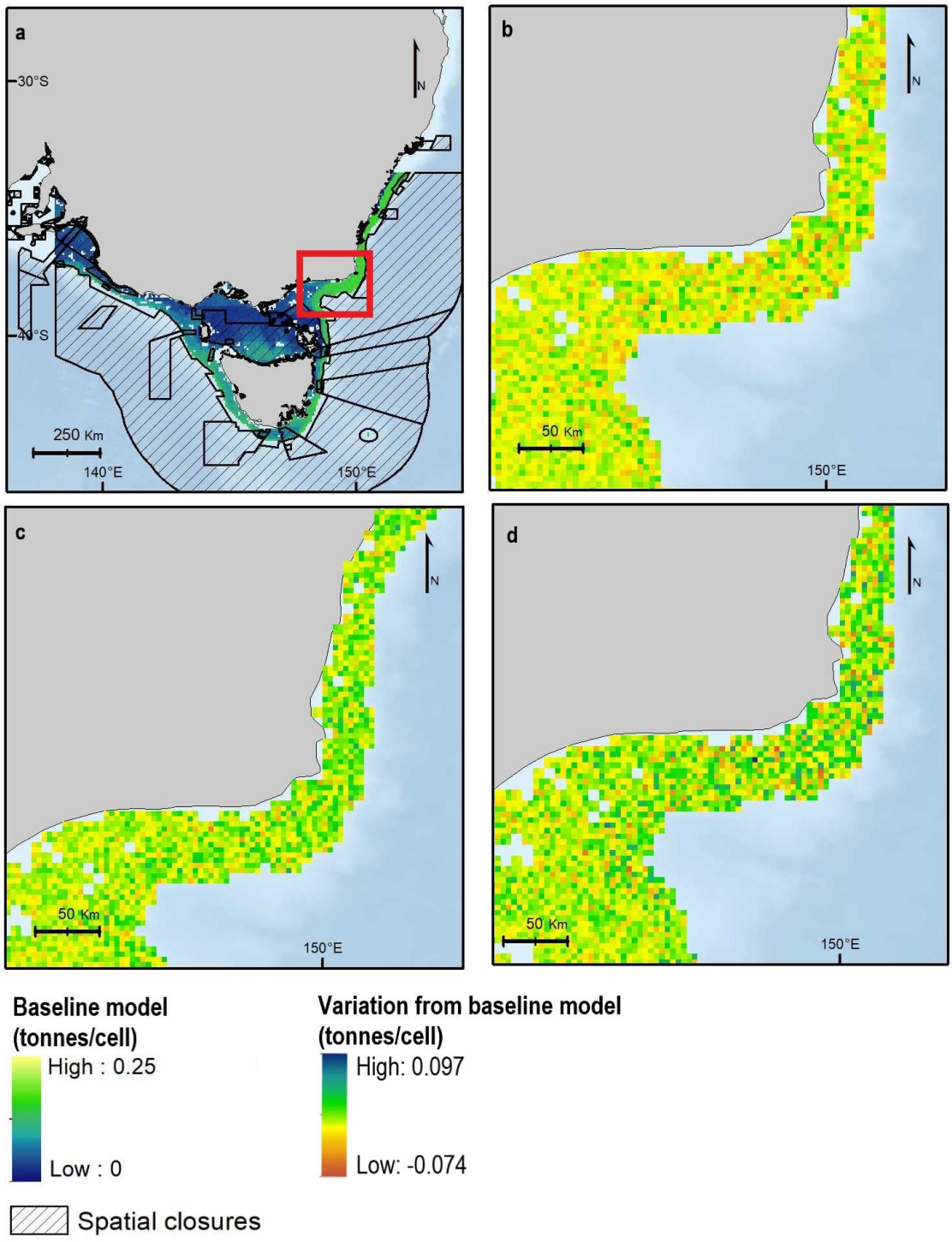

Figure 5.4: Spatial distribution and abundance of adult pink ling in tonnes per cell. Abundance is shown for baseline (panel **a**) and detail of differences in abundance from the baseline scenario in Eastern Victoria area for alternative fisheries management strategies (panel **b** Fishery Scenario, panel **c** Closure Scenario, panel **d** Fishery and Closure Scenario). Data shows the simulation results at timestep 30 for sedentary fish. Spatial closures according to the Fishery Report Status 2019 (Patterson et al. 2019) are shown in the top left panel (a). Red rectangle shows the area highlighted in maps b, c and d. Maps in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

5.4 Discussion

Population viability analysis revealed that more knowledge around pink ling movements is required to ensure more realistic and reliable models to inform fisheries managers. Even with significant management intervention, such as increased spatial closures and reduced fishing pink ling abundance is declining. Pink link abundance showed to be influenced by the distance of movements undertaken by individuals. Furthermore, movement tended to dampen the effect of alternative management strategies such that no single strategy explored here appeared to be more beneficial than others.

The current fisheries management regime led to a universal decline in pink ling abundance over the next 30 years. However, these declines were ameliorated when ling were allowed to make larger movements. Intuitively, when adult pink ling are capable of movement at broader scales throughout this seascape, a larger proportion of fish would be in regions that are not fished, increasing their long-term probability of survival. Despite the overall negative trend, pink ling abundance remained above current targets and indicators, and had low vulnerability to fishing. These results are consistent with the information from recent stock assessment reports which showed that pink ling is not overfished (Patterson et al. 2019). There is poor evidence of stock recovery despite changes to trawling fisheries management in south-east Australia date back to mid-2000s, and explicit recovery strategies are adopted (Novaglio et al. 2018). Reducing TAC is a common approach to reduce exploitation but globally only a low percentage of stocks have recovered despite these management decisions (Trzcinski and Bowen 2016, Hilborn et al. 2020). Changes in fishing pressure appeared to have a limited influence on pink ling abundance. These results indicate that the current fishery targets are likely appropriate for managing pink ling fisheries, and further reducing fishing pressures would not bring substantial benefits to the pink ling stock, even when this is combined with larger spatial closures. Additionally, uncertainty around stock structure is an unresolved issue for ling species and had hindered effective management of the fishery in the past (Daley et al. 2000) and might have influenced our simulations. Here, some models' parameters were assumed to

be the same for western and eastern stock due to little knowledge of the differences between these two stocks, however, more details on the stock-specific characteristics might improve the reliability of models' predictions.

Increased closures were most effective when pink ling were assumed not to move far, while reducing fishing pressure was more effective when movements are included. These results indicate that spatial management tools may be more effective for sedentary species while focussing on fishing catch could be more beneficial when targeting highly mobile species which might move across a larger area (Le Quesne and Codling 2008, Breen et al. 2015). We expected that combining reduced fishing mortality and increased spatial closure size would amplify the benefits to pink ling viability. However, this result was only clearly observed when ling were assumed to make large movements (Fig. 5.2). Despite Marine Protected Areas (MPAs) and permanent spatial closures being actively promoted by many fisheries scientists, there is some equivocal evidence on their effectiveness. Variations in MPAs size, larval and adult distance movements, generation time and connectivity can result in different spatial and temporal population trends and thus influence the efficacy of MPAs (Grüss et al. 2011, Moffit et al. 2013, White et al. 2014). Different amounts of success have been demonstrated for sedentary and highly mobile species. These more general findings raise questions on the spatial extent of closures and which life stage actually needs to be protected to facilitate population recovery (Le Quesne and Codling 2008). Positive effects of spatial closures have been demonstrated for deep sea south-east Australia species. For example, data-driven closures proved to be useful for managing sharks when combining networks of closures developed based on sharks vertical migration and horizontal movement patterns (Daley et al. 2015). Greater understanding of life history and movements is needed, ensuring an optimal placement of spatial closures around spawning and nursery areas that could lead to more sustainable management of the stocks.

The significance of understanding a species' movement behaviours is key to spatial management (Heath et al. 2008, Hutchinson 2008, Punt et al. 2016). This was clearly

illustrated in our results where model projections of abundance changed considerably depending on movement behaviour. An unstable persistence trend was observed when movements were absent or limited to 10 km. Our predicted temporal variability in abundance under these model parametrisations mirrors the variability actually observed in the catch of pink ling in south-east Australian waters (Bruce et al. 2002). Our finding also corroborates previous suggestions that ling only make small scale movements across their lifetime (Punt et al. 2016). It is well-known that abundance variability has a detrimental effect on population persistence, and it is interpreted as population vulnerability to exploitation (Akçakaya 2000).

In our models we assumed that fish can move equally in all directions through suitable habitat. It is, however, common for fish to display directionality in their movements due to the presence of currents, or feeding (Daley et al. 2000, Woolnough et al. 2009). Here, we did not consider the ability of fish to actively avoid trawling, a behaviour observed in pink ling (Piasente et al. 2004), or movement associated with spawning (Horn 2005). The knowledge of movement associated to spawning and spawning aggregations locations in south-east Australia might implement the predictions of our models, and provide new insight on optimal position of spatial closures targeting these regions.

Spatial differences in abundance between eastern and western regions emerged. The western stock was less abundant and fishing mortality was more intense than the current fishing mortality used for managing eastern stock. Despite the presence of areas with high fishing effort, the eastern stock was more persistent than western stock. Our simulations did, however, assume fixed fishing mortality across all timesteps and thus did not account for any temporal and spatial variation in fishing catches (Cordue 2018, Patterson et al. 2019). Other SESSF species display spatial differences in biomass such as gemfish and deepwater sharks, and different management strategies are applied for eastern and western zones (Patterson et al. 2019). Variations in population dynamics are generally incorporated for species where spatial separation among components is clear, however this approach leads to underestimating population diversity for species where stock separation is more cryptic but

equally important (Schindler et al. 2010). The integration of genetic data may be more informative to understand this separation and better manage the stocks (Dudgeon et al. 2012).

One of the characteristics of spatially explicit population viability analyses is that they can account for spatial closures and variation in spatial management tools can be easily simulated (Carroll et al. 2003, Carroll and Miquelle 2006). Studying the spatial structure of marine populations is useful to understand which areas are more productive and persistent. Likewise, PVA results can help the design of spatial management tools, prioritizing sites to protect (Carroll et al. 2003, Newbold and Siikamäki 2009). This approach is helpful to inform on optimal locations or size of new protected areas.

The accuracy and precision of PVA predictions are strongly influenced by the quality of biological understanding underpinning model construction (Naujokaitis-Lewis et al. 2009). We found our models to be highly sensitive to demographic parameters but less sensitive to carrying capacity and habitat suitability. Pink ling is commonly found in a variety of habitats in Australian waters (Daley et al. 2000), and for this reason might be less sensitive to variation in habitat characteristics and, as a consequence to carrying capacity, which here was assumed to be related to habitat suitability. PVA has been used for decades and best practices are well documented, allowing appropriate results interpretation, use of sensitivity analysis and model validation (McCarthy et al. 1995, Coulson et al. 2001, Akçakaya et al. 2004). Another advantage of population viability analysis is the opportunity to understand relative impact of management strategies and compare alternative options evaluating populations vulnerability to extinction or to fall below persistence indicators. Population viability analysis might provide a suitable alternative when ecosystem-based fisheries management is not possible because of the lack of species interactions data. This approach seems appropriate for SESSF, due to the very limited knowledge of species interactions (Bruce et al. 2002).

Limitations on using population viability analysis are generally relative to the quality of available data (Brook et al. 2000). Using fishery-dependent and fishery-independent data often leads to different models results. Fishery-dependent data may influence the designation

of suitable habitat, and therefore pink ling distribution. In general, fishery-dependent data is better at predicting temporal trends of presences and absences because longer time series are usually available, while fishery-independent data produced more spatially accurate predictions since surveys are designed to sample all habitat types (Pennino et al. 2016). Increased knowledge of how pink ling distribution and abundance varies across the region, and how it responds to particular habitat types, would increase the reliability of our models. Assumptions often have to be made about demographic parameters, individual behaviours or larval stage details for marine species as this data is not readily available (Brooks et al. 2009). Indeed, a more detailed knowledge of pink ling home range movements is required to better understand the impact of fisheries management on ling. Natural mortality of many marine species could also be affected by other stressors, including climate change and habitat loss (Dulvy et al. 2003), which we omitted in our analyses. Though population viability analysis potentially allows the inclusion of habitat changes, but here we only considered fluctuations due to environmental stochasticity, while suitable habitat availability was stable for all timesteps.

Pink ling persistence was influenced by life history characteristics such as survival and reproduction. Therefore, future research to understand and characterise natural mortality, larval stage and movements of pink ling could improve the reliability of our models. In particular, focusing research effort on the pink ling larval stage, such as larval duration and behaviour, will help parameterise the spatial scales of dispersal and identifying spawning locations and timing. Better knowledge of spatial heterogeneity of demographic parameters and habitat could benefit fisheries management decision, by improving the understanding of how persistence changes regionally. In general, studies on fishing indicators not evaluate the influence of habitat conditions, even if this approach showed the potential of overestimate or underestimate fishing effects on aquatic species (Nash et al. 2016). Further exploration of population viability analysis modelling approach and its use for fisheries management is needed to understand the benefits and the weaknesses of using this method.

To conclude, pink ling showed a general but limited decrease in its simulated future stock abundance based on the current fisheries management but remains above reference indicators. Neither increased size of existing spatial closures and/or and overall reduction in fishing mortality proved best in increasing stock abundance. Knowing pink ling dynamics would help to explore alternative management strategies identifying for example new spatial closures areas, instead of modifying the existing ones. Our population viability analysis results were largely influenced by movement behaviours, suggesting that a better knowledge of pink ling movements could contribute to inform fisheries management.

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Chapter 6

General discussion

6.1 The benefits of using spatially explicit ecological models to manage living marine resources

Many life history aspects of marine species are uncertain or unknown, largely due to the challenges of obtaining empirical *in situ* data for large populations distributed throughout vast seascapes. However, ecological modelling approaches can be used to help put these limited data into broader context, as well as help direct future research directions. Models are also critical in managing marine species: they can simulate future scenarios of persistence, distribution and population dynamics, helping managers to understand the impact of potential management actions and decisions on marine ecosystems (Hilborn 2012). This often results in more sustainable and cost-effective practices, improving the design of protected areas (Holland 2002) and management of marine living resources (Fulton et al. 2011). Recent advancements in computational power allow for building more reliable, realistic, and detailed models and performing ecological simulations on larger spatial and temporal scales (Bunnefeld et al. 2011). In this respect, many ecological models are now spatially explicit and incorporate real-world landscapes and complex environments, allowing for the investigation of metapopulation dynamics. These realistic ecological models, in addition to proving critical management guidance, help us understand how species might respond to habitat fragmentation and loss and climate change (Dunning Jr et al. 1995).

This thesis applied spatially explicit ecological models to several important species found in south-east Australian waters, a critical region characterised by high biodiversity as well as significant human impact, such as fishing pressure, increasing population, and oil and gas exploration (Commonwealth of Australia 2015). The focal species are significant to this region

for their economic and ecological relevance. Blacklip abalone is one of the most important commercial species in Victoria (Savage 2015), and snapper, King George whiting and pink ling are important fisheries species (Bruce et al. 2002, Hamer et al. 2011, Jenkins et al. 2016). Sea urchins are keystone species within the shallow rocky reef systems of this seascape and may be experiencing a recent range expansion, strongly linked to Australian waters warming (Ling et al. 2010, Ling et al. 2015, Ling et al. 2019). Together these species were chosen as representative of the south-eastern Australian marine ecosystem ensuring that the modelling approaches and ecological outcomes can be broadly applied to other species and regions.

The overarching aim of this thesis was to quantify the persistence of marine species living along the south-east Australian coast and investigate the combined effects of i) species-specific life history characteristics and habitat requirements, and ii) various fisheries management strategies. In this work, I applied a range of spatially explicit ecological models to study marine populations. For example, in Chapter 3 I presented a novel method to effectively integrate important connectivity-related information into species distribution models (SDMs), and in Chapter 2 I extended the use of spatially explicit population viability analysis (PVA) to inform commercial fisheries management. In Chapter 2, I demonstrate the power of integrating habitat spatial and temporal heterogeneity in a spatially explicit PVA to assess the impact of various fisheries management strategies. In my thesis, I explored the use of spatially explicit PVA in the fisheries management context, an approach of intermediate complexity not yet explored. I showed that spatially explicit PVA is a flexible tool to predict future species persistence and assess the impact of alternative management strategies (Akçakaya et al. 2004). In chapter 2, I developed a PVA which included realistic temporal and spatial variability to simulate habitat loss. I demonstrated that these dynamic habitat characteristics play a major role in determining the persistence of abalone, and that PVA proved uniquely suitable for incorporating these dynamics. The results of this abalone PVA demonstrate that it is critical for models to account for habitat heterogeneity and its subsequent impacts. This might be particularly significant for species threatened by the loss of habitat due to climate change,

those experiencing range expansion, invasive species, as well as those impacted by destructive fishing methods (e.g., bottom trawling).

Spatially explicit models are not only useful in fisheries management but are fundamental in many marine conservation efforts. Spatial management tools such as marine protected areas are largely used to protect key habitats and species (Breen et al. 2015). Spatially explicit models that predict a species' geographic range and movements throughout the seascape are necessary to inform these conservation decisions (Dunning Jr et al. 1995). For example, results from Chapter 3 identified potential conservation priorities around hotspots of connectivity, which were associated with high suitability habitat. Similarly, in Chapter 4, the results identified 'stepping-stones' as well as connectivity hotspots, providing information on key habitats that can be useful for managing the species. Clearly, using spatially explicit ecological models is incredibly valuable in informing marine conservation and fisheries management, and research on how to improve and apply these models is important in achieving conservations goals.

6.2 A new opportunity to assess fisheries management strategies: Population Viability Analysis

Many tools exist to understand the impact of fisheries management strategies on marine populations and they have been in use for decades (Hilborn 2012). Models evolved from traditional single-species stock assessment approaches to complex ecosystem-based models (Smith et al. 2007). In Chapter 2, I identified six criteria to compare three common categories of models: stock assessments, spatially explicit population viability analysis and ecosystem-based fisheries management modelling tools. This chapter demonstrated that population viability analysis is a flexible tool, of intermediate complexity, suitable to assess fisheries management strategies. The criteria identified to compare these modelling approaches were: inclusion of key life-history traits, spatial heterogeneity of the habitat, efficient management strategies comparison, ecosystem-based approach, fisheries data requirements and ability to perform sensitivity analysis. Despite modern models can potentially accommodate these

features in different ways, these criteria are not always implemented in models applied for management decisions. Common traits to all the three modelling frameworks are the ability of efficiently comparing management strategies impact on marine species, the opportunity to include the spatial structure of populations and inclusion of key life history traits. EBFM modelling tools are explicitly built based on an ecosystem and multi-species approach (Smith et al. 2007), yet spatially explicit PVAs tools have recently been shown to also include multi-species methods (Pastorok et al. 2003, Kianirad et al. 2006). A reliable modelling approach should also include a robust sensitivity analysis to quantify and communicate uncertainties and variability, particularly within management contexts. Sensitivity analysis can be performed within classic stock assessments, as well as population viability analyses, while the complexities of most ecosystem-based models do not always allow for sensitivity analysis, making it difficult to assess uncertainties in predictions. Based on these criteria, I showed how spatially explicit PVA is a powerful and flexible approach, capable of including adequate complexities. An important advantage of this approach is the ability to simulate realistic spatial and temporal variations in populations dynamics and habitats characteristics.

In Chapter 5, I used spatially explicit PVA to explore the population persistence of pink ling across four management approaches. Approaches included a baseline scenario of current fisheries management using quotas, and explored three alternative management scenarios. I built scenarios based on traditional fisheries indicators such as fishing mortality, as well as spatial management tools like spatial closures. No strategy emerged as the most beneficial to the long-term persistence of pink ling, and all scenarios showed significant temporal fluctuations in persistence, supporting existing reports of south-east Australian marine species (Bruce et al. 2002).

By explicitly including the spatial component into my PVAs, I could identify where the most abundant and more vulnerable populations were distributed. Many abundant pink ling populations were found in eastern Victoria. This is a key area of the south-eastern Australian waters, as highlighted in different chapters of my thesis. In Chapter 3, I identified hubs of

connectivity for snapper and purple sea urchin in eastern Victoria, while in Chapter 4, the same area corresponded to important patches for ensuring metapopulation persistence across various taxa. Eastern Victoria is a key region, corresponding to a thermal gradient where major ocean currents converge, and where faunal breaks and habitat discontinuity have been identified (Colton and Swearer 2012).

6.3 The contribution of connectivity in modelling marine species dispersal and distribution

The marine environment is strongly affected by human activities resulting in significant habitat loss and fragmentation (Halpern et al. 2019). In such fragmented habitats, connectivity between habitat patches, becomes critical to ensure population persistence (Hanski and Ovaskainen 2003). In my thesis, I investigated many aspects of metapopulation dynamics and persistence of key marine species of south-east Australia. I explored marine connectivity, investigating its role in determining species spatial distribution in Chapter 3, and metapopulation persistence in Chapter 4. In Chapter 5, connectivity was also highlighted as important, here in terms of the movement behaviour of fish. Pink ling movements are largely unknown, and in my results I showed how predictions of persistence was influenced by movement behaviour, suggesting that this improved knowledge is necessary to obtain reliable persistence predictions and to manage this fishery more sustainably.

Understanding habitat characteristics and species distributions is essential for effective conservation and management. Species distribution models (SDMs) are powerful and efficient tools to characterize the environmental drivers and geographic distributions (Elith and Leathwick 2009). However, the dynamic nature of the marine environment, limitations and challenges in sampling, and the paucity of data, make marine-based SDMs particularly challenging (Robinson et al. 2017). In Chapter 3, I investigated whether incorporating connectivity into marine-based SMDs might improve the models' predictive power. Only a few studies have tried to integrate connectivity into SDMs for terrestrial species using graph-based metrics (Foltête et al. 2012, Clauzel et al. 2013, Girardet et al. 2013), and these suggested

that including connectivity can improve the predictive performance (Foltête et al. 2012). Many studies have analysed marine connectivity using a graph or network-based approach (e.g., Treml et al. 2008, Treml et al. 2012, Andrello et al. 2013, Andrello et al. 2015, Treml et al. 2015, Krueck et al. 2017), but none have integrated these connectivity estimates into SDMs. In Chapter 3, I took advantage of least cost paths analysis and biophysical models to quantify seascape connectivity and assigned patch-level values of centrality (betweenness centrality, degree centrality, eigenvector centrality) to quantify the importance of each habitat patch and then included this in correlative SDMs. Seascape connectivity appeared to have a strong influence in predicting species spatial distribution.

In my thesis, I developed a new understanding of which network-based connectivity metric might be the most influential in determining species distribution and metapopulation persistence. In Chapter 3 and Chapter 4, degree centrality, a node-level metric quantifying the number of incoming and outgoing connections to each habitat node, emerged as the most important connectivity metric. Degree centrality was the connectivity metric with the largest influence in predicting spatial distribution. Although despite degree centrality was not as influential as temperature and bathymetry, it had a significant contribution to SDM predictions.

In my work on metapopulation modelling, I showed that high values of degree centrality, quantified as in-degree or out-degree, are critical to ensure metapopulation persistence, revealing hubs of connectivity as key nodes to marine metapopulation dynamics (Cecino and Treml, in press). Dispersal has a significant role in controlling population dynamics and many studies have quantified the influence of connectivity in metapopulation persistence. However, most studies focussed on a small subset of node-level metrics and network properties (Vuilleumier and Possingham 2006, Bode et al. 2008, Artzy-Randrup and Stone 2010, Kleinhans and Jonsson 2011, Watson et al. 2011, Shtilerman and Stone 2015), or on the role of self-seeding (Zamborain-Mason et al. 2017), often presenting example for theoretical networks. For this reason, an extensive study on a broad set of connectivity metrics and realistic marine metapopulation was needed. Knowing which network metric is the most

influential in terms of metapopulation persistence can inform managers on which habitat patches to prioritize to ensure metapopulation-wide outcomes. Together with several previous studies, I show evidences that hubs of connectivity and habitats with large degree are critical for stability of metapopulations (Minor and Urban 2007, Shtilerman and Stone 2015, Zamborain-Mason et al. 2017).

For many marine species, it is the larval stage which is critical for maintaining connectivity among subpopulations. In Chapter 4, I explored persistence focussing on a group of real-world metapopulations representative of different life history traits and dispersal characteristics, with extended or restricted larval dispersal capabilities. In this chapter an additional analysis was completed to understand which early life history trait mostly influences persistence. The length of pre-competency window resulted as the most significant trait among a set of life-history characteristics. Together, this information can help conservation scientists to better understand which species may be more vulnerable when some key habitats are impacted by excessive fishery or habitat loss.

Movement ecology is often unknown for many fish species, particularly for fish inhabiting the continental shelf and slope (Afonso et al. 2014). In Chapter 5, I investigated different movement patterns in pink link, an important commercial fish in the region, and quantified the impact of different fisheries management scenarios. Pink ling abundance displayed different trends for each movement behaviour and across all management scenarios. This chapter's results suggest that better knowledge on movement ecology is necessary, because it largely influences the efficacy of a range of fisheries management strategies.

6.4 Key limitations

In this section, I discuss some of the general limitations of this thesis while specific limitations for chapters 2-5 were discussed in each chapter. Through this thesis I made significant advancements in the field of marine connectivity and distribution modelling, but there are

various sources of variability in predicting metapopulations dynamics that may influence model results.

In an effort to reflect realistic metapopulation processes, I included many parameters without local-based estimates or validation. For instance, larval mortality is often unknown for many marine species, requiring one to estimate mortality in the models, often using data from related species (e.g. same family). I attempted to minimise these parameter issues by choosing common and well-studied species across the study region where information was largely available from the literature, and often the parameters were estimated in local-based studies. However, when studying the metapopulation persistence of species where larval mortality is completely unknown and assumptions are required, sensitivity analysis allows to understand the model uncertainty around this parameter. Another common limitation of models studying marine connectivity is the absence of data representing the spatial heterogeneity of species life histories and habitats. The marine connectivity model used here (Treml et al. 2012) addressed this limitation by including spatial data of habitat heterogeneity and used these data as a proxy for reproductive output and larval settlement cues. Similar issues on data availability were found in modelling metapopulation persistence using PVA. Population models and fisheries management models are known for their significant data requirements and their reliability often depends on accuracy of the data used (Brook et al. 2000). Throughout, I relied on transparency in my methods and results, and sensitivity analyses to communicate potential impacts.

Another limitation of the spatial models presented in this thesis is related to the characteristics of the environmental data used. Environmental data are often summarised as long-term (e.g., annual or decadal) averages and there might be a discrepancy between these periods among the different environmental data layers used. For instance, the environmental variables used in the SDMs (e.g., temperature, salinity) of this thesis were downloaded from the Bio-Oracle database (Tyberghein et al. 2012), where data largely consists of long-term averages, describing periods of few years or decades. This potential temporal mismatch between data

layers might result in discrepancies in how I characterised the marine environment. However, I feel the impact would be minor and again, I relied on clear transparency in the modelling approaches and data used in this thesis, also ensuring repeatability.

The limitations of this thesis largely depend on data availability and quality, and this is a common trait of models trying to understand marine ecology and population dynamics. In all the models presented in this work, the parameters were carefully chosen and clearly explained, limiting the number of assumptions. The most suitable modelling tools were selected based on the best available data and to obtain the most realistic and reliable predictions. For example, BRT algorithms were preferred to other approaches in Chapter 3, because BRT have been documented to perform well in presence-only SDMs (Elith et al. 2008). Sensitivity analysis and model validation were also included and explained for all chapters, where appropriate. Where not explicitly included, the studies investigating model sensitivities were appropriately cited (e.g. larval connectivity model sensitivities in Chapter 4).

6.5 Opportunities for future research

This thesis highlights new approaches to study marine species distribution, connectivity and how to employ modelling tools widely used in conservation science to address issues within the fisheries management context. The results of my thesis suggest that future research is recommended, specifically around connectivity. Research on integrating connectivity in the study of species distributions is increasing (e.g., Maiorano et al. 2019, Jennings et al. 2020, Tarabon et al. 2020) and this work provides a clear foundation for future marine-based models. This thesis explored the role of connectivity in predicting marine species distribution only for a couple species with limited dispersal. Future work should expand the analysis to more species, with longer dispersal range and associated with different habitat types.

The role of life history traits in determining metapopulation dynamics is of great interest to marine ecologists and managers alike, and previous studies have explored which life history traits influences connectivity (Treml et al. 2012), gene flow patterns (Galarza et al. 2009) and

adult distribution (Clarke et al. 2001). In Chapter 4, I presented important results on which early life history traits might be the most influential to metapopulation persistence. In my thesis, the extent of the larval pre-competency period was shown to be the most influential, but future research is recommended to investigate a larger group of traits and species. Broadening the knowledge in this research area might be of great benefit to marine conservation, and knowing which larval trait is indicative of persistence might help us understand which species is more vulnerable or more persistent based on its life history traits.

Network approaches have proved to be powerful and flexible in quantifying and visualising connectivity. This approach is widely used in marine conservation, largely for prioritising conservation and placing marine protected areas (e.g., Andrello et al. 2013, Andrello et al. 2015, Krueck et al. 2017). A potential opportunity of future research is the development of new models integrating graph-based metrics within fisheries models. This is particularly significant for ecosystem-based fisheries management models, where network approaches may provide new methods for including the connectivity process and patterns in these to ecosystem-based models.

Future research could also focus on implementing spatially explicit PVA models integrating spatial and temporal habitats variability, which would be critical in the context of quantifying the impact of future climate change. Similarly, future work is needed around the application of these models to evaluate the effect of marine habitat loss, for example due to the use of trawling, coupled to the assessment of fisheries management strategies, and how habitat loss might have different impacts on species when applying semelparous or iteroparous strategies. Finally, the possibility of developing multispecies PVA models may encourage future research on the use of these models applied to ecosystem-based fisheries management.

6.6 Concluding remarks

The growing pressure of fisheries and the challenges of understanding marine population dynamics in a changing world, require the implementation of accurate and reliable models that

facilitate marine species management. The shortcomings of many traditional models (e.g., the simplification of spatial structure of populations and lack of information on population dynamics) are well known specifically on how they have often failed to ensure persistent marine populations. New ecosystem-based modelling approaches are recommended, but often these approaches have a high level of ecological and computational complexity, making these models appropriate to study only a limited number of key species or well-known ecosystems. In this thesis, models of intermediate complexity were suggested as suitable tools to be used in the fisheries management context. With fisheries pressure increasing, and many species disappearing or extremely vulnerable to extinction, the need for less data intensive and time-consuming models may be required to increase our modelling capacity and understanding across more taxa.

Connectivity is emerging as key feature in many areas of marine ecology, specifically marine spatial planning, yet limited knowledge of dispersal dynamics and movement ecology led to the omission of this process within marine species distribution models and most population dynamics models. Population connectivity is known to significantly influence metapopulation dynamics and much more effort is needed to develop new methods to integrate and explore the influence of connectivity. This thesis develops a new understanding on the role of connectivity, proposing a new method to integrate connectivity into predicting marine species distributions. I demonstrated how graph-based metrics provide rich information on habitat or subpopulation importance, suitable for marine management decisions. Overall, connectivity emerged as critical in determining metapopulation persistence, significant in predicting species distributions, and helpful in informing fisheries management decisions. This clearly demonstrated the need of field-based data and modelling tools to better understand the characteristics of marine species connectivity.

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Appendix 1

Population Viability Analysis of blacklip abalone, *H. rubra.*

Population viability analysis requires habitat suitability layers that describe the relative likelihood of an environmental cell supporting the presence of the target species. Habitat suitability layers contain values of habitat suitability index between 0 (inhabitable) and 1 (habitable). In our PVA we used spatial layers consisting of rasters, with each layer corresponds to one of the three Victorian abalone management zones (Fig. 2.1 in Chapter 2). The model extent size varied according to each zone (Western 6900 km^2, Central 34000 km^2, Eastern 8350 km^2) at 5-ha resolution. Cell size was chosen to reflect the abalone population size previously used in a local study (Hart & Gorfine, 1997). Habitat suitability layers were obtained from species distribution models (SDMs) using 'dismo' package (Hijmans et al., 2017) within R v3.6.2 (R Core Team, 2019). Blacklip abalone SDMs predict species spatial distribution using occurrence data from Atlas of Living Australia, ALA (https://www.ala.org.au), abalone absence data were not available and pseudo-absence data were used in the model. Environmental parameters for the SDMs consisted of bathymetry (GEBCO, General Bathymetric Chart of the Oceans, https://www.gebco.net), monthly average sea surface temperature, and the magnitude of currents, chlorophyll concentration, all available from AODN portal (Beggs et al., 2010; Johnson et al. 2013; IMOS, https://imos.org.au/). Other habitat data used to build the SDMs were seabed gravel (Jin Li, 2010) and sand content (Jin Li, 2011) available from data.gov.au for the entire Australian Exclusive Economic Zone. SDMs were performed using generalized additive models (GAM), in which the probability of species presence, the linear response variable y, depends on smooth functions of the environmental predictor variables, $f(x_n)$, as per Eq. 1. (see below) Model results were used to develop and map habitat suitability scores for each model cell.

$$y = \beta_0 + f(x_1) + f(x_2) + \cdots + f(x_n) + \varepsilon, \qquad \varepsilon \sim N(0, \sigma^2) \tag{1}$$

Key life history traits have been included in the model through several parameters such as stage matrix, populations size, N, and carrying capacity, *k* (Hart & Gorfine, 1997; Bardos et al., 2006; Fordham et al., 2013). Specifically, a stage-structured approach was used to model populations with stages defined on the stage matrix available from COMADRE database, a demographic database containing matrix population models of hundreds of plants and animals (Salguero-Gómez et al., 2016). A seven stages matrix is available from this database for abalone (Fordham et al., 2013). We applied competition density-dependent processes using a growth rate (R_{max}) of 1.82 (Fordham et al., 2013) to life-stage transition matrix, adjusting the vital rates in each cell based on the carrying capacity in the cell and Beverton-Holt density dependence function (see equation 2 below and Fig. A1.1). We built a stochasticity matrix to describe the uncertainty around the stage matrix transition probabilities (as standard deviations) and it is used to simulate environmental stochasticity, where zeros indicating no stochasticity, i.e. there is no uncertainty about environmental fluctuations in our system.

$$\frac{dN}{dt} = R_{max} N \frac{k - N}{N} \tag{2}$$

The initial abundance of abalones for each stage was derived using stable state age distributions multiplied by the carrying capacity of the seascape, and then drawn from a multinomial distribution to return whole integers. Carrying capacity of the landscape was estimated from the upper bound estimation of abundance of adults from fishery-independent survey data (Hart & Gorfine, 1997), following an approach used in population viability analysis (Mebane & Arthaud, 2010)and it was assumed to affect only adult stages.

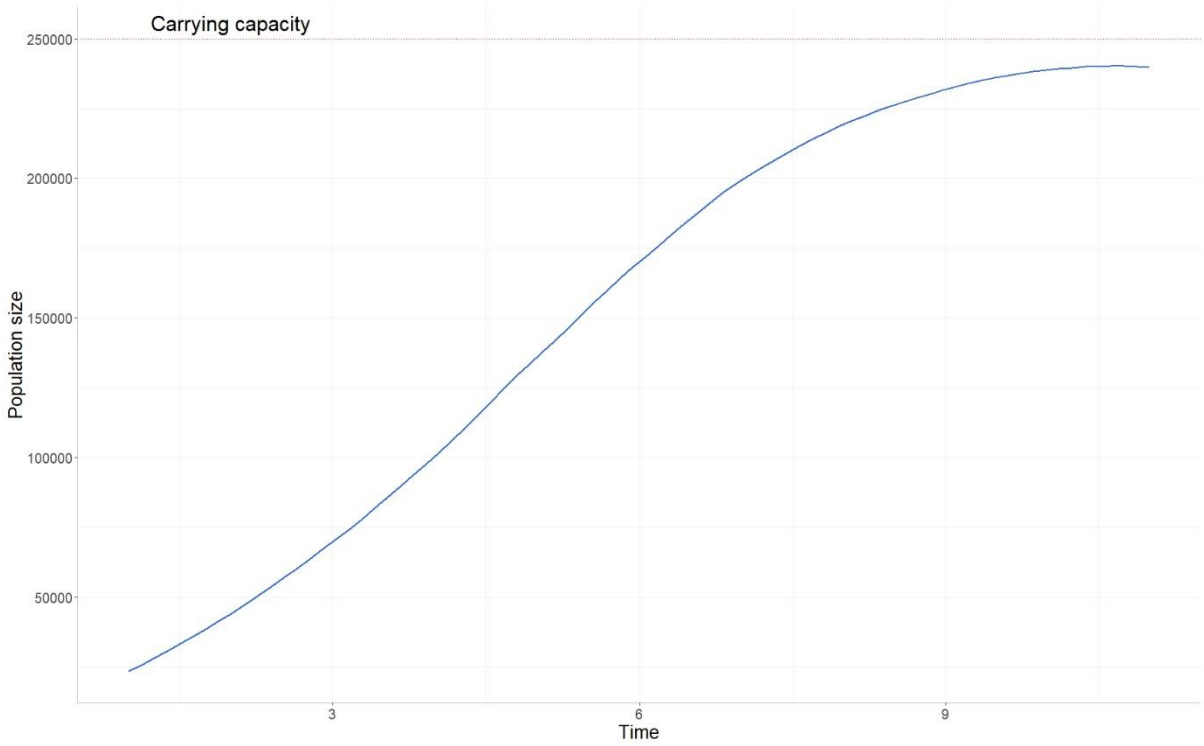

Figure A1.1: Growth curve (in blue) representing population size over time. Dashed line shows the carrying capacity of the system.

Dispersal can be incorporated in PVA models; however, dispersal is not included in this work as there is disagreement around dispersal ability of abalone. Formerly it was assumed that abalone populations are substantially closed and rely for individual replacement only on local larval retention (Bardos et al., 2006). Recent advancements have identified evidence of both long and short distance larval dispersal (Miyake et al., 2017). However, due to the cryptic nature of the juvenile stage, juveniles' movements are almost unknown, while adults settle on reefs. The illustrative purpose of our case study, we decided to assume blacklip abalone populations are closed.

STEPS package (Visintin et al., 2020) allows one to incorporate functions to describe management actions into the models (Fig. A1.2). Fishing can be either included in form of fishing mortality function, if available, or using an "origin" and "destinations" layer. An "origins" layer contains information on the number of individuals removed per cell each timestep. A "destinations" layer contains value representing the number of individuals left in each cell after fishing; in this case destination layers contained 0 values in each cell where fishing is allowed.

Area of marine parks, marine reserves and Marine Protected Areas (MPAs) were downloaded from World Marine Protected Areas Database (UNEP-WCMC and IUCN 2020). In these areas, together with Port Philip Bay region, where commercial fishery is not allowed, no fishing pressure is applied. The number of individuals removed from the environment was obtained from Fisheries Victoria reporting of annual TACC (Victorian Fisheries Authority, 2019). Fishing pressure was only applied to individuals vulnerable to capture, i.e. the recruit stage. Spatial distribution of fishing effort is not known and so it was assumed to be equally distributed across the fishing zones. Due to the limited knowledge of recreational and indigenous fishing we focussed on commercial fisheries catch only.

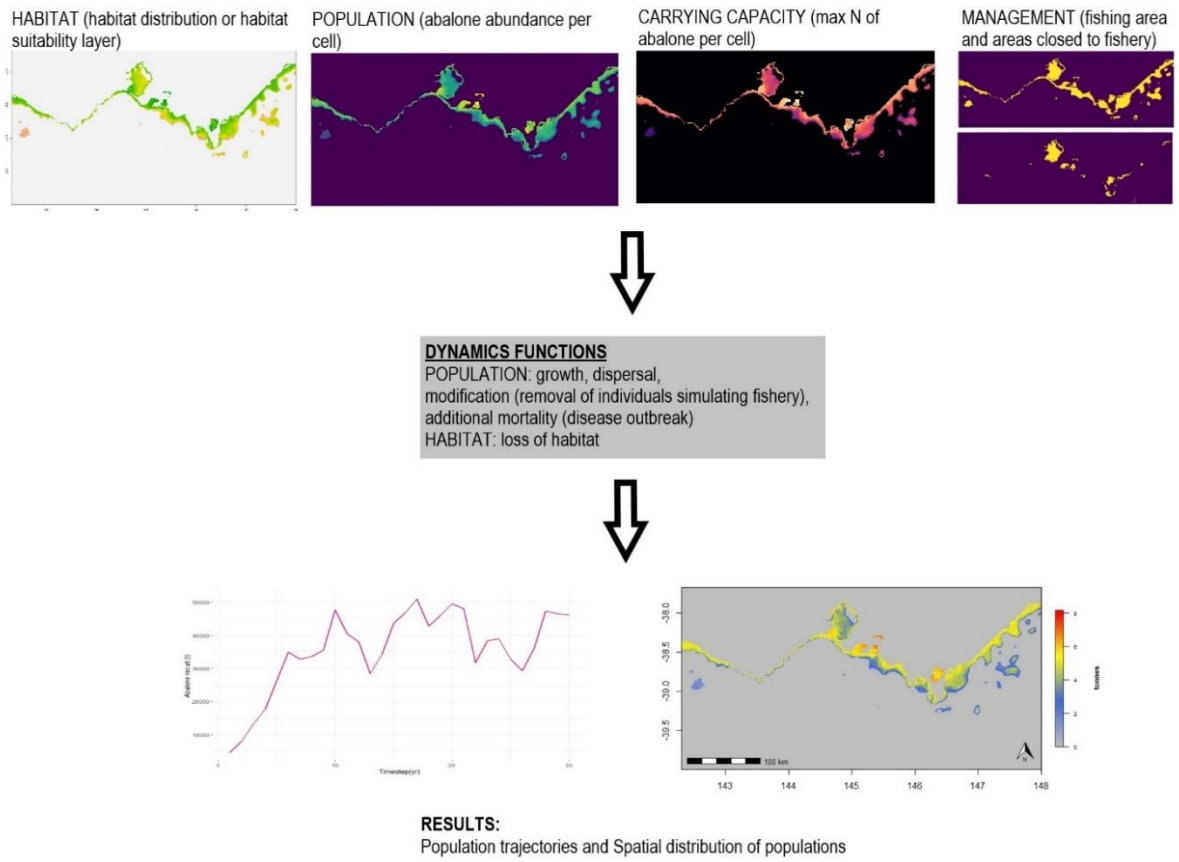

Figure A1.2: STEPS (Visintin et al. 2020) basic structure. During the simulations dynamic are applied to the seascape at each iteration (timestep) and stored in a "results" object (as per Visintin et al. 2020). Dynamic functions that are applied are population growth, dispersal, modifications (i.e., management actions) and additional function such as mortality. Model outputs include metapopulation trajectories and spatial distribution of the populations across the seascape.

We modelled three different scenarios. For the Central Zone we simulated fishery as the only modification that influences populations. For the Eastern zone habitat loss was simulated. We applied a coefficient of loss of available habitat of 0.1 affecting all years. This coefficient is used in all timesteps to gradually reduce suitability of habitat, which then influences other model parameters such as abalone abundance and carrying capacity. In the past decade, a large loss (up to 90%) of abalone habitat has been recorded due to urchin grazing (Department of Primary Industries, 2012). Despite culling measures recently enacted to limit sea urchins to spread (Gorfine et al., 2012), we selected a loss rate of 10% of habitat because we assume that the Victorian coast might still experience future habitat loss albeit at a lower than rates detected in the past. In the Western Zone we simulated the effect of a disease outbreak. Abalone Western stock experienced an outbreak of abalone viral ganglioneuritis (AVG). We simulated a potential future disease outbreak that could increase the mortality across the population by adding AVG mortality to natural and fishing mortality. A value of viral mortality of 0.8 due to AVG was selected based on literature information about past published models (Gorfine et al., 2008).

We simulated population trajectories over 30 timesteps with each timestep representing one year. We chose to model abalone growth for 30 years because this is comparable to fisheries management reports where long-term targets for abalone are set referring to one or few decades (Department of Primary Industries, 2012). Simulations also operate with a one-year timestep so all the events that happen within each timestep only occur once per year (except for disease outbreaks). This timestep duration is set because fisheries data are reported for each year fishing season. Also, even if is often unknown and it can vary across species, many haliotids naturally spawn only once a year (Counihan et al., 2001). We performed three replicates of each model simulation and averaged results over these to increase model precision. Greater replication can be of value but was not implemented here due to the computational effort of our PVAs. When analysing our results, we looked for areas with abundance under the quasi-extinction threshold of 0.33 abalone/ha, below which the

population is expected to become extinct (Catton et al., 2016). We perform one-at-time sensitivity analysis for relevant simulation parameters common to all scenarios to test their influence on population persistence. A rate of 10% increase and decrease was applied to key model's parameters. Sensitivity analysis results were presented by visualising the abundance trends of all perturbated models and quantifying the total average rate of variations in model output in both directions. The perturbated parameters included survival and fecundity included into the stage matrix, changes in fisheries catches, and modification in carrying capacity and habitat suitability. For Eastern and western Zones, we also tested for sensitivity to variability of habitat loss rate and disease-dependent mortality.

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Abalone abundance maps

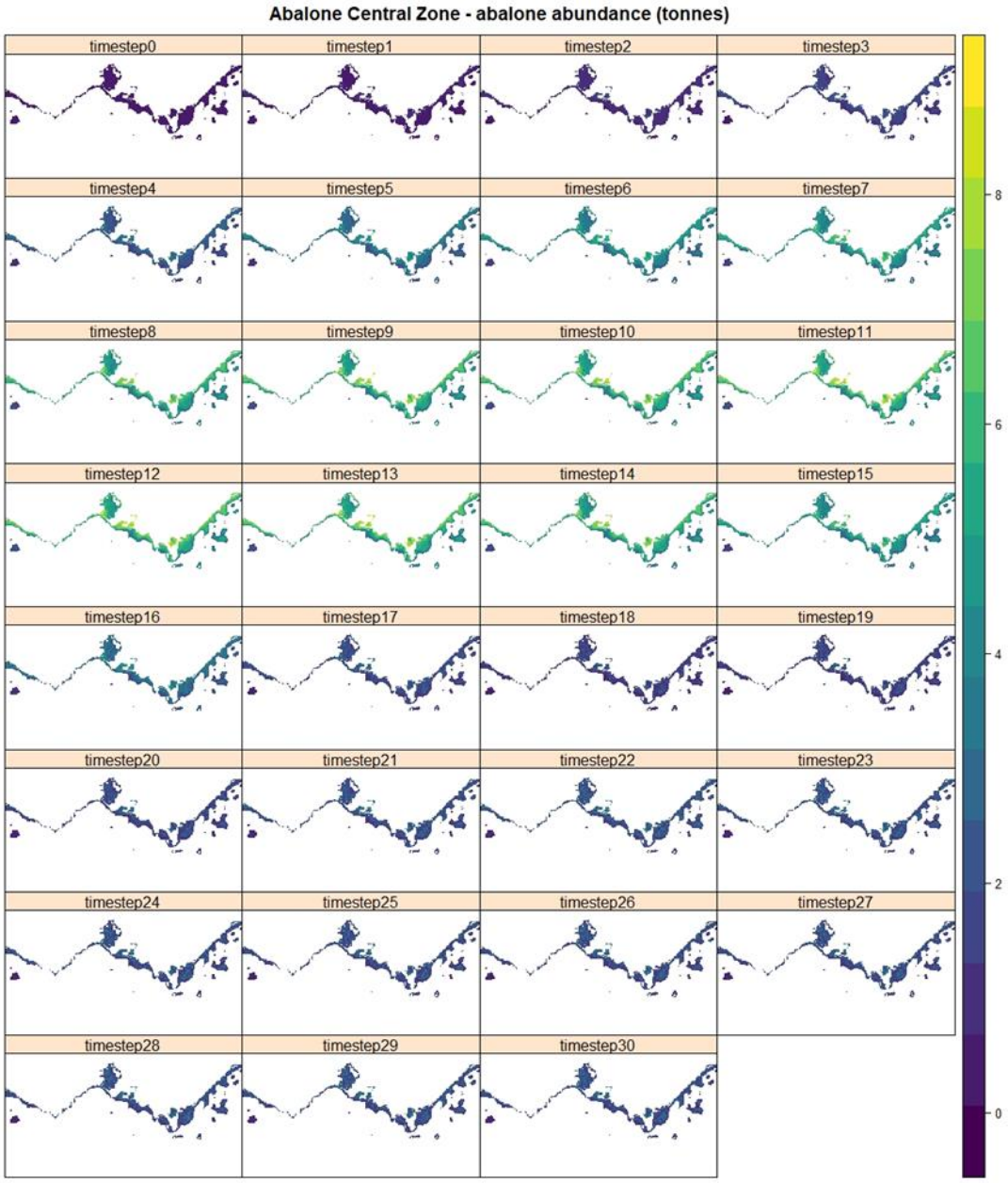

Figure A1.3: Abundance of abalone (recruitment stage) for all timestep simulated, average over 3 replicates, for baseline scenario for Abalone Central Management Zone. Abundance is measured in tonnes for cell. Maps use EPSG projection 4326 – World Geodetic System (WGS) 84.

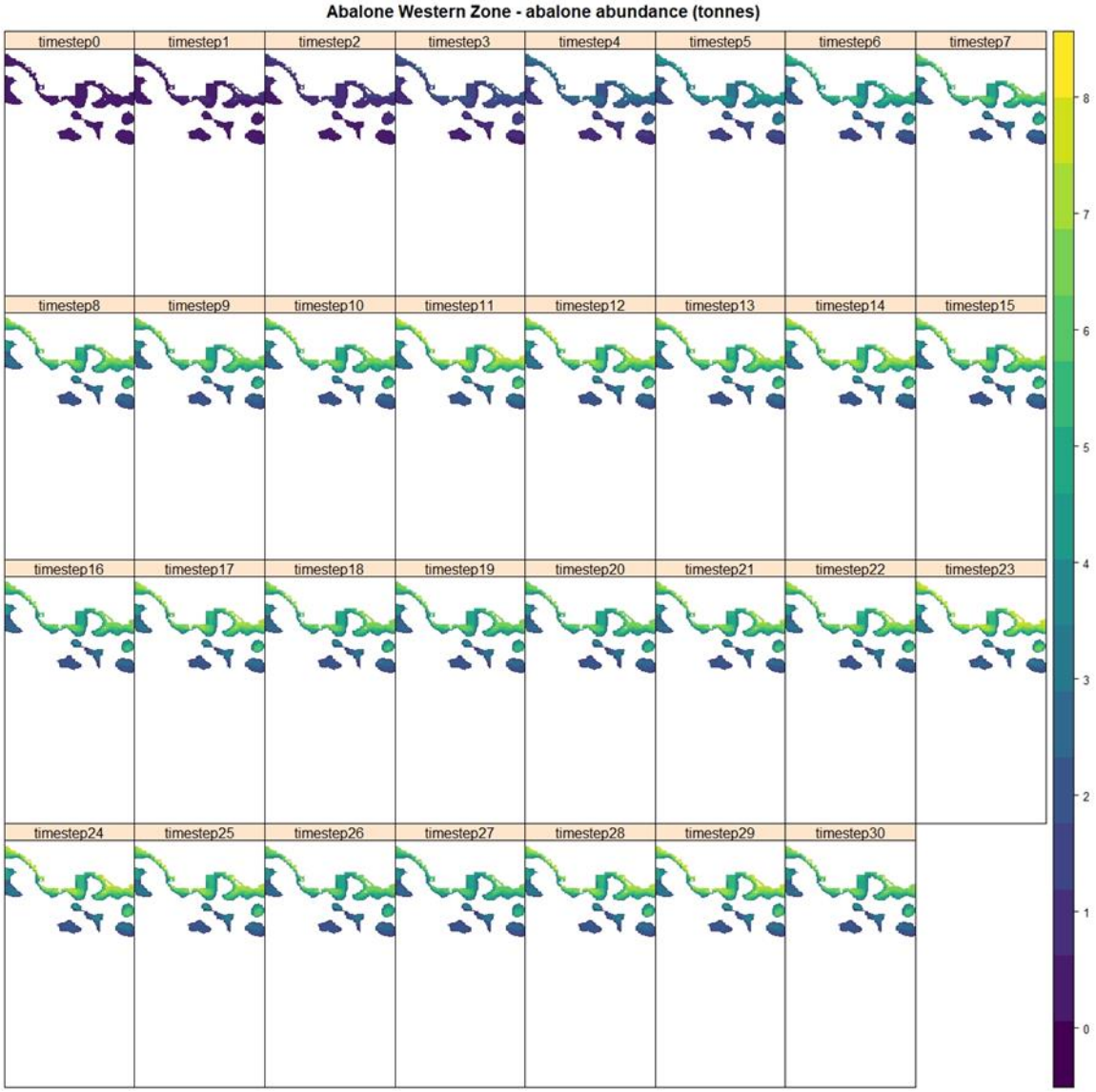

Figure A1.4: Abundance of abalone (recruitment stage) for all timestep simulated, average over 3 replicates, for baseline scenario for Abalone Western Management Zone. Abundance is measured in tonnes for cell. Maps use EPSG projection 4326 – World Geodetic System (WGS) 84.

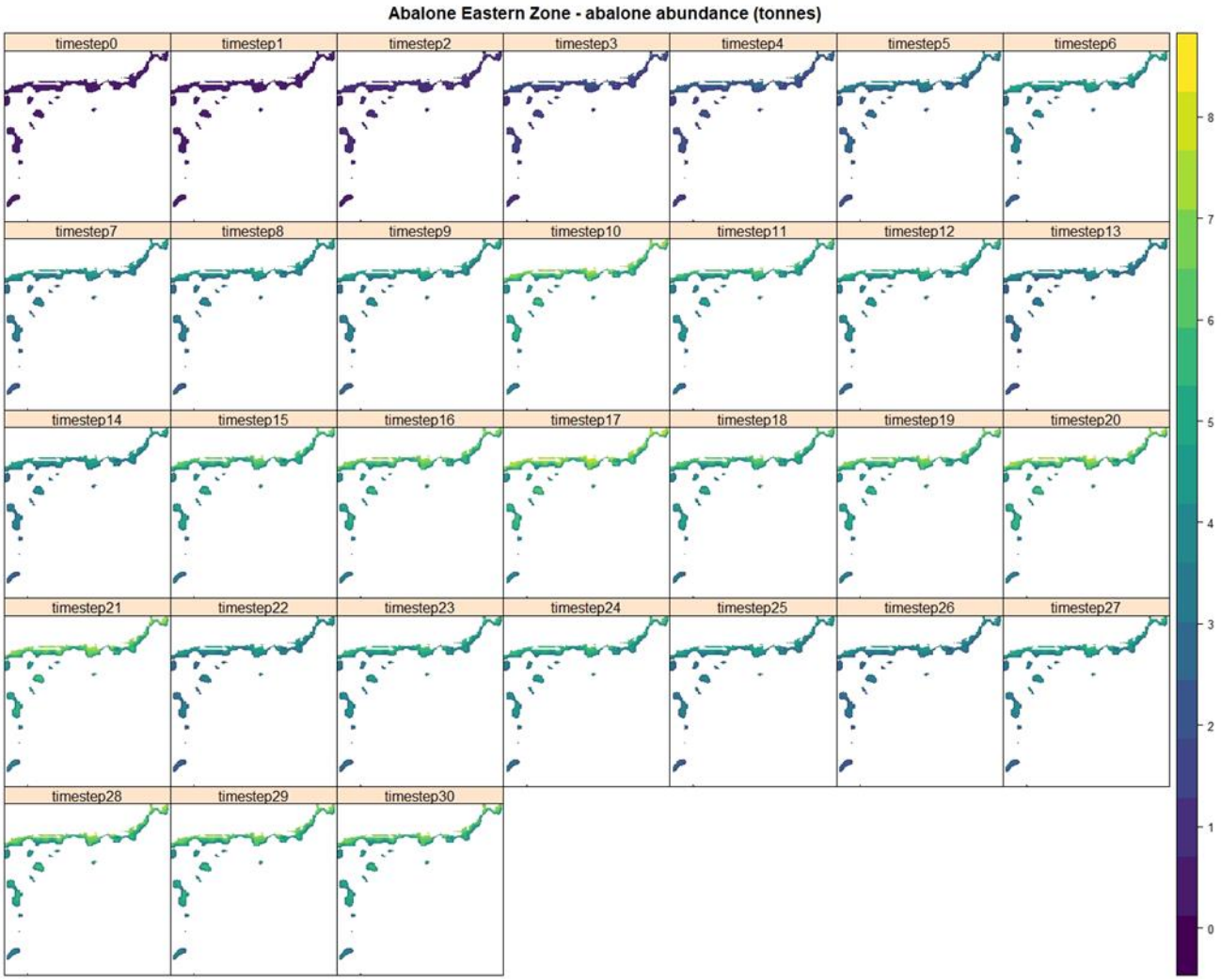

Figure A1.5: Abundance of abalone (recruitment stage) for all timestep simulated, average over 3 replicates, for baseline scenario for Abalone Eastern Management Zone. Abundance is measured in tonnes for cell. Maps use EPSG projection 4326 – World Geodetic System (WGS) 84.

Appendix 2

Seascape connectivity

Seascape connectivity for *C. auratus*

Linkage Mapper 2.0.0 (McRae and Kavanagh 2011) uses circuit theory to run Circuitscape (McRae and Shah 2009) to produce linkages. Input data required to use Linkage Mapper consists of a movement cost surface (Fig. A2.1) and a map representing snapper habitat patches. Cost surface was generated according to currents magnitude and directions, assuming the minimum cost when moving following the ocean currents. Currents were derived from HYCOM database (HYCOM, http://hycom.org) from the surface to 50 m depth, representing the adult snapper habitat. Cost surface scores were estimated on a scale from 1 to 10, after assessing several scales and verifying that the chosen scale did not influence seascape connectivity spatial patterns and number of links. A cut-off of maximum link length was applied according to maximum swimming distance recorded in snapper populations across southeast Australia (Fowler et al. 2017) to eliminate all links exceeding this threshold and increasing model realism. Linkage Mapper output for *C. auratus* is presented in Fig. A2.3.

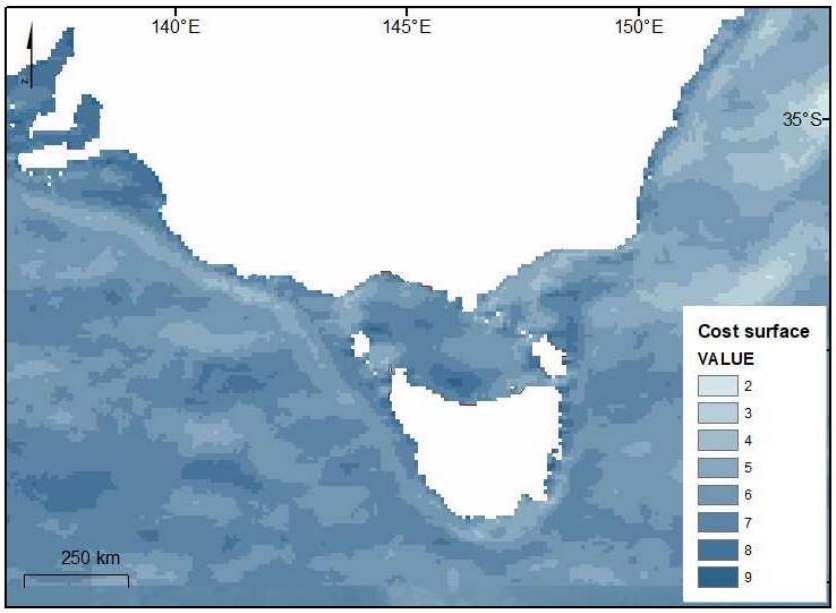

Figure A2.1: Cost surface raster used to identify least cost paths and quantify connectivity for adult of *C. auratus*.

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Seascape connectivity for *H. erythrogramma*

A biophysical model (Treml et al. 2012) was used to estimate *H. erythrogramma* connectivity. The input data of this model consists of 1) a habitat patch map, 2) currents data from a hydrodynamic model (HYCOM, http://hycom.org) and 3) species-specific demographic parameters (Table A2.1).

This model was used to simulate larval dispersal among habitat patches, revealing the structure of habitat connectivity. The model simulated larval dispersal as clouds of larvae, which were released from a habitat patch and tracked as they moved through the seascape. Larval dispersal depends on biophysical parameters (Table A2.1). An advection transport algorithm (Smolarkiewicz 1983, Smolarkiewicz & Margolin 1998, Smolarkiewicz 2006) was used to move the dispersal kernel through current velocity fields. When larvae came in contact with suitable habitat they settled, and quantity of settled larvae were recorded. Model connectivity output is presented in Fig. A2.2.

Table A2.1: Marine connectivity model parameters (*H. erythrogramma*).

Parameter	***H. erythrogramma* (purple sea urchin)**
Depth	0-35m[1]
Max PLD	5 d[2]
Competency period	3 to 5 days[3]
Spawning period	December and March [4]
Diffusivity	100 m^2s^{-1} [5]
Larval settlement likelihood	90%
Larval mortality	16% per day[6]

References: 1. Huggett et al. 2008, 2. Williams and Anderson 1975, 3. Swanson et al. 2012, 4. Williams and Anderson 1975, Laegdsgaard et al. 1991, 5. Okubo 1971, 6. Rumrill 1990, Lamare and Barker 1999.

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Connectivity maps

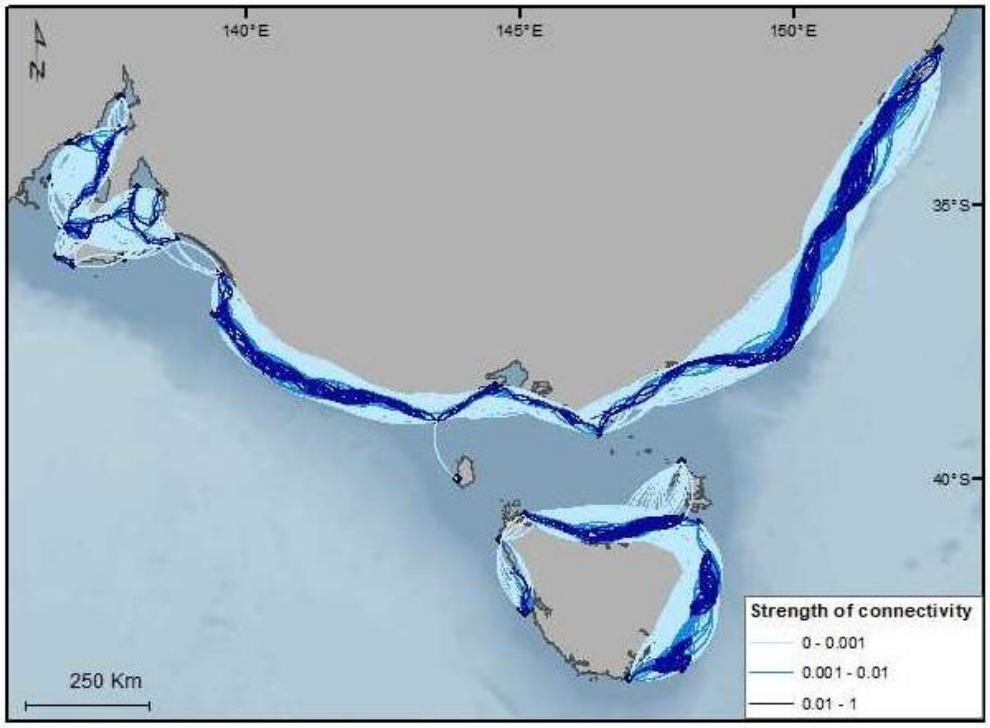


Figure A2.2: Purple sea urchin *H. erythrogramma* connectivity. The weight of the connections is indicative of the strength of dispersal and the directionality is implied by following the arcs in a clockwise direction.

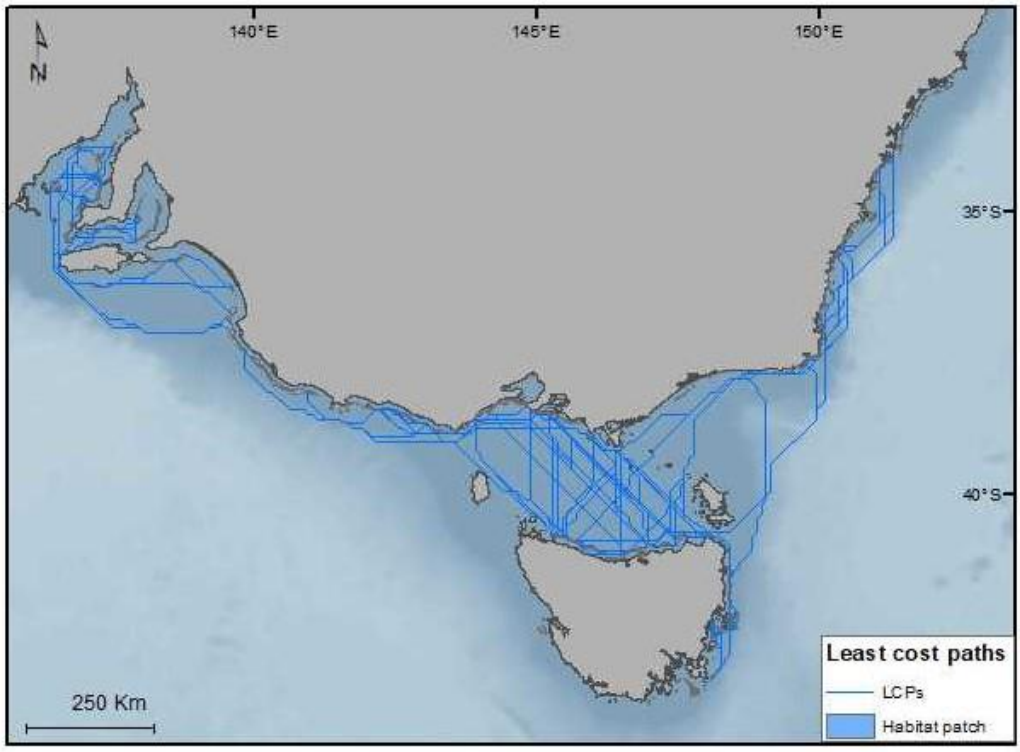


Figure A2.3: Snapper *C. auratus* connectivity.

Species distribution models (SDMs)

Table A2.2: Details of the environmental parameters used in the SDMs.

Name	Description	Units	Source	Start year	End year
Bathymetry	Depth of the seafloor	m	Gebco/EMODnet Bathymetry	2016	2016
pH	Measure of ocean's acidity	-	In-situ measurements	1910	2007
Chlorophyll concentration	Mean mass concentration of chlorophyll in sea water	mg/m^3	Model	2000	2014
Salinity	Dissolved salt content in the ocean	PSS	In-situ measurements	1961	2009
Temperature	Mean sea water temperature	°C	Model	2000	2014
Primary production	Mean net primary productivity of carbon	mg/m3/day	Model	2000	2014
Dissolved oxygen	Mole concentration of molecular oxygen in sea water	mol/m3	Model	2000	2014
Current velocity	Sea water velocity	m/s	Model	2000	2014

Source: Bio-ORACLE (Tyberghein et al., 2012, Assis et al., 2017). All data are in long-lat coordinates (WGS84) and cell size is 0.08333 degree.*

*Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F. & De Clerck, O. (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecology and Biogeography, 21, 272-281.

Assis, J., Tyberghein, L., Bosh, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2017). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography.

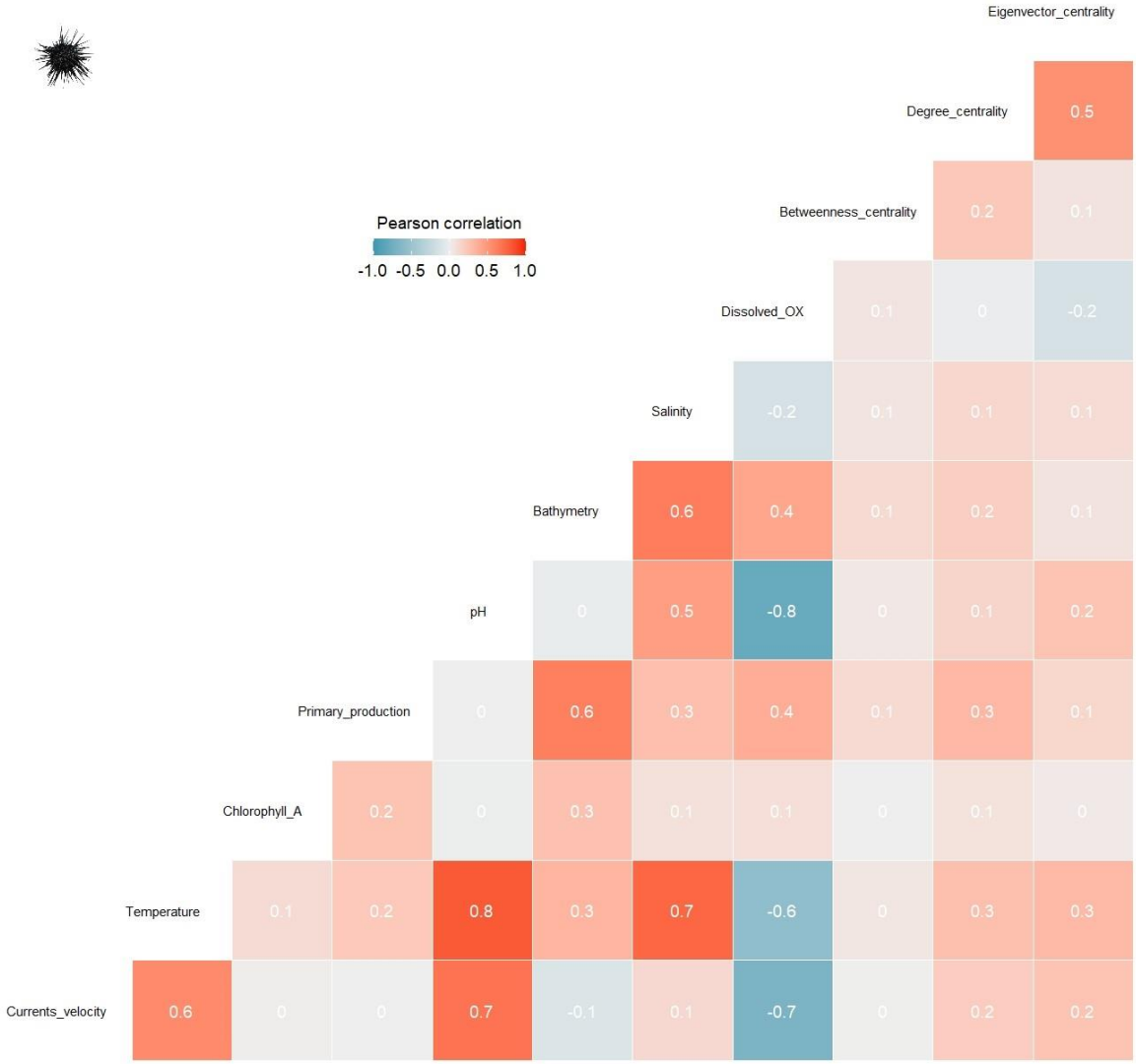


Figure A2.4: Pearson correlation (r) of environmental variables for *H. erythrogramma*.

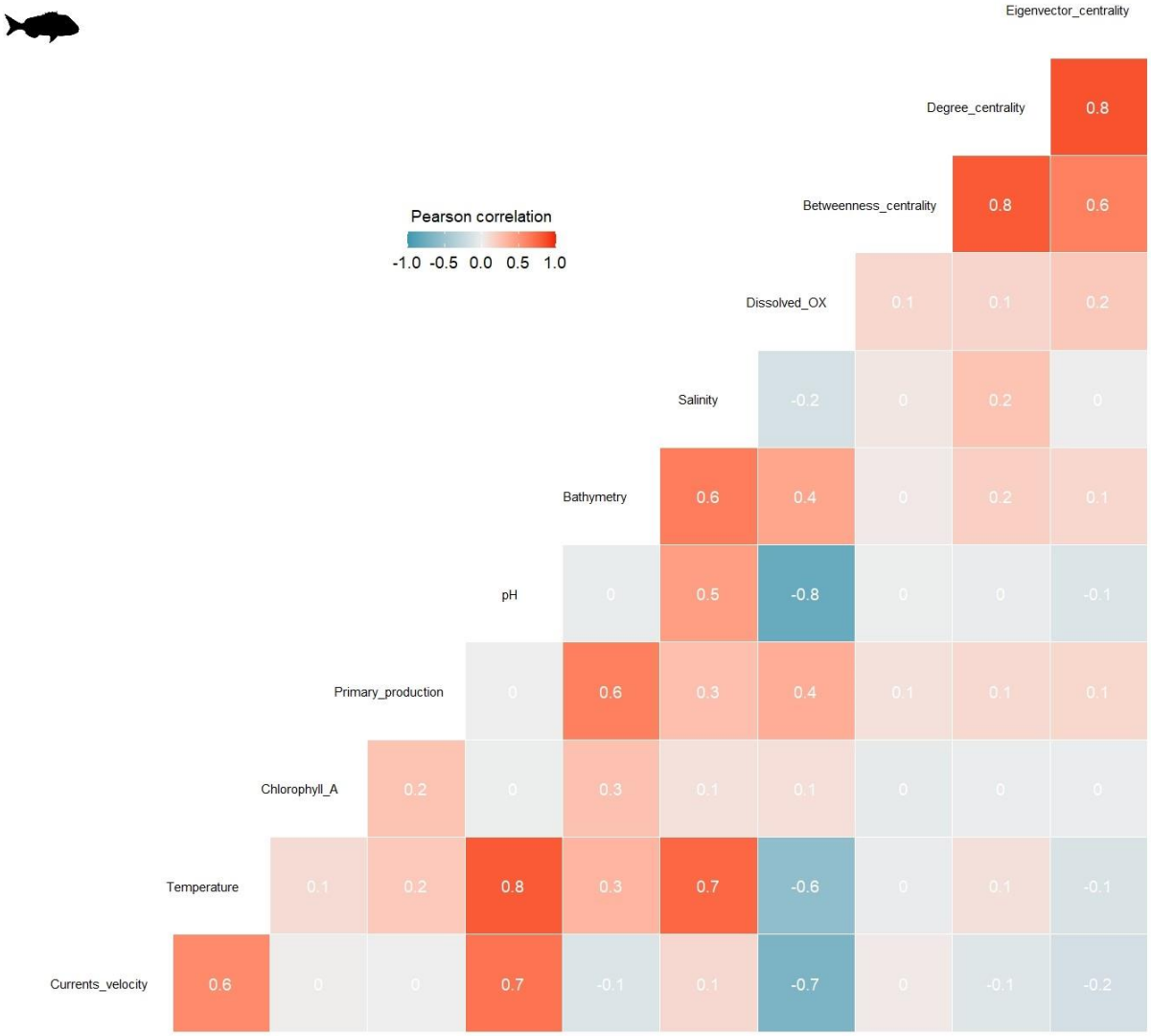
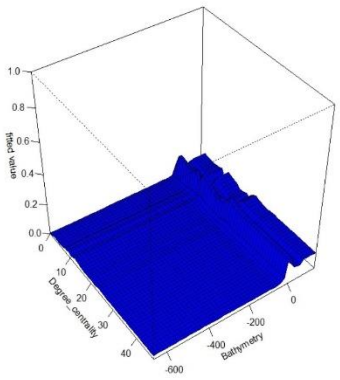
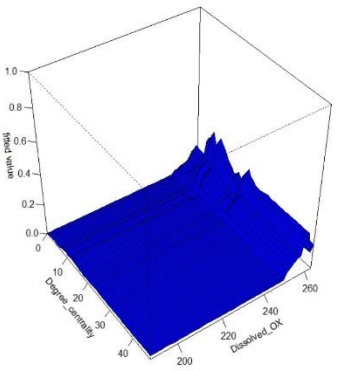


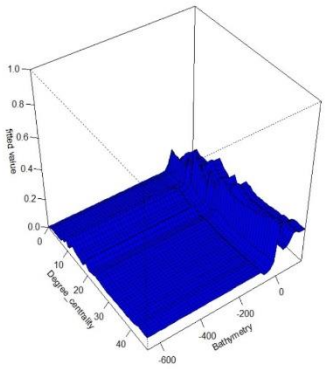
Figure A2.5: Pearson correlation (r) of environmental variables for *C. auratus*.

a


fitted value
Degree_centrality
Bathymetry


fitted value
Degree_centrality
Dissolved_OX

b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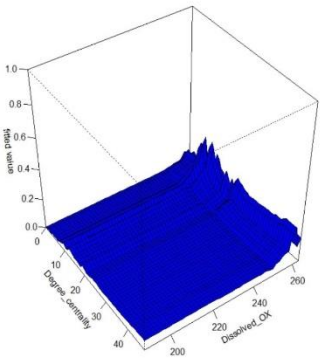
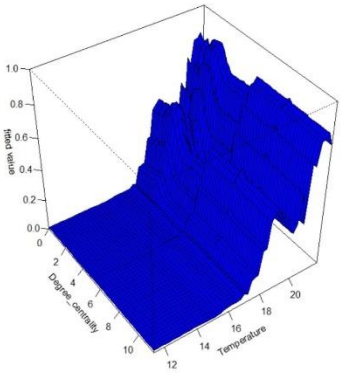
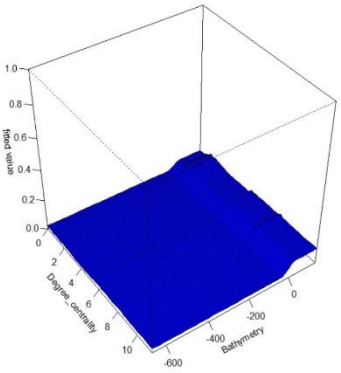
Degree_centrality
Bathymetry

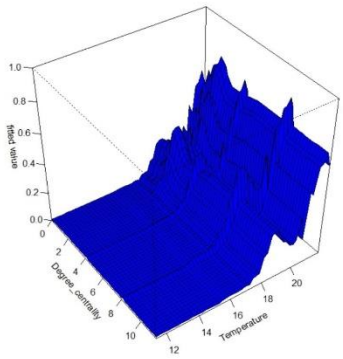

fitted value
Degree_centrality
Dissolved_OX

c


fitted value
Degree_centrality
Temperature


fitted value
Degree_centrality
Bathymetry

d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Degree_centrality
Temperature

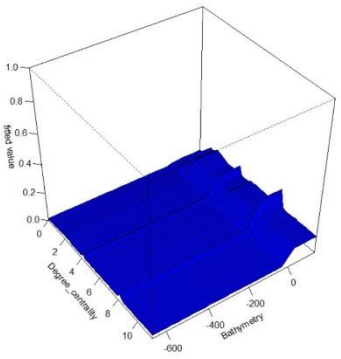
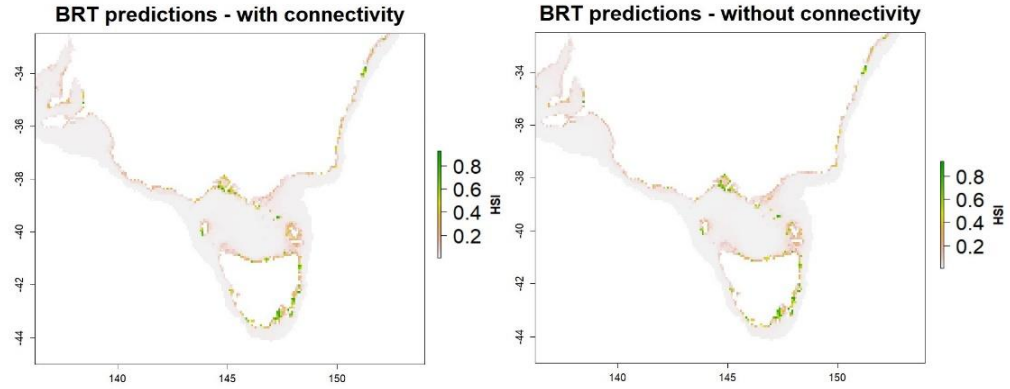

fitted value
Degree_centrality
Bathymetry

Figure A2.6: Plots of the interactions between degree centrality and the two most important environmental variables interacting with degree centrality. Plots showing interactions for BRT models fitted including all connectivity variables for *H. erythrogramma* (top) with maximum fitted value 0.2 for bathymetry plot and 0.37 for dissolved oxygen (a) and *C. auratus* (bottom) with maximum fitted value 0.88 for temperature plot and 0.12 for bathymetry (c). Plots showing fitted functions for BRT models fitted including degree centrality only for *H. erythrogramma* (top) with maximum fitted value 0.35 for bathymetry plot and 0.31 for dissolved oxygen (b) and *C. auratus* (bottom) with maximum fitted value 0.84 for temperature plot and 0.24 for bathymetry (d).

SDMs spatial predictions and connectivity

a



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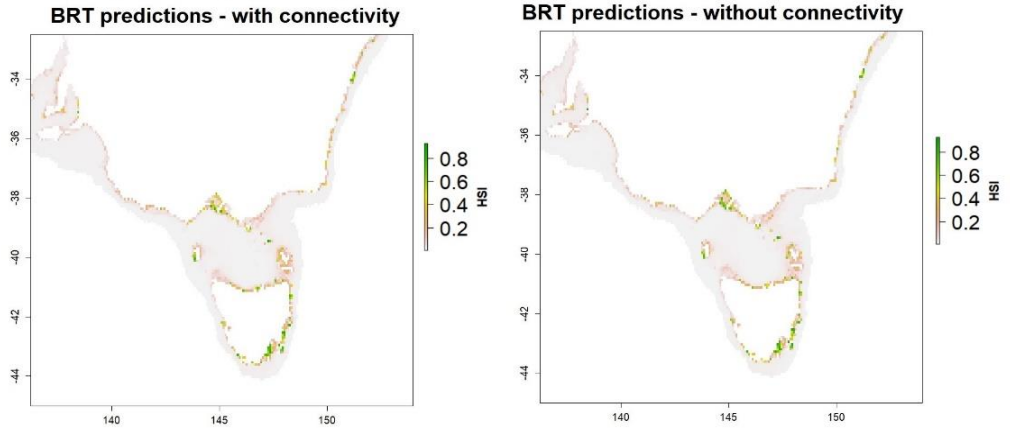
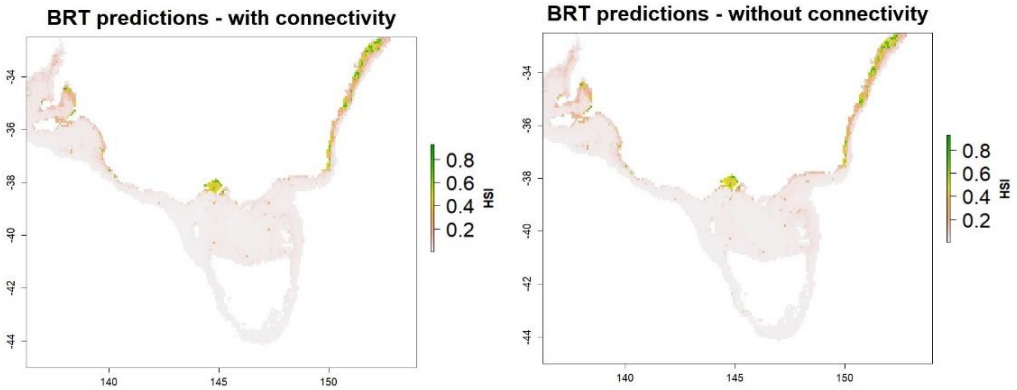


c



d

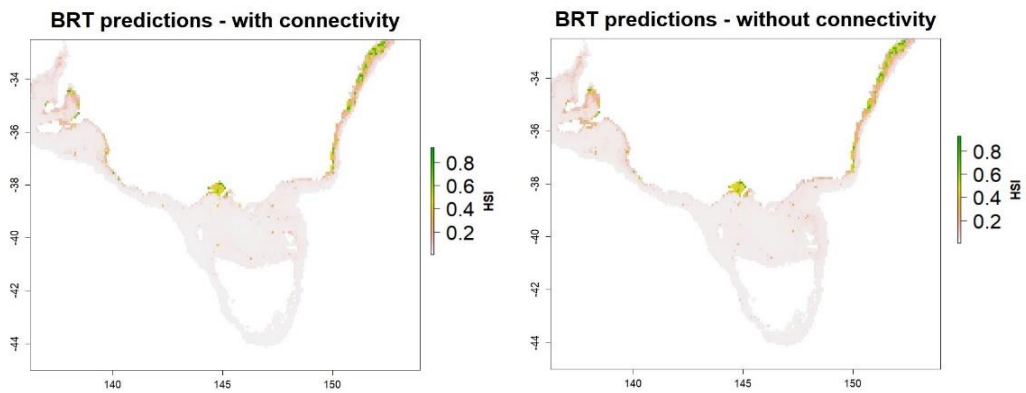


Figure A2.7: Habitat suitability index for *H. erythrogramma* (top) and *C. auratus* (bottom) with and without connectivity. Figure A2.7a and A2.7c show habitat suitability for SDMs models including all connectivity metrics. Figure A2.7b and A2.7d, show habitat suitability for the models where only degree centrality was used to fit the SDMs.

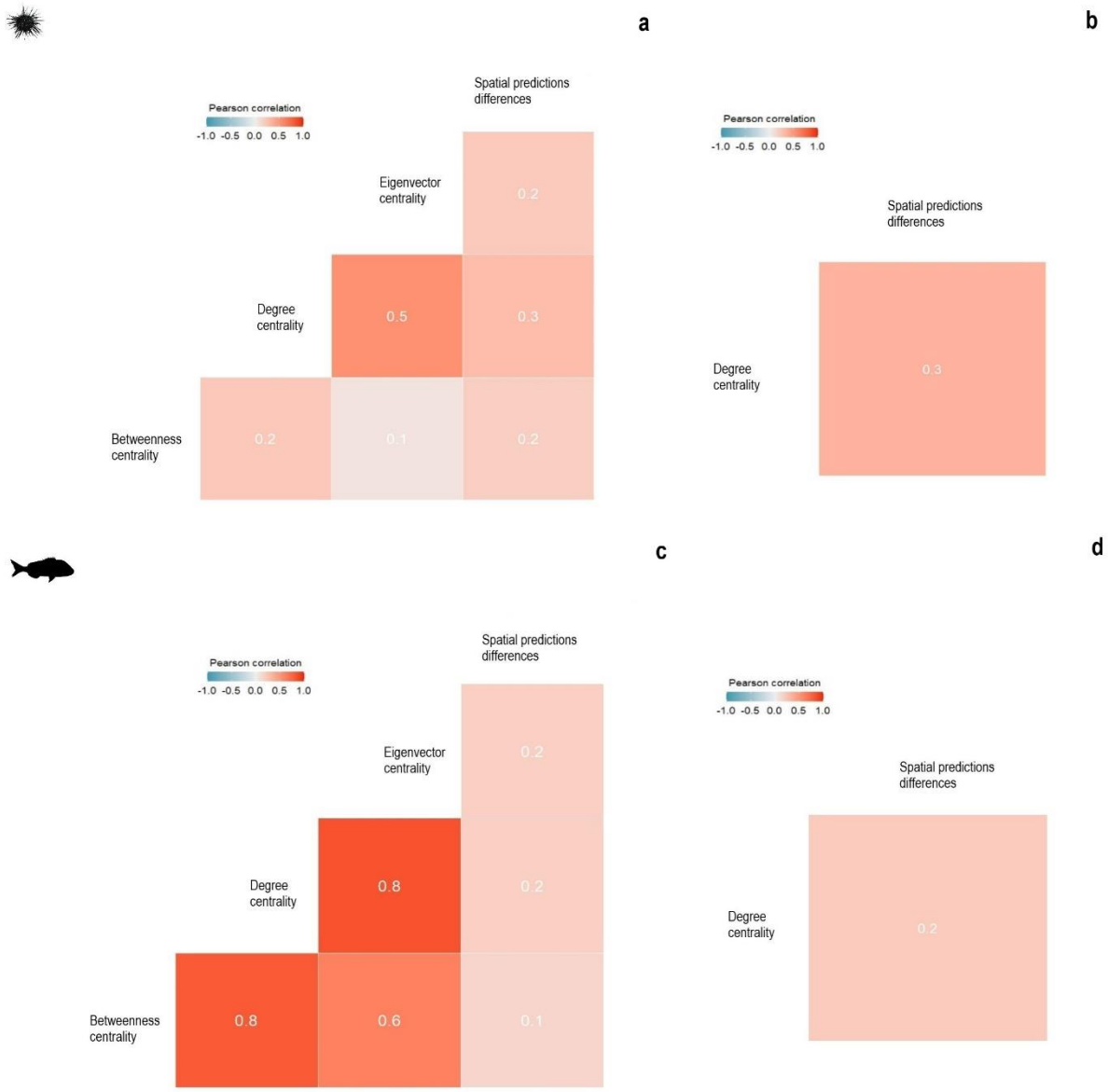


Figure A2.8: a) Correlation (r) of differences in spatial predictions of habitat suitability (with and without connectivity) and betweenness centrality, degree centrality, eigenvector centrality. b) Correlation (r) of differences in spatial predictions of habitat suitability (with and without connectivity) and degree centrality for *H. erythrogramma* (top). c) Correlation (r) of differences in spatial predictions of habitat suitability (with and without connectivity) and betweenness centrality, degree centrality, eigenvector centrality. d) Correlation (r) of differences in spatial predictions of habitat suitability (with and without connectivity) and degree centrality for *C.* auratus (bottom).

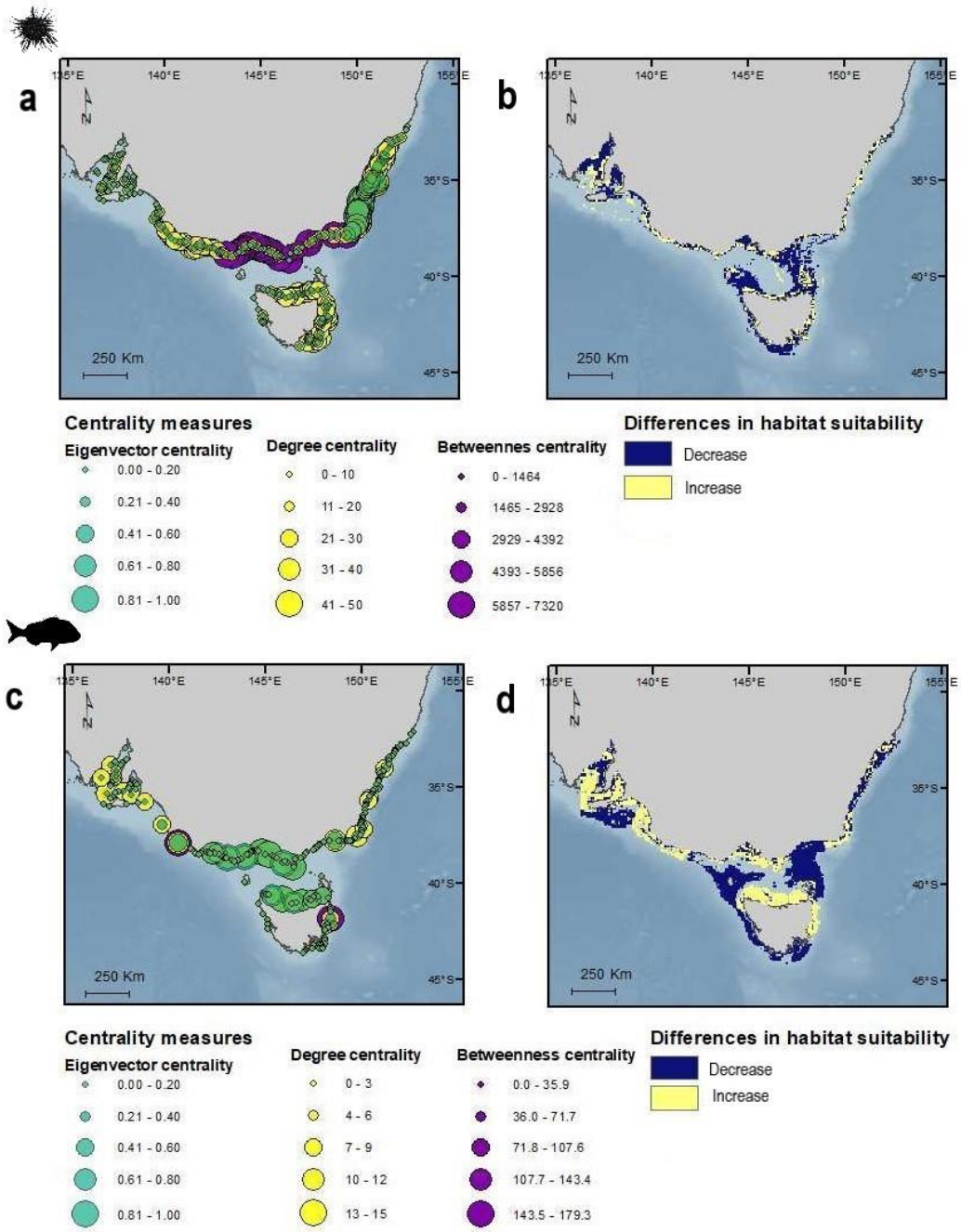


Figure A2.9: Maps showing the geographic distribution of centrality measures (a and c) and differences in spatial predictions of habitat suitability (b and d) for sea urchin *H. erythrogramma* (top) and snapper, *C. auratus* (bottom). Centrality values (a and c) are shown as dots corresponding to the habitat patches centroids. Values of habitat suitability are classified as 'Increase' when predicted habitat suitability is larger for SDM incorporating connectivity compared to the SDM without connectivity. Values are classified as 'Decrease' when predicted habitat suitability is lower for SDM incorporating connectivity compared to the SDM without connectivity. Maps in WGS84.

Appendix 3

Quantifying marine larval connectivity

Habitat patches

Habitat maps for *H. rubra*, *C. rodgersii* and *H. erythrogramma* were quantified using species distribution models (SDMs) in R, using the 'dismo' package. These models used occurrence data from a biological database and environmental data from several sources (see main text). We used presence and background data and fitted the models using GAMs within the 'mgcv' R package. Models were evaluated and selected using Akaike information criterion (AIC) values (*H. rubra* AIC = 207.62, *C. rodgersii* AIC = 87.40 and *H. erythrogramma* AIC = 135.98). Habitat maps for *C. auratus* and *S. punctatus* were built in ArcGIS. All mapped predictions were imported in ArcGIS to calculate proportion of habitat and each assigned a unique identifier, and imported to the biophysical model. For the other two species, *C. auratus* and *S. punctatus*, habitat patches were mapped using the species-specific known location of spawning and settlement (Fowler et al. 2000, Jenkins et al. 2000, Fowler and Jennings 2003, Hamer et al. 2011, Hamer and Conron 2016, Jenkins et al. 2016), as described in the main text.

Biophysical model

A geographically explicit biophysical model was used to quantify larval dispersal between habitat patches for the five species across southeast Australia (additional detailed methods and sensitivity analysis can be found in Treml et al. 2012). The model's spatial resolution, 5x5 km cells, was chosen as a compromise between the resolution of the hydrodynamic data available from the HYCOM oceanographic model and the finer resolution in the habitat maps. To capture a wide range of current conditions we completed dispersal simulation across all years of available data, 1992-2012. Three-hourly, depth-averaged ocean current velocities

from HYCOM were interpolated to the spatial model across all years. A diffusivity parameter (Table 4.1 in the main text) was used to represent sub-scale turbulence below the scale of the oceanographic data.

The species-specific biological parameters (Table 4.1, main text) were based on known or presumed values (see references in caption of Table 4.1, main text), representing a range of larval dispersal capacities. Species-specific spatial parameters, such as habitat location and proportion of available habitat (our proxy for reproductive output) were defined by habitat patch attributes, as determined, above. Larvae were released weekly for a 3-hourly time-steps, throughout the entire species-specific spawning period (Table 4.1, main text). The lengths of the simulations were determined by each species' maximum pelagic larval duration. The specific values of the biological parameters and other model parameters are listed in Table 1 in the main text. Settlement of larvae to suitable habitat was controlled by the competency characteristics, a daily settlement likelihood, and homing behavior. For homing, larvae either settle in proportion to the available habitat per model cell (no homing), or larvae were allowed to swim towards and settle to any available habitat within the 5 x 5 km model cell (with homing). Larval vertical movement was not included in the model as the parameters to support this behavior are largely unknown. As a result, larvae are effectively evenly distributed throughout the top water column (top 10 m). Daily larval mortality was incorporated into the model as a Weibull function, incorporated every day through the simulation (e.g., Connolly and Baird 2010).

The larval dispersal kernel (probability density function) was modelled as a cloud of larvae moving through time and space, concentrated or dispersed in the seascape, based on the model parameters described above. The multidimensional positive definite advection transport algorithm was used for moving larvae (Smolarkiewicz 1983, Smolarkiewicz & Margolin 1998, Smolarkiewicz 2006). This approach is accurate (3rd order or more), minimizes numerical diffusion and maximises computational efficiencies (Treml et al. 2012). At the end of the

simulation, larvae that age beyond the maximum larval duration do not settle, do not survive, and do not contribute to output.

Simulation data were saved as a 3-dimensional matrix, representing the cumulative proportion of larvae released from patch *i* (row) that have settled to patch *j* (column) at the time-step *t*. The matrix was then converted to represent the flow of larvae between patches, based on reproductive output and the proportion of suitable habitat per source patch. These matrices were averaged through time to represent the average potential of connectivity for each species. Several matrices were used in the population modelling. For our model we used a migration matrix M, which represents the proportion of settlers to each destination patch *j* that came from each source patch *i*, the diagonal of this matrix quantifies self- recruitment, which was maintained in our analysis. This matrix is consistent with the existing work in this area (e.g., Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). Defining a critical level of recruitment is necessary for making meaningful predictions on demographically-significant connectivity, for this reason we used a migration rate threshold, representing a minimum proportion of larvae that successfully settle. We set this lower threshold to 0.001, or a level of 1 out of 1,000 settlers, to focus the analysis on the demographically-significant connections important in metapopulation dynamics. For further details on this approach see Treml et al. 2012.

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Table A3.1: Definition of the network metrics of interest in this work.

Network metrics	Definition	Ecological relevance and relationship with metapopulation persistence
In-degree	Node-level metric indicating the number of edges going into a node. (Minor and Urban 2007).	In-degree is an indicator of immigration to a patch. Patches with high in-degree are considered destinations able to receive individuals from a lot of patches (Minor and Urban 2007, Zamborain-Mason et al. 2017); these patches may be more likely to persist despite some neighbouring patches going extinct.
Out-degree	Node-level metric indicating the number of edges going out from a node. (Minor and Urban 2007).	Out-degree is an indicator for the number of downstream connections from a patch. Patches with high out-degree could be considered sources, capable of contributing to many destinations. For this reason these nodes may be considered critical for ensuring metapopulation persistence (Minor and Urban 2007, Zamborain-Mason et al. 2017).
Eigenvector centrality	This node-level centrality metric represents the summed connections to all the other graph nodes, weighted by their centralities (Bonacich 1987).	Eigenvector centrality (EC) may highlight which subpopulation has the greatest number of connections with the important nodes. EC may identify which subpopulation, when removed, may cause a rapid and far-reaching decline impacting metapopulation dynamics (Watson et al. 2011, Zamborain-Mason et al. 2017).
Alpha centrality	Node-level metric used for directed and non-symmetric networks. It is considered a	As a generalization of eigenvector centrality, its relevance can be considered the same. Alpha centrality identifies which subpopulation may be highly connected to other important nodes. AC,

	generalization of eigenvector centrality (Bonacich and Lloyd 2001).	similarly to EC, may be used to identify which subpopulations have a large influence on metapopulation dynamics (Watson et al. 2011, Zamborain-Mason et al. 2017).
Closeness centrality	Node-level metric calculated as the inverse of the average distance between the node *i* and the other nodes (Freeman 1978).	Closeness centrality (CC) represents the proximity of a node to all other nodes. Nodes with high values of CC may interact rapidly with the other nodes (Estrada and Bodin 2008, Gonzalez et al. 2010) and captures how close the site is to the network's central region. Metapopulation persistence may be strongly influenced by these central subpopulations (Zamborain-Mason et al. 2017).
Betweenness centrality	This node metric defines the number of shortest paths that pass through a given node; a shortest path is the minimum number of edges connecting two nodes (Freeman 1978).	Nodes with high betweenness centrality (BC) are significant for ensuring network-wide metapopulation dynamics, efficiently connecting areas across the network. BC may also identify critical metapopulation stepping-stones. Nodes with high BC are also important for forming dispersal corridors (Bodin and Norberg 2007, Minor and Urban 2007, Zamborain-Mason et al. 2017).
Asymmetry	Networks are asymmetric when the strength of connection from patch *i* to patch *j* is different from patch *j* to patch *i*. The degree of symmetry, γ, is calculated as indicator of	Presence of asymmetry may be important for marine metapopulations, as ocean currents are often strong directional, influencing the directionality and symmetry of connections. Strongly asymmetric networks may be vulnerable to extinction resulting from many patches that only act as sources. These patches might be unable to

	network-wide asymmetry (Vuilleumier and Possingham, 2006).	survive because of inadequate replenishment, negatively affecting metapopulation persistence (Artzy-Randrup and Stone 2010, Vuilleumier et al. 2010, Zamborain-Mason et al. 2017)
Cycles	For directed networks a cycle represents a closed loop of at least 3 nodes with the same starting and ending node: A→B→C→A (Artzy-Randrup and Stone 2010).	Presence of cycles has been shown to be important in metapopulation persistence. An increased presence of cycles leads to increased persistence. A cycle represents the ability of 'returning home', which is the ability of future offspring to recruit back to the original, natal, patch source. At local scales, the absence of cycles or feedback loops may negatively impact metapopulation persistence (Artzy-Randrup and Stone 2010, Zamborain-Mason et al. 2017).
Heterogeneity	Heterogeneity refers to the variability in node-level connections (i.e., degree) across the network. A coefficient of variability in node degree is an informative measure of network-wide heterogeneity (Artzy-Randrup and Stone 2010).	In our model, network heterogeneity is defined as the difference between in and out degree for nodes. Heterogeneity can have variable consequences on metapopulation persistence, depending on the level of correlation between in and out degree. Evidence suggests when the in and out degree of all nodes in a network are highly and positively correlated, the metapopulation may be much more resilient. (Shtilerman and Stone 2015, Zamborain-Mason et al. 2017).

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Table A3.2: Network analysis results with a threshold of 0.001 (0.1% of contribution to settled larvae).

Species	Graph size *# of edges*	Graph components *(size)*	Degree *mean(min-max)*	Betweenness centrality *mean(min-max) [component]*	Closeness centrality *mean(min-max) [component]*	Eigenvector centrality *mean(min-max) [component]*	Alpha centrality *mean(min-max) [component]*	Asymmetry	Heterogeneity	Number of cycles
Haliotis rubra	2380	4 (2192[1] – 65[2] – 122[3] – 1[4])	13.6 (1-38) in-degree 13.6 (1-39) out-degree 55.43 (0-177.61) w in-degree 55.43 (0-180.94) W out-degree	972.3 (0-7107) [1] 5.8 (0-24) [2] 14.07 (0-55) [3] 0 (0-0) [4]	0.06 (0.04-0.08) [1] 0.45 (0.02-0.62) [2] 0.23 (0.12-0.3) [3] 0 (0-0) [4]	0.14 (0-1) [1] 0.62 (0.08-1) [2] 0.55 (0 -1) [3] 1 (1-1) [4]	0.12 (-12.45-22.38) [1] -0.19 (-1.09-0.2) [2] 0.34 (-17.53-8.9) [3] 1 (1-1) [4]	0.65	0.36 (in-degree) 0.5 (w in- degree) 0.39 (out-degree) 0.45 (w out-degree)	4674
Heliocidaris erythrogramma	2339	5 (162[1] - 1[2] - 203[3] - 3[4] - 1970[5])	9.25 (1-27) in-degree 9.25 (1-27) out-degree 33.14 (0-111.99) w in-degree 33.14 (0-104.35) w out-degree	23.41 (0-63) [1] 0 (0-0) [2] 79.97 (0-300) [3] 0 (0-0) [4] 718.3 (0-4252) [5]	0.25 (0.15-0.34) [1] 0 (0-0) [2] 0.12 (0.07-0.18) [3] 0.37 (0.37 - 0.37) [4] 0.02 (0.01 – 0.03) [5]	0.68 (0.24-1) [1] 1 (1-1) [2] 0.3 (0.003-1) [3] 0.5 (0-1) [4] 0.1 (0-1) [5]	-0.14 (-0.8-0.68) [1] 1 (1-1) [2] -0.16 (-5.96-6.9) [3] 1.73 (1-2.450) [4] - 0.7 (-496.94-514.84) [5]	0. 74	0.29 (in-degree) 0.45 (w in-degree) 0.31 (out-degree) 0.39 (w out-degree)	3346

Centrostephanus rodgersii	8838	1	57.02 (22-110) in-degree 57.02 (0-155) out-degree 281.8 (89.84-575.41) w in-degree 281.8 (0-772) w out-degree	118.6 (0-3749) [1]	0.21 (0.17-0.38) [1]	0.38 (0.02-1) [1]	0.001 (-0.85-3) [1]	0.35	0.25 (in-degree) 0.32 (w in-degree) 0.65 (out-degree) 0.51 (w out-degree)	37609
Chrysophrys auratus	590	2 (232[1]-358[2])	12.29 (3-17) in-degree 12.29 (3-18) out-degree 41.71 (7.54-63.33) w in-degree 41.71 (9.95-67.76) w out-degree	8 (0-56) [1] 34 (0-209) [2]	0.32 (0.17-0.43) [1] 0.11 (0.08-0.15) [2]	0.78 (0.14-1) [1] 0.44 (0.0119 -1) [2]	-0.53 (-23.05-19.63) [1] -0.05 (-0.35-0.47) [2]	0. 86	0.09 (in-degree) 0.12 (w in-degree) 0.1 (out-degree) 0.14 (w out-degree)	1583

Sillaginodes punctatus	861	1	5.48 (0-10) in-degree 5.48 (0-72) out-degree 16.71 (0-41.24) w in-degree 16.71 (0-311.32) w out-degree	0 [1]	0.17 (0.11-0.22 [1]	0 [1]	9.35 (1-21.62) [1]	0	0.31 (in-degree) 0.41 (w in-degree) 8.74 (out-degree) 9.77 (w out-degree)	0

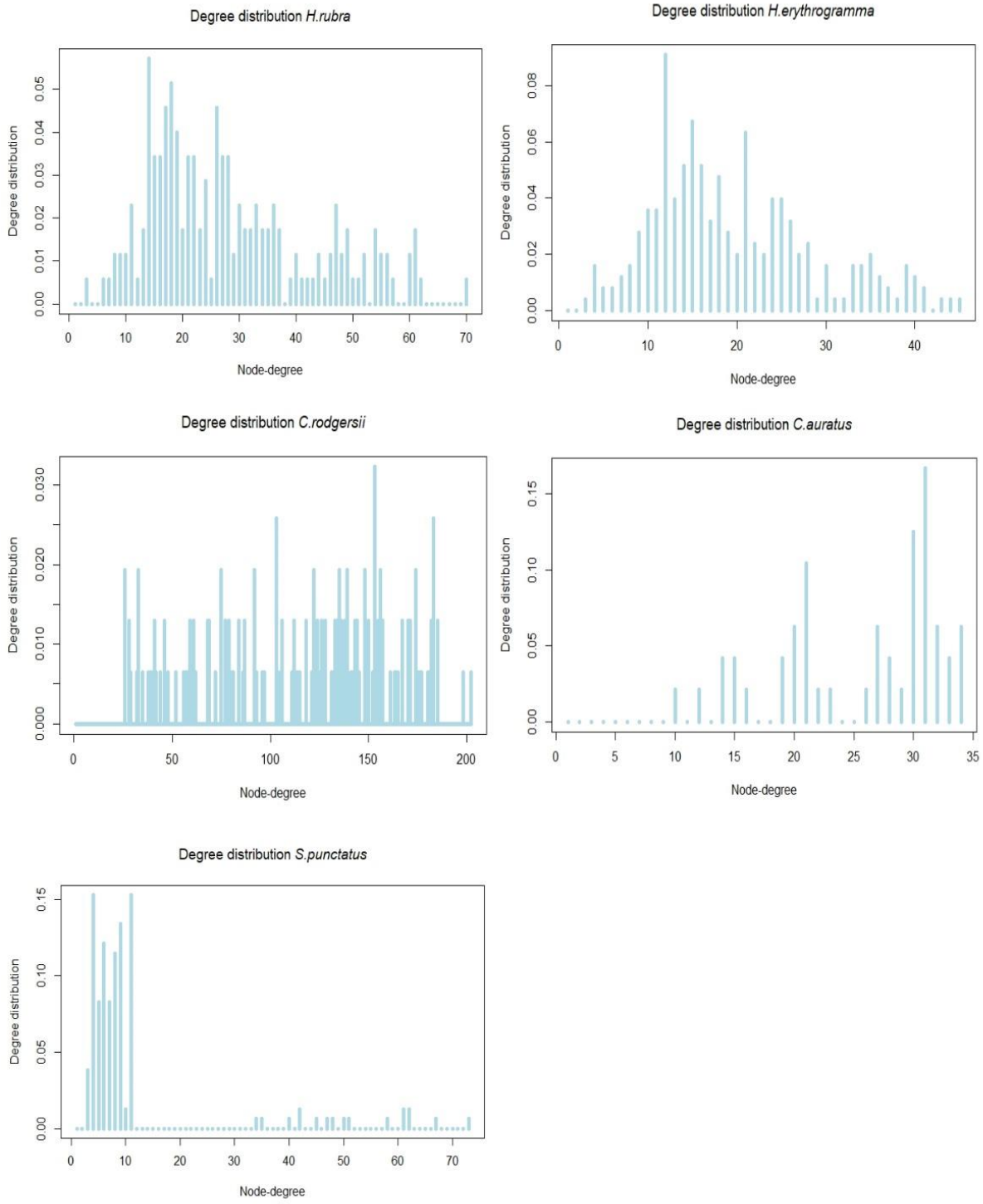


Figure A3.1: Node-degree distribution for all species. Node degree frequency distributions represents the fraction of nodes corresponding to each node-degree value (x-axis).

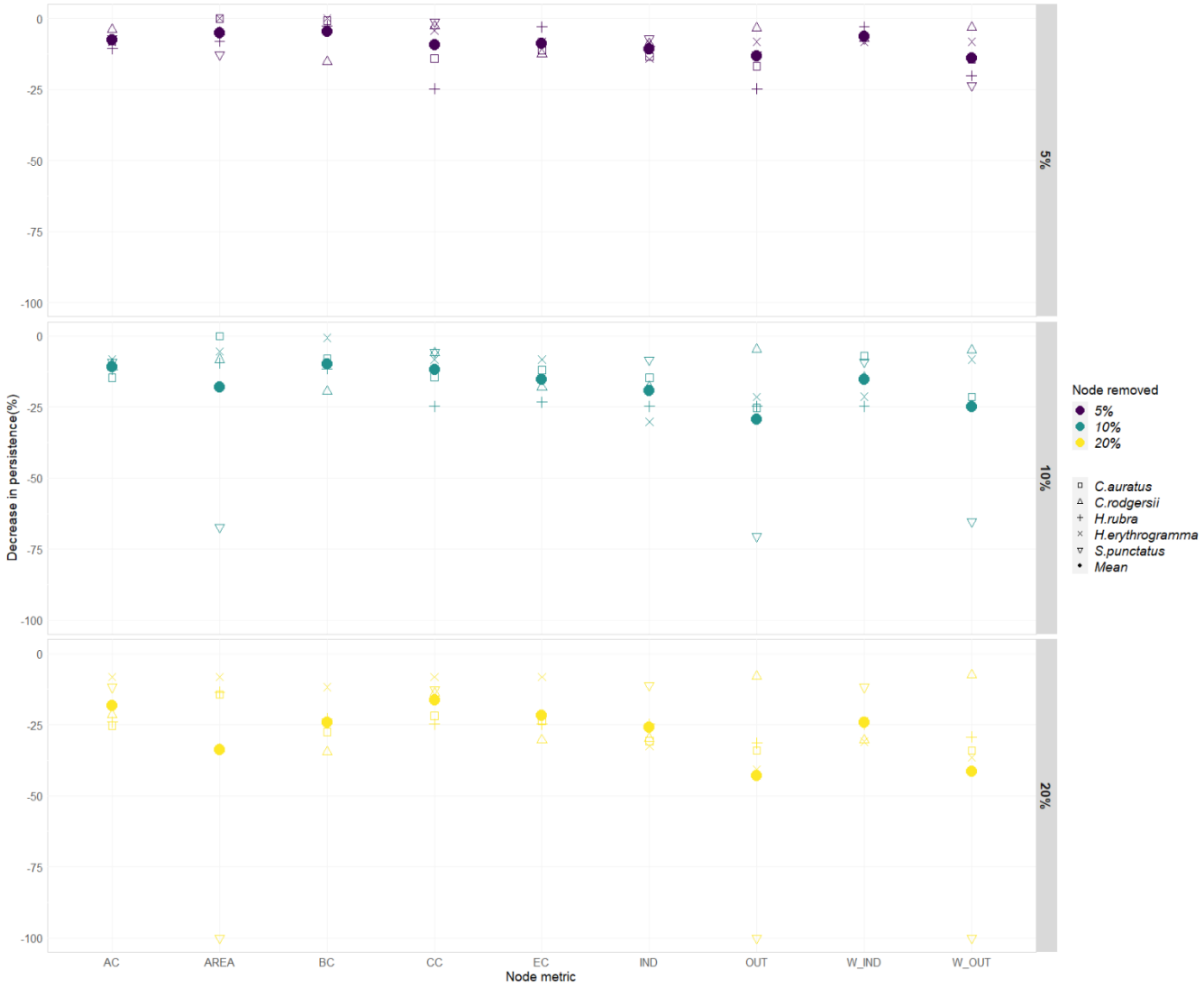


Figure A3.2: Decrease in persistence by network metric. Decrease in metapopulation persistence (%) when removing top 5%, 10% and 20% of nodes in a network, determined by each node-level network metrics. Data are shown for each species, as well as the mean across all species. Metrics used to identify those nodes to be removed include AC (alpha centrality), Area, BC (betweenness centrality), CC (closeness centrality), EC (eigenvector centrality), IND (in-degree), OUT (out-degree), W_IND (weighted in-degree) and W_OUT (weighted out-degree).

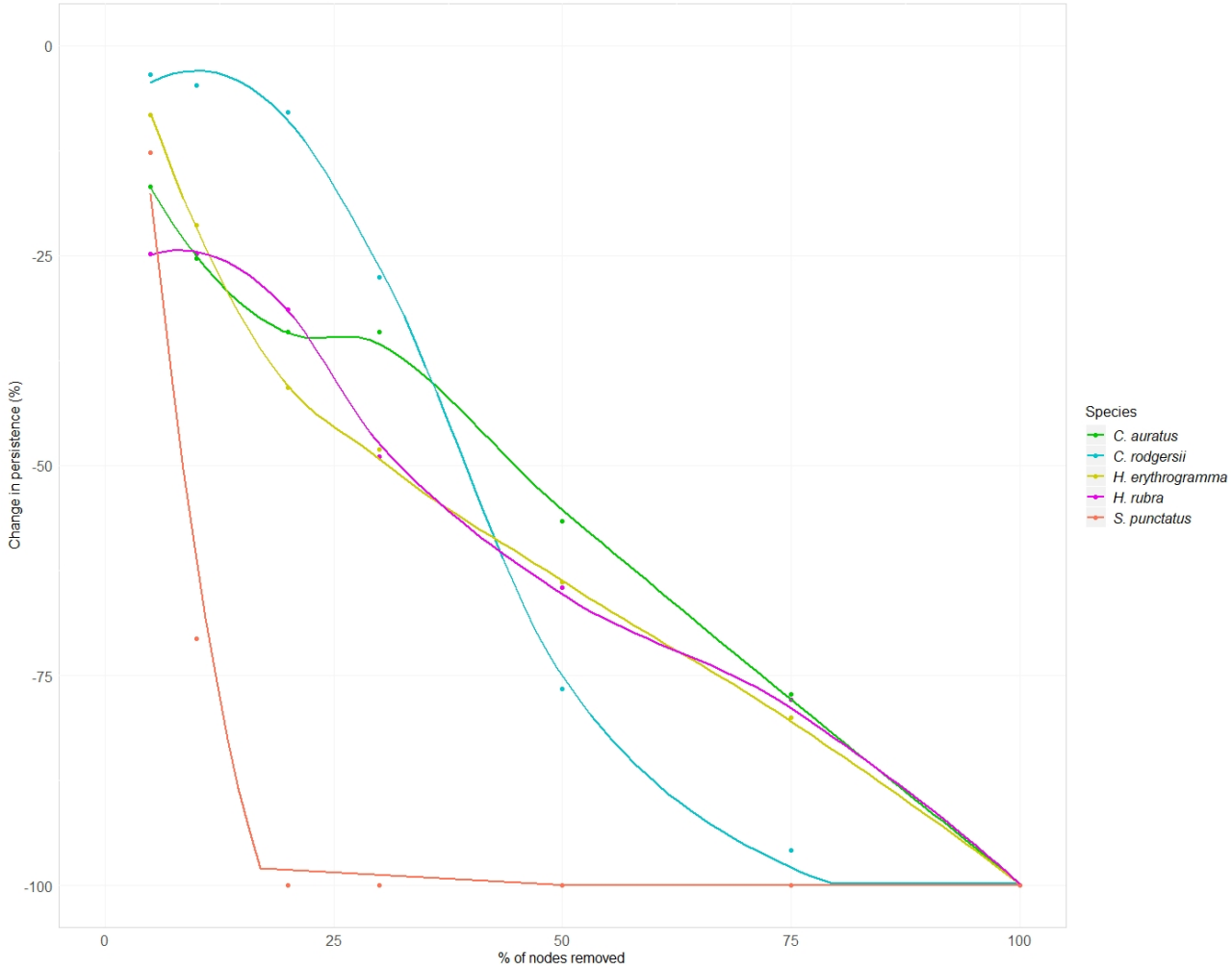


Figure A3.3: **Decline in population persistence with nodes removed.** Decrease in population persistence (-% on y-axis) with increased proportion of nodes removed, prioritised from highest to lowest out-degree.

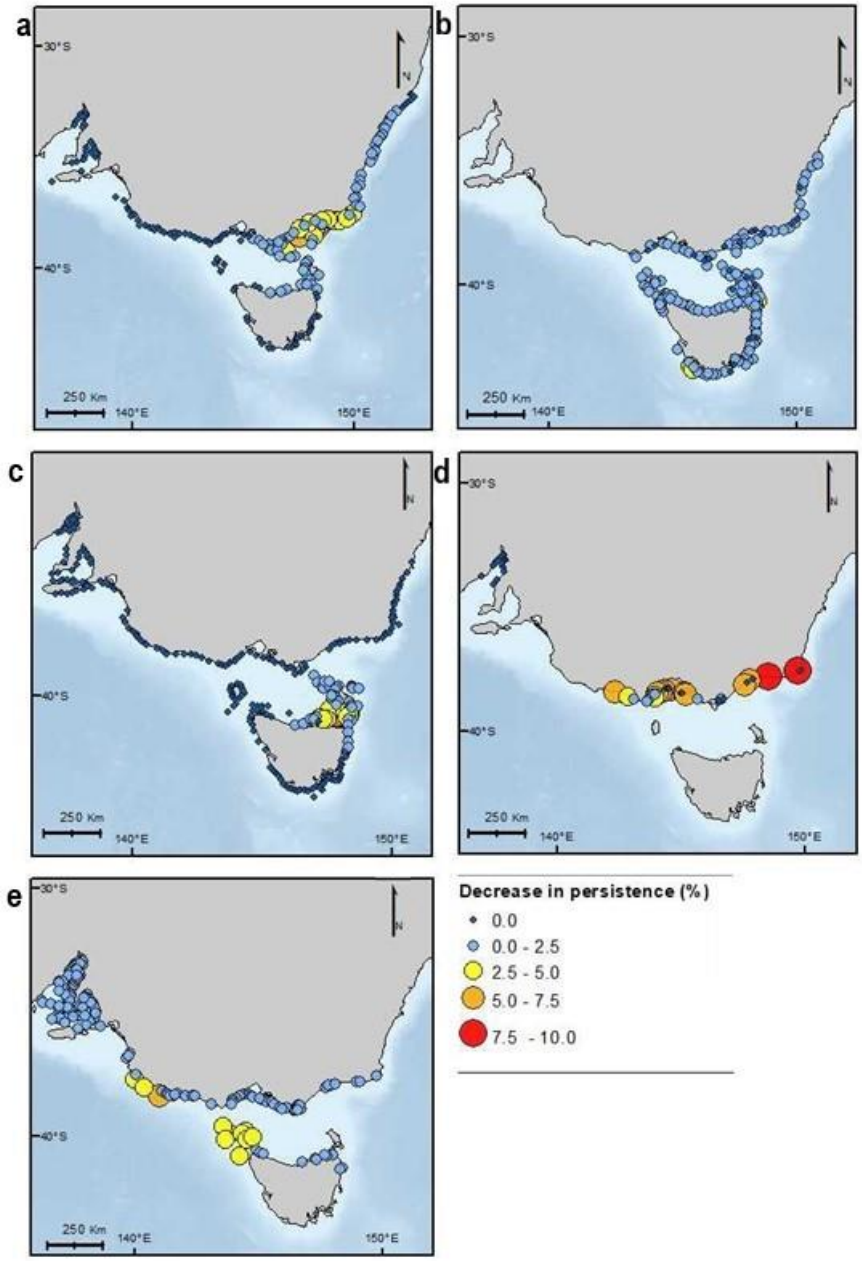


Figure A3.4: Decrease in persistence based on iterative node-removal exercise. Each node's influence on metapopulation persistence was evaluated based on the relative decrease in persistence when each focal node was removed. Mapped for all species: a) *H. rubra*; b) *C. rodgersii*; c) *H. erythrogramma*; d) *C. auratus*; e) *S. punctatus*. Map is in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

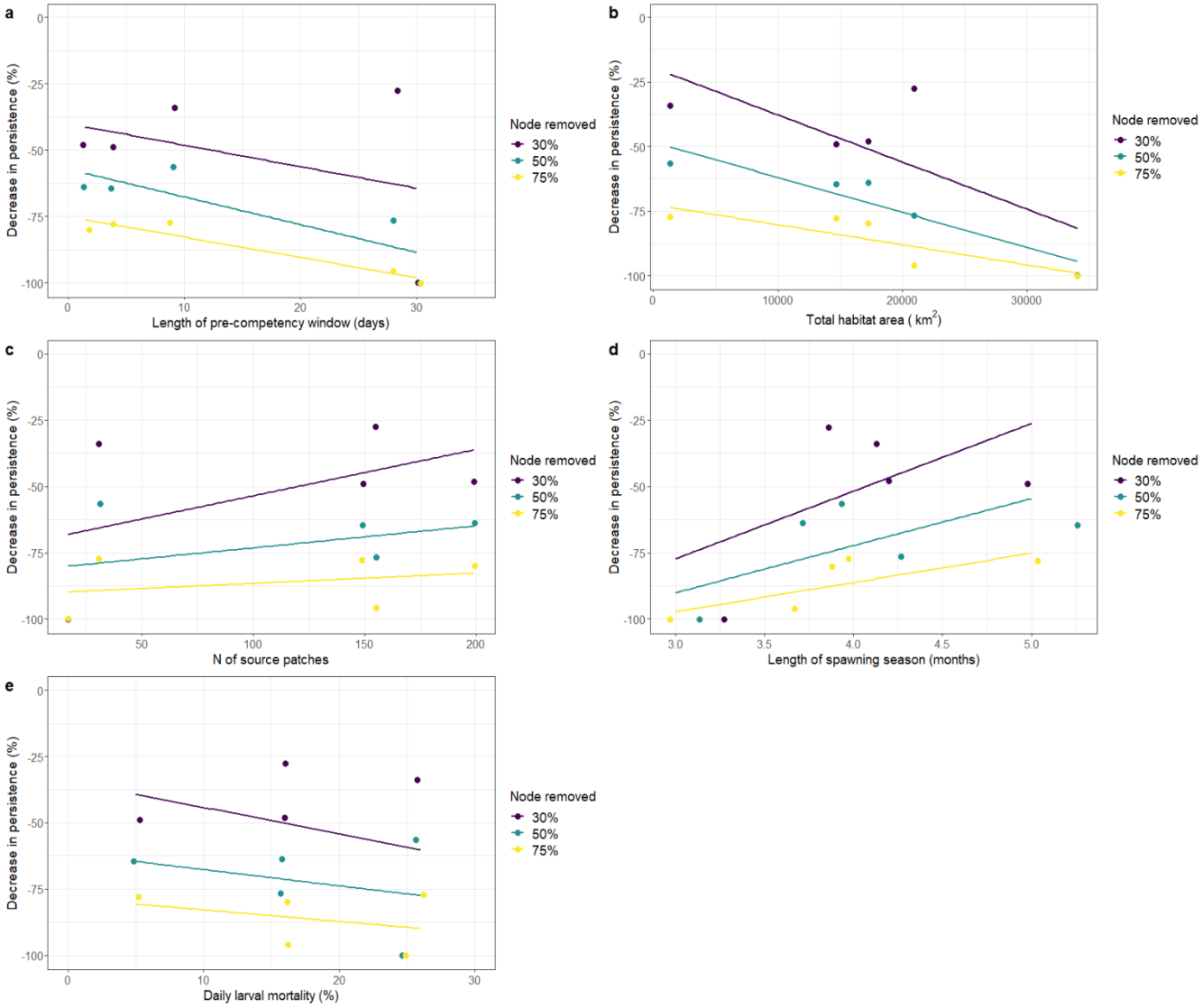


Figure A3.5: Correlation between life history characteristics and response in metapopulation persistence. a) Relationship between length of pre-competency window (days) and decrease in metapopulation persistence (% decrease). Respectively at 30%,50%,75% change in persistence R = -0.39, n = 5, p = 0.52; R = -0.83, n = 5, p =0.08; **R = -0.96, n = 5, p = 0.01**. b) Relationship between total habitat area (km^2) and decrease in metapopulation persistence. Respectively at 30%,50%,75% change in persistence R = -0.75, n = 5, p = 0.14; **R = -0.93, n = 5, p =0.02**; R = -0.84, n = 5, p = 0.07. c) Relationship between number of source habitat patches and decrease in metapopulation persistence. Respectively at 30%,50%,75% change in persistence R = 0.50, n = 5, p = 0.39; R = 0.40, n = 5, p =0.51; R = 0.29, n = 5, p = 0.64. d) Relationship between length of spawning season (months) and decrease in metapopulation persistence. Respectively at 30%,50%,75% change in persistence R = 0.63, n = 5, p = 0.25; R = 0.73, n = 5, p =0.16; R = 0.72, n = 5, p = 0.17. e) Relationship between daily larval mortality (%) and decrease in metapopulation persistence. Respectively at 30%,50%,75% change in persistence R = -0.30, n = 5, p = 0.63; R = -0.31, n = 5, p =0.62; R = -0.34, n = 5, p = 0.57.

Appendix 4

Network analysis results: node-level metrics

Species	IDs	Longitude	Latitude	In-degree	Out-degree	Weighted in-degree	Weighted out-degree	Betweenness centrality	Closeness centrality	Eigenvector centrality	Alpha centrality	Graph component
Haliotis rubra	1	842101.06	-3761308	9	7	33.67	28.14	0	0.04	0	-0.3	1
Haliotis rubra	2	847101.06	-3768808	9	6	30.71	33.31	0	0.04	0	0.1	1
Haliotis rubra	3	857101.06	-3773808	9	11	29.51	58.55	0	0.04	0	1.75	1
Haliotis rubra	4	839601.06	-3795236.5	9	17	31.43	50.16	567	0.04	0	0.87	1
Haliotis rubra	5	822101.06	-3813808	9	7	33.12	37.23	0	0.04	0	1.64	1
Haliotis rubra	6	811101.06	-3825808	9	19	33.92	59.21	147	0.04	0	2.96	1
Haliotis rubra	7	800434.38	-3842141.25	9	16	33.02	65.06	0	0.04	0.01	-0.5	1
Haliotis rubra	8	-797898.94	-3866308	7	5	24.66	15.35	0	0.32	0.71	-0.43	2
Haliotis rubra	9	-787898.94	-3873808	8	4	28.08	17.34	0	0.39	0.78	-0.02	2
Haliotis rubra	10	-818565.63	-3882474.5	8	8	32.84	15.07	24	0.41	1	-0.43	2
Haliotis rubra	11	-792898.94	-3893808	8	5	26.24	22.59	0	0.63	0.83	0.2	2
Haliotis rubra	12	-807898.94	-3898808	7	7	24.53	35.33	0	0.6	0.8	0.11	2
Haliotis rubra	13	772101.06	-3858544.75	8	21	29.98	60.76	201	0.05	0.01	0.98	1
Haliotis rubra	14	-832898.94	-3906308	7	8	19.57	34.54	11	0.5	0.53	0.05	2
Haliotis rubra	15	737101.06	-3908808	15	7	62.09	38.11	0	0.05	0.04	3.76	1

Haliotis rubra	16	-842898.94	-3921308	7	3	19.62	8.72	1	0.48	0.62	0.01	2
Haliotis rubra	17	727101.06	-3921308	14	11	54.3	47.28	0	0.05	0.04	-0.25	1
Haliotis rubra	18	720851.06	-3935058	16	14	62.75	51.6	62	0.05	0.05	-1.75	1
Haliotis rubra	19	-850398.94	-3941308	5	5	14.04	15.63	2	0.26	0.31	-0.34	2
Haliotis rubra	20	-798148.94	-3938058	5	10	20.25	14.68	15	0.62	0.54	-1.09	2
Haliotis rubra	21	707101.06	-3958808	19	6	73.86	31.76	0	0.05	0.12	-2.84	1
Haliotis rubra	22	712101.06	-3963808	20	7	79.55	36.7	0	0.05	0.12	1.62	1
Haliotis rubra	23	-808613.25	-3958093.5	3	10	5.15	35.74	5	0.46	0.08	0.01	2
Haliotis rubra	24	699601.06	-4001308	19	16	73.75	71.68	2493	0.05	0.11	2.8	1
Haliotis rubra	25	689601.06	-4016308	17	13	70.34	61.27	0	0.05	0.11	2.6	1
Haliotis rubra	26	-764327.5	-4045950.75	9	4	36.17	14.11	0	0.19	0.77	8.9	3
Haliotis rubra	27	-755898.94	-4066808	11	6	44.14	23.6	14	0.23	0.87	-8.72	3
Haliotis rubra	28	-787898.94	-4078808	12	4	43.87	22.42	0	0.29	0.91	1.62	3
Haliotis rubra	29	661767.69	-4067474.5	12	20	46.5	62.58	432	0.06	0.04	-2.45	1
Haliotis rubra	30	-747541.81	-4089522.25	9	10	33.67	23.27	29	0.28	0.71	-11.45	3
Haliotis rubra	31	-760398.94	-4103808	11	9	40.53	49.03	0	0.27	0.83	6.63	3
Haliotis rubra	32	662101.06	-4101308	15	15	59.64	72.69	6	0.06	0.08	4.07	1
Haliotis rubra	33	-787898.94	-4101308	12	11	52.12	49.79	7	0.27	1	0.34	3
Haliotis rubra	34	-757898.94	-4118808	9	9	28.48	47.12	0	0.27	0.56	2.12	3
Haliotis rubra	35	-794717.13	-4128353.25	7	13	27.36	39.21	39	0.31	0.46	0.4	3
Haliotis rubra	36	-742482.31	-4137141.25	8	11	28.12	34.14	3	0.22	0.54	-17.53	3
Haliotis rubra	37	-797898.94	-4153808	8	12	29.44	48.76	55	0.23	0.38	-1.17	3
Haliotis rubra	38	-837898.94	-4163808	5	5	14.1	15.54	24	0.17	0.12	7.56	3

Haliotis rubra	39	650315.31	-4135236.5	12	19	49.46	59.39	813	0.06	0.09	-6.36	1
Haliotis rubra	40	-861232.31	-4170474.5	4	3	8.47	8.46	0	0.16	0.05	4.33	3
Haliotis rubra	41	-813898.94	-4227308	1	4	0	10.74	0	0.12	0	1	3
Haliotis rubra	42	592101.06	-4243808	19	8	81.75	37.36	0	0.06	0.49	6.09	1
Haliotis rubra	43	589601.06	-4283808	30	16	137.23	60.55	5525	0.07	0.78	2.27	1
Haliotis rubra	44	-957898.94	-4291308	1	1	0	0	0	0	1	1	4
Haliotis rubra	45	584601.06	-4308808	34	9	156.36	38.94	0	0.07	0.88	-3.88	1
Haliotis rubra	46	572101.06	-4323808	33	8	158.09	44.09	0	0.07	0.81	-10.26	1
Haliotis rubra	47	-637898.94	-4388808	11	7	36.31	33.48	0	0.04	0	-0.41	1
Haliotis rubra	48	569601.06	-4383808	37	12	172.75	37.5	1769	0.07	0.96	9.97	1
Haliotis rubra	49	557101.06	-4396308	34	8	161.86	37.79	0	0.07	0.9	22.38	1
Haliotis rubra	50	-597898.94	-4406308	9	8	33.14	31.02	0	0.04	0	0.19	1
Haliotis rubra	51	567101.06	-4433808	37	7	175.25	44.57	0	0.07	1	5.59	1
Haliotis rubra	52	-582898.94	-4451308	11	11	37.95	46.88	0	0.04	0	-0.13	1
Haliotis rubra	53	589101.06	-4447808	38	12	177.61	50.93	139	0.07	1	-4.36	1
Haliotis rubra	54	-572898.94	-4463808	10	8	33.52	35.18	0	0.04	0	-0.54	1
Haliotis rubra	55	-566648.94	-4475058	12	15	50	63.57	0	0.04	0	0	1
Haliotis rubra	56	532101.06	-4498808	28	7	128.61	39.42	0	0.07	0.72	-2.17	1
Haliotis rubra	57	549373.75	-4491989.5	31	20	138.58	81.69	2635	0.07	0.75	0.77	1
Haliotis rubra	58	-562898.94	-4503808	16	13	70.05	68.93	0	0.04	0	-0.05	1
Haliotis rubra	59	-546827.5	-4497379.5	13	19	55.79	54.52	1126	0.04	0	-1.54	1
Haliotis rubra	60	452934.38	-4533391	30	30	130.51	101.29	54	0.07	0.57	1.34	1
Haliotis rubra	61	489184.38	-4531308	28	26	116.4	91.39	0	0.07	0.54	-8.45	1

Haliotis rubra	62	-525206.63	-4534577	15	19	66.17	54.31	142	0.04	0	0.46	1
Haliotis rubra	63	404601.03	-4548808	30	25	123.36	133.58	0	0.07	0.55	1.35	1
Haliotis rubra	64	397101.03	-4553808	30	15	122.59	92.43	0	0.07	0.53	-0.07	1
Haliotis rubra	65	-522898.97	-4563808	17	16	68.63	86.02	0	0.05	0	0.18	1
Haliotis rubra	66	-492898.97	-4561308	13	20	55.12	65.68	0	0.04	0	0.67	1
Haliotis rubra	67	381101.03	-4568808	28	31	113.58	110.34	477	0.08	0.55	17.51	1
Haliotis rubra	68	-426232.28	-4577141	14	13	53.49	64.32	0	0.05	0	0.14	1
Haliotis rubra	69	319601.03	-4583808	29	24	124.2	130.78	1	0.07	0.47	-5.37	1
Haliotis rubra	70	370101.03	-4582808	28	25	117.94	132.16	0	0.08	0.56	4.99	1
Haliotis rubra	71	-470251.91	-4582043	19	24	78.17	84.88	2673	0.05	0	-0.56	1
Haliotis rubra	72	-445398.97	-4590474.5	18	18	68	82.2	0	0.05	0	-0.24	1
Haliotis rubra	73	341101.03	-4590808	28	31	111.58	143.95	0	0.08	0.49	-12.45	1
Haliotis rubra	74	-412898.97	-4591308	16	20	60.67	84.98	0	0.05	0	0.78	1
Haliotis rubra	75	-395398.97	-4608808	16	11	56.31	57.78	0	0.05	0	-0.34	1
Haliotis rubra	76	-85398.96	-4613808	8	5	25.19	18.32	0	0.06	0	-0.86	1
Haliotis rubra	77	-366535.31	-4613808	17	21	67.72	75.56	10	0.05	0	-0.06	1
Haliotis rubra	78	352555.59	-4611989.5	29	31	129.7	105.61	3818	0.08	0.59	-6.58	1
Haliotis rubra	79	-98898.96	-4620808	8	9	26.08	31.82	3491	0.05	0	0.24	1
Haliotis rubra	80	-28315.63	-4611724.5	9	14	39.02	54.22	6043	0.06	0	0.62	1
Haliotis rubra	81	354601.03	-4633808	28	20	131.35	101.89	0	0.07	0.58	-0.93	1
Haliotis rubra	82	-112898.96	-4636308	9	7	33.26	24.43	0	0.05	0	-1.03	1
Haliotis rubra	83	-341232.28	-4642141	18	14	67.17	81.14	1375	0.05	0	-0.4	1
Haliotis rubra	84	332726.03	-4545370.5	18	29	81.5	114.76	0	0.07	0.32	-2.99	1

Haliotis rubra	85	287656.59	-4635474.5	31	38	134.13	161.9	2637	0.08	0.43	-0.96	1
Haliotis rubra	86	-120398.96	-4653808	13	8	61.43	31.3	1981	0.06	0	1.7	1
Haliotis rubra	87	216476.05	-4647558	15	24	62.67	126.04	0	0.07	0.13	0.62	1
Haliotis rubra	88	352101.03	-4653808	23	6	101.32	36.12	0	0.07	0.47	8.83	1
Haliotis rubra	89	-292898.97	-4616308	12	19	50.99	62.54	125	0.06	0	-0.08	1
Haliotis rubra	90	-187898.95	-4663808	12	6	41.74	24.19	1104	0.05	0	1.25	1
Haliotis rubra	91	-137898.95	-4658808	14	8	65.02	26.51	5204	0.06	0	-0.2	1
Haliotis rubra	92	-12898.96	-4663808	14	1	53.62	3.98	0	0.07	0	7.53	1
Haliotis rubra	93	187101.05	-4663808	11	6	44.16	31.66	0	0.07	0.07	-1.49	1
Haliotis rubra	94	-172898.95	-4671308	12	6	39.57	25.7	1824	0.05	0	-1.17	1
Haliotis rubra	95	-165398.95	-4683808	17	8	63.58	34.47	3694	0.06	0	-0.36	1
Haliotis rubra	96	193919.22	-4683808	20	31	81.75	136.66	1200	0.07	0.14	2.13	1
Haliotis rubra	97	342656.59	-4686585.5	22	24	97.97	113	97	0.07	0.43	0.95	1
Haliotis rubra	98	171191.95	-4688353.5	17	22	77.71	97.58	102	0.07	0.09	3.04	1
Haliotis rubra	99	129392.7	-4687766	8	18	32.97	73.35	0	0.07	0.01	-0.61	1
Haliotis rubra	100	167101.05	-4708808	17	4	63.19	21.99	0	0.07	0.07	-1.29	1
Haliotis rubra	101	132101.05	-4713808	16	7	75.58	34.63	0	0.07	0.05	1.77	1
Haliotis rubra	102	142101.05	-4720058	18	17	78.27	80.95	2967	0.07	0.06	1.46	1
Haliotis rubra	103	169601.05	-4726308	25	15	110.23	76.01	43	0.08	0.17	-2.72	1
Haliotis rubra	104	220101.05	-4729808	24	37	112.34	180.94	4013	0.08	0.26	2.21	1
Haliotis rubra	105	184601.05	-4763808	22	33	109.01	165.9	1337	0.08	0.19	-1.15	1
Haliotis rubra	106	262815.31	-4759165	17	31	74.21	123.35	7107	0.08	0.28	2.17	1
Haliotis rubra	107	328529.63	-4790950.5	10	11	39.61	47.71	336	0.07	0.05	-0.17	1

Haliotis rubra	108	312101.03	-4808808	11	9	45.68	40.9	0	0.07	0.07	-1.36	1
Haliotis rubra	109	-95756.1	-4815950.5	5	9	18.48	42.07	1984	0.07	0	-0.76	1
Haliotis rubra	110	-140232.3	-4810474.5	4	9	11.37	37.69	2	0.07	0	-1.43	1
Haliotis rubra	111	-115398.96	-4861308	5	4	16.98	11.03	2	0.07	0	0.11	1
Haliotis rubra	112	311267.72	-4837697	9	16	34.69	60.27	165	0.07	0.03	0.24	1
Haliotis rubra	113	320434.38	-4882974.5	12	13	51.65	46.1	218	0.06	0.01	-0.32	1
Haliotis rubra	114	382101.03	-4887974.5	12	6	45.97	30.72	103	0.06	0	0.93	1
Haliotis rubra	115	338101.03	-4912808	10	9	32.63	35.81	1	0.06	0	-0.16	1
Haliotis rubra	116	344601.03	-4943808	16	10	68.11	40.1	423	0.06	0	3.18	1
Haliotis rubra	117	292656.59	-4945197	13	16	47.46	54.55	6969	0.06	0	-1.64	1
Haliotis rubra	118	-42898.96	-4966308	3	5	7.7	19	4241	0.05	0	-1.09	1
Haliotis rubra	119	59601.04	-4957974.5	5	9	17.46	38.42	4340	0.05	0	-0.74	1
Haliotis rubra	120	372101.03	-4978808	10	7	36.41	28.33	2447	0.05	0	-1.25	1
Haliotis rubra	121	-49898.96	-4984808	2	6	1.39	26.21	2014	0.05	0	0.9	1
Haliotis rubra	122	219878.81	-4978530	11	15	43.09	58.38	4643	0.06	0	0.04	1
Haliotis rubra	123	136545.48	-4999363.5	6	12	16.34	42.96	4470	0.06	0	-1.28	1
Haliotis rubra	124	368767.72	-5010474.5	8	5	35.17	17.42	0	0.05	0	0.32	1
Haliotis rubra	125	375226.03	-5029433	10	7	45.81	24.24	2466	0.05	0	1.08	1
Haliotis rubra	126	377101.03	-5158808	13	4	50.19	18.7	2205	0.04	0	-2.13	1
Haliotis rubra	127	16684.37	-5166724.5	4	6	15.62	19.74	2208	0.05	0	-0.39	1
Haliotis rubra	128	22101.04	-5188808	4	2	16.46	9.12	0	0.05	0	-0.26	1
Haliotis rubra	129	339767.72	-5218141	6	7	18.83	16.17	294	0.04	0	-1.43	1
Haliotis rubra	130	336101.03	-5245808	8	5	30.78	10.72	0	0.04	0	0.87	1

Haliotis rubra	131	334601.03	-5261308	11	5	43.7	14.82	560	0.04	0	-0.1	1
Haliotis rubra	132	290434.38	-5292141	5	4	19.86	14.84	0	0.04	0	-0.39	1
Haliotis rubra	133	84958.18	-5315236.5	4	7	12.56	23.44	0	0.04	0	0.17	1
Haliotis rubra	134	274206.31	-5308808	8	8	28.29	27.17	295	0.04	0	-0.56	1
Haliotis rubra	135	264601.03	-5348808	9	6	28.38	24.54	0	0.04	0	-0.8	1
Haliotis rubra	136	97485.66	-5346115.5	5	8	14.6	23.65	2069	0.04	0	-0.04	1
Haliotis rubra	137	244601.05	-5366308	7	8	23.24	29.85	3	0.04	0	-0.61	1
Haliotis rubra	138	224408.73	-5369961.5	6	8	14.31	30.18	952	0.04	0	0.84	1
Haliotis rubra	139	147101.05	-5378808	5	9	12.97	28.72	1923	0.04	0	-0.09	1
Haliotis rubra	140	-730398.94	-4116808	7	9	24.5	29.92	0	0.21	0.46	7.12	3
Haliotis rubra	141	-743353.5	-4116989.75	9	12	33.5	28.37	40	0.27	0.66	3.91	3
Haliotis rubra	142	-450398.97	-4576308	16	19	63.09	78.61	0	0.05	0	0.1	1
Haliotis rubra	143	-219565.63	-4655474.5	14	12	57.19	46.57	3001	0.06	0	-0.13	1
Haliotis rubra	144	-241398.95	-4642808	12	13	46.35	48.2	0	0.06	0	0.16	1
Haliotis rubra	145	-341148.97	-4611558	17	19	75.02	55.96	1157	0.05	0	-1.63	1
Haliotis rubra	146	-132898.95	-4778808	4	16	9.01	76.22	1728	0.08	0	-0.6	1
Haliotis rubra	147	-55676.74	-4598252.5	8	9	30.81	35.92	0	0.06	0	-0.54	1
Haliotis rubra	148	6574.72	-4627492	7	14	25.92	55.91	34	0.07	0	-0.86	1
Haliotis rubra	149	47907.49	-4648324	7	18	24.84	58.47	6495	0.07	0	1.69	1
Haliotis rubra	150	82101.04	-4659879.5	7	16	25.12	61.69	0	0.07	0	-0.63	1
Haliotis rubra	151	103351.04	-4683183	9	14	34.3	53.69	2719	0.07	0.01	1.75	1
Haliotis rubra	152	176101.05	-4667308	11	23	47.24	100.68	1	0.07	0.07	-1.49	1
Haliotis rubra	153	238053.42	-4630712.5	17	36	71.48	138.85	360	0.08	0.14	-3.42	1

Haliotis rubra	154	257395.16	-4606749	12	36	46.05	164.9	0	0.07	0.12	2.45	1
Haliotis rubra	155	285249.19	-4586400.5	21	39	98.62	137.57	755	0.08	0.35	0.18	1
Haliotis rubra	156	427101.03	-4528808	22	25	92.65	122.22	0	0.07	0.43	2.45	1
Haliotis rubra	157	397101.03	-4533558	26	30	118.64	92.51	107	0.07	0.49	1.41	1
Haliotis rubra	158	364601.03	-4532974.5	18	27	79.13	117.06	0	0.07	0.33	-1.87	1
Haliotis rubra	159	306476.03	-4560370.5	15	31	65.13	126.08	0	0.07	0.22	0.73	1
Haliotis rubra	160	519101.03	-4520308	30	24	130	89.49	999	0.07	0.72	-0.72	1
Haliotis rubra	161	639601.06	-4163450.75	15	18	64.91	73.56	279	0.06	0.27	3.12	1
Haliotis rubra	162	646476.06	-4116933	9	15	34.26	61.12	0	0.06	0.04	-8.55	1
Haliotis rubra	163	675434.38	-4034919	13	18	53.21	66.17	0	0.05	0.04	-7.59	1
Haliotis rubra	164	747101.06	-3886535.25	12	22	51.72	82.07	1067	0.05	0.02	-4.2	1
Haliotis rubra	165	238101.05	-4769308	17	29	77.35	135.97	2406	0.08	0.26	-0.85	1
Haliotis rubra	166	302101.03	-4854808	12	16	46.2	67.31	6317	0.07	0.02	-2.83	1
Haliotis rubra	167	318976.03	-4946933	14	12	56.36	50.1	0	0.06	0	0.09	1
Haliotis rubra	168	189828.31	-4991535	7	14	22.13	52.8	0	0.06	0	0.82	1
Haliotis rubra	169	80434.38	-4972141	5	8	12.01	31.53	4384	0.05	0	2.16	1
Haliotis rubra	170	132601.05	-5374808	5	9	11.81	33.32	0	0.04	0	-0.04	1
Haliotis rubra	171	356434.38	-5164474.5	3	4	7.85	9.88	0	0.04	0	-1.17	1
Haliotis rubra	172	346684.38	-5190474.5	5	7	13.11	22.2	293	0.04	0	1.33	1
Haliotis rubra	173	-319148.97	-4615058	13	19	55.82	64.17	0	0.05	0	1.71	1
Haliotis rubra	174	-266648.97	-4623808	10	17	37.59	58.57	0	0.06	0	0.27	1
Haliotis rubra	176	27101.04	-4631308	6	11	19.2	54.07	0	0.07	0	-1.42	1
Centrostephanus rodgersii	1	648351.06	-4123808	109	18	567.43	113.93	0	0.19	0.93	-0.12	1

Centrostephanus rodgersii	2	624243.88	-4174165	110	24	575.41	151.24	153	0.19	0.95	0.05	1
Centrostephanus rodgersii	3	583886.75	-4278808	104	33	548.15	200.25	0	0.2	0.92	-0.72	1
Centrostephanus rodgersii	4	573101.06	-4291808	103	0	545.06	0	0	0.2	0.91	-0.73	1
Centrostephanus rodgersii	5	579323.25	-4313252.5	103	21	546.35	135.92	0	0.2	0.93	-0.07	1
Centrostephanus rodgersii	6	569601.06	-4383808	98	27	529.17	172.62	0	0.2	0.87	-0.09	1
Centrostephanus rodgersii	7	588038.56	-4443808	102	50	547.45	285.7	26	0.21	0.94	-0.01	1
Centrostephanus rodgersii	8	557101.06	-4466308	78	0	416.73	0	0	0.21	0.53	0.09	1
Centrostephanus rodgersii	9	532101.06	-4498808	71	0	374.71	0	0	0.21	0.42	0.76	1
Centrostephanus rodgersii	10	552395.19	-4492631.5	79	56	424.19	322.29	0	0.21	0.54	-0.08	1
Centrostephanus rodgersii	11	369601.03	-4528808	45	0	219.93	0	0	0.21	0.16	-0.16	1
Centrostephanus rodgersii	12	352101.03	-4533808	43	0	207.51	0	0	0.21	0.12	-0.06	1
Centrostephanus rodgersii	13	452601.03	-4532808	53	68	264.97	378.65	181	0.22	0.23	-0.16	1
Centrostephanus rodgersii	14	404601.03	-4548808	51	0	252.18	0	0	0.21	0.2	-0.24	1
Centrostephanus rodgersii	15	397101.03	-4553808	56	0	284.61	0	0	0.21	0.24	-0.17	1
Centrostephanus rodgersii	16	318038.53	-4550370.5	41	33	195.19	205.22	0	0.21	0.07	0.16	1

Centrostephanus rodgersii	17	322815.31	-4583093.5	45	50	218.94	279.98	0	0.22	0.16	-0.16	1
Centrostephanus rodgersii	18	285434.38	-4583808	41	50	198.71	280.18	183	0.22	0.07	0.19	1
Centrostephanus rodgersii	19	302101.03	-4593808	41	0	194.91	0	0	0.21	0.07	0.17	1
Centrostephanus rodgersii	20	380434.38	-4581308	66	70	340.51	388.21	0	0.22	0.39	-0.14	1
Centrostephanus rodgersii	21	-44822.04	-4599961.5	26	41	116.03	242.63	195	0.19	0.02	0.01	1
Centrostephanus rodgersii	22	324601.03	-4606308	47	21	229.33	136.57	0	0.22	0.18	0.13	1
Centrostephanus rodgersii	23	-82898.96	-4613808	25	0	110.28	0	0	0.19	0.02	0	1
Centrostephanus rodgersii	24	252656.59	-4608252.5	34	23	155.04	147.82	0	0.21	0.04	0.1	1
Centrostephanus rodgersii	25	289601.03	-4611308	41	4	195.84	27.26	0	0.21	0.07	0.18	1
Centrostephanus rodgersii	26	-100398.96	-4618808	22	3	89.84	20.02	0	0.19	0.02	0	1
Centrostephanus rodgersii	27	-24565.63	-4612974.5	27	5	120.66	33.28	0	0.19	0.02	0	1
Centrostephanus rodgersii	28	348489.94	-4603252.5	52	80	256.72	438.82	47	0.23	0.23	0.02	1
Centrostephanus rodgersii	29	233529.61	-4624522	32	0	143.47	0	0	0.21	0.03	0.02	1
Centrostephanus rodgersii	30	12101.04	-4627379.5	28	55	125.27	310	407	0.2	0.03	-0.01	1
Centrostephanus rodgersii	31	-112898.96	-4643808	25	0	109.79	0	0	0.19	0.02	-0.02	1

Centrostephanus rodgersii	32	286545.5	-4637141	41	36	194.02	215.8	0	0.22	0.06	0.16	1
Centrostephanus rodgersii	33	50042.21	-4644396	26	41	110.63	238.59	0	0.2	0.02	0.03	1
Centrostephanus rodgersii	34	-172898.95	-4668808	26	6	112.94	40.12	0	0.19	0.08	-0.02	1
Centrostephanus rodgersii	35	286029.63	-4659522	41	50	193.09	285.13	0	0.22	0.11	-0.2	1
Centrostephanus rodgersii	36	94601.04	-4668808	27	0	115.21	0	0	0.21	0.02	-0.18	1
Centrostephanus rodgersii	37	-165398.95	-4683808	24	13	102.41	71.81	0	0.19	0.03	-0.04	1
Centrostephanus rodgersii	38	119101.04	-4680308	27	7	114.89	47.26	0	0.21	0.02	-0.2	1
Centrostephanus rodgersii	39	176191.95	-4672444	28	11	118.27	67.7	0	0.21	0.02	0.02	1
Centrostephanus rodgersii	40	162101.05	-4693808	28	0	118.85	0	0	0.21	0.02	0.02	1
Centrostephanus rodgersii	41	142101.05	-4703808	27	0	114.38	0	0	0.2	0.02	-0.2	1
Centrostephanus rodgersii	42	154601.05	-4731308	28	3	117.45	20.53	0	0.22	0.02	0.03	1
Centrostephanus rodgersii	43	219024.11	-4729192.5	39	40	186.84	241.09	0	0.22	0.06	0.29	1
Centrostephanus rodgersii	44	252101.05	-4761308	40	0	186.08	0	0	0.22	0.11	-0.03	1
Centrostephanus rodgersii	45	262934.38	-4763808	42	41	199.42	250.86	0	0.22	0.15	-0.12	1
Centrostephanus rodgersii	46	-120206.65	-4774192.5	27	106	119.05	519.55	263	0.22	0.04	-0.04	1

Centrostephanus rodgersii	47	235851.05	-4775058	38	36	176.71	225.09	0	0.22	0.06	0.2	1
Centrostephanus rodgersii	48	334601.03	-4781308	59	37	297.38	237.47	0	0.21	0.36	0.11	1
Centrostephanus rodgersii	49	382101.03	-4778808	89	45	474.68	272.09	0	0.2	0.78	0.17	1
Centrostephanus rodgersii	50	260434.38	-4795474.5	37	1	168.17	6.91	0	0.22	0.06	0.07	1
Centrostephanus rodgersii	51	332101.03	-4798808	78	0	414.95	0	0	0.2	0.64	3	1
Centrostephanus rodgersii	52	-137898.95	-4801308	26	48	113.39	280.29	0	0.21	0.07	-0.06	1
Centrostephanus rodgersii	53	293976.03	-4792870.5	44	96	207.79	516.32	1	0.23	0.18	0.16	1
Centrostephanus rodgersii	54	314601.03	-4806308	55	47	276.57	293.28	0	0.21	0.3	-0.16	1
Centrostephanus rodgersii	55	352101.03	-4808808	86	0	461.11	0	0	0.2	0.77	-0.1	1
Centrostephanus rodgersii	56	-54565.63	-4822141	26	106	108.59	587.89	0	0.23	0.03	-0.03	1
Centrostephanus rodgersii	57	304601.03	-4823808	49	56	238.55	348.24	0	0.21	0.21	0	1
Centrostephanus rodgersii	58	372101.03	-4838808	102	0	534.51	0	0	0.19	0.89	1.68	1
Centrostephanus rodgersii	59	-127898.96	-4851308	30	38	127.21	228.32	0	0.22	0.1	0.03	1
Centrostephanus rodgersii	60	-93523.96	-4855370.5	29	144	125.3	614.18	0	0.25	0.08	-0.04	1
Centrostephanus rodgersii	61	300562.59	-4851500	48	90	233.87	499.82	0	0.22	0.19	-0.05	1

Centrostephanus rodgersii	62	267101.03	-4868808	40	0	187.17	0	0	0.22	0.13	0.11	1
Centrostephanus rodgersii	63	288767.72	-4867141	45	15	215.38	101.44	0	0.21	0.18	0.11	1
Centrostephanus rodgersii	64	373101.03	-4872808	102	40	525.97	249.14	0	0.19	0.91	0	1
Centrostephanus rodgersii	65	262101.05	-4881308	39	8	181.55	53.73	0	0.22	0.11	-0.12	1
Centrostephanus rodgersii	66	332555.59	-4877899	46	74	219.65	450.43	0	0.21	0.19	0.03	1
Centrostephanus rodgersii	67	379601.03	-4888808	103	7	530.15	47.93	0	0.19	0.9	-0.06	1
Centrostephanus rodgersii	68	-91648.96	-4879120.5	29	155	125.11	633.02	4	0.25	0.08	-0.07	1
Centrostephanus rodgersii	69	-70398.96	-4908808	26	117	106.3	662.03	0	0.23	0.07	0	1
Centrostephanus rodgersii	70	314601.03	-4904363.5	45	107	214.46	578.36	0	0.22	0.17	-0.03	1
Centrostephanus rodgersii	71	307101.03	-4936308	57	23	291.55	152.05	0	0.2	0.39	0.37	1
Centrostephanus rodgersii	72	3101.04	-4920808	27	146	116.11	534.66	173	0.26	0.03	0.03	1
Centrostephanus rodgersii	73	67101.04	-4966308	27	59	114.38	364.36	0	0.21	0.03	0.01	1
Centrostephanus rodgersii	74	79601.04	-4968808	28	93	119.62	545.06	0	0.21	0.03	-0.01	1
Centrostephanus rodgersii	75	95226.04	-4985683	29	104	127.16	556.91	0	0.21	0.03	0.03	1
Centrostephanus rodgersii	76	117101.04	-4993808	31	27	138.35	181.72	0	0.21	0.04	0.08	1

Centrostephanus rodgersii	77	272101.03	-4970650	45	109	218.24	526.78	221	0.23	0.2	0.03	1
Centrostephanus rodgersii	78	154878.81	-5001308	33	115	148.76	600.34	61	0.22	0.05	0	1
Centrostephanus rodgersii	79	-57158.22	-4948808	27	155	111.23	410.71	274	0.38	0.08	-0.02	1
Centrostephanus rodgersii	80	370947.19	-5047654	106	68	541.67	334.79	582	0.19	0.99	0.2	1
Centrostephanus rodgersii	81	369601.03	-5098808	102	64	520.76	314.48	11	0.18	0.91	0.1	1
Centrostephanus rodgersii	82	374101.03	-5131308	102	58	521.63	313.85	0	0.18	0.91	-0.04	1
Centrostephanus rodgersii	83	377101.03	-5153808	102	0	523.15	0	0	0.17	0.91	0.01	1
Centrostephanus rodgersii	84	342101.03	-5163808	76	0	376.59	0	0	0.17	0.71	-0.82	1
Centrostephanus rodgersii	85	357555.59	-5160626	76	0	377.64	0	0	0.17	0.71	-0.83	1
Centrostephanus rodgersii	86	352101.03	-5178808	82	3	410.78	20.64	0	0.17	0.72	-0.24	1
Centrostephanus rodgersii	87	377101.03	-5176308	99	36	505.07	230.28	0	0.17	0.88	-0.02	1
Centrostephanus rodgersii	88	19958.18	-5229998.5	48	73	241.15	309.14	375	0.23	0.46	0.01	1
Centrostephanus rodgersii	89	341476.03	-5220058	92	60	467.71	310.69	0	0.17	0.8	0.16	1
Centrostephanus rodgersii	90	357101.03	-5288808	101	42	518.41	242.05	0	0.17	0.93	-0.42	1
Centrostephanus rodgersii	91	339408.72	-5292654	93	62	474.74	292.68	138	0.18	0.85	0.09	1

Centrostephanus rodgersii	92	279601.03	-5303808	56	58	265.24	284.57	0	0.19	0.6	-0.08	1
Centrostephanus rodgersii	93	272101.03	-5323808	58	0	277.34	0	0	0.17	0.62	-0.54	1
Centrostephanus rodgersii	94	328886.75	-5320236.5	71	59	348.24	290.77	0	0.18	0.69	-0.82	1
Centrostephanus rodgersii	95	257101.05	-5368808	61	0	294.35	0	0	0.17	0.64	-0.85	1
Centrostephanus rodgersii	96	231386.75	-5368331.5	64	59	314.78	290.05	151	0.18	0.65	-0.24	1
Centrostephanus rodgersii	97	78291.52	-5326903	67	80	330.87	348.99	759	0.21	0.65	-0.05	1
Centrostephanus rodgersii	98	330851.03	-4917141	47	80	225.99	468.4	0	0.21	0.24	0.01	1
Centrostephanus rodgersii	99	317983.41	-4948219.5	74	90	390.2	467	0	0.22	0.66	0.06	1
Centrostephanus rodgersii	100	390989.94	-4908252.5	106	67	548.86	370.77	0	0.2	0.93	0.15	1
Centrostephanus rodgersii	101	368976.03	-4923183	86	89	458.51	433.01	12	0.23	0.8	0.06	1
Centrostephanus rodgersii	102	382501.03	-4938208	105	96	540.64	437.45	3003	0.22	0.94	0.06	1
Centrostephanus rodgersii	103	341767.72	-4941808	90	91	480.68	457.38	0	0.22	0.84	-0.08	1
Centrostephanus rodgersii	104	362378.81	-4945752.5	101	96	527.68	447.45	185	0.22	0.9	-0.13	1
Centrostephanus rodgersii	105	381101.03	-4976808	108	61	552.33	339.78	0	0.19	0.97	-0.35	1
Centrostephanus rodgersii	106	374288.53	-5001620.5	107	69	546.54	341.85	198	0.19	0.96	-0.26	1

Centrostephanus rodgersii	107	374101.03	-5021808	107	59	546.96	320.13	0	0.18	1	0.61	1
Centrostephanus rodgersii	108	376101.03	-5069808	108	47	555.39	276.79	78	0.18	0.99	0.17	1
Centrostephanus rodgersii	109	197101.05	-5383808	65	47	318.14	227.92	0	0.17	0.66	0.25	1
Centrostephanus rodgersii	110	177726.05	-5378183	65	46	319.72	225.71	0	0.17	0.64	0.16	1
Centrostephanus rodgersii	111	154913.55	-5390370.5	71	67	353.1	283.67	99	0.18	0.71	-0.04	1
Centrostephanus rodgersii	112	132364.2	-5376176.5	64	61	309.48	274.34	0	0.18	0.66	0.26	1
Centrostephanus rodgersii	113	107656.59	-5363808	67	50	331.27	226.26	0	0.18	0.65	0.03	1
Centrostephanus rodgersii	114	91163.54	-5348495.5	68	79	336.08	348.53	3749	0.2	0.67	0.04	1
Centrostephanus rodgersii	115	70601.04	-5305308	68	70	347.9	312.78	0	0.22	0.66	0	1
Centrostephanus rodgersii	116	-40398.96	-4893808	26	128	105.99	615.79	0	0.22	0.03	0.04	1
Centrostephanus rodgersii	117	-26787.85	-4899363.5	26	130	105.8	603.39	0	0.22	0.03	-0.01	1
Centrostephanus rodgersii	118	-39327.53	-4916308	26	155	105.93	611.83	21	0.25	0.03	0.03	1
Centrostephanus rodgersii	119	-49262.6	-4933126	25	155	99.06	466.7	0	0.33	0.05	-0.19	1
Centrostephanus rodgersii	120	-45171.69	-5004717	27	152	107.69	772.02	0	0.23	0.07	-0.03	1
Centrostephanus rodgersii	121	-56232.29	-4979998.5	27	155	109.04	476.49	517	0.32	0.07	-0.03	1

Centrostephanus rodgersii	122	189601.05	-4993808	34	26	154.35	174.11	0	0.21	0.05	-0.13	1
Centrostephanus rodgersii	123	210101.05	-4979058	35	114	158.82	551.37	0	0.23	0.06	-0.01	1
Centrostephanus rodgersii	124	237328.31	-4972444	40	116	190.06	516.38	262	0.24	0.13	0.01	1
Centrostephanus rodgersii	125	256476.05	-4963183	44	108	212.64	577.6	0	0.22	0.18	0.02	1
Centrostephanus rodgersii	126	287983.41	-4947925.5	48	107	235.19	539.13	25	0.23	0.24	-0.1	1
Centrostephanus rodgersii	127	-1232.29	-4905474.5	26	121	109.65	559.88	0	0.22	0.02	0	1
Centrostephanus rodgersii	128	-20398.96	-4921308	29	141	125.76	654.14	0	0.22	0.07	-0.03	1
Centrostephanus rodgersii	129	39601.04	-4950474.5	28	121	121.21	551.96	0	0.23	0.03	0.01	1
Centrostephanus rodgersii	130	18919.22	-4936308	28	141	122.55	524.59	76	0.27	0.03	-0.01	1
Centrostephanus rodgersii	131	524601.06	-4519165	70	61	367.54	347.17	0	0.22	0.42	0.06	1
Centrostephanus rodgersii	132	496601.03	-4531558	67	70	352.91	384.26	208	0.22	0.38	0.19	1
Centrostephanus rodgersii	133	420336.34	-4534984.5	49	42	240.32	247.46	0	0.22	0.19	-0.27	1
Centrostephanus rodgersii	134	-82148.96	-4818058	26	137	109.43	533.88	6	0.26	0.03	-0.01	1
Centrostephanus rodgersii	135	-80648.96	-4835058	28	142	122.03	538.22	105	0.26	0.07	-0.05	1
Centrostephanus rodgersii	136	-115398.96	-4861308	29	105	121.56	518.74	0	0.23	0.07	-0.03	1

Centrostephanus rodgersii	137	363767.72	-5190474.5	93	58	471.1	309.87	0	0.17	0.8	0.17	1
Centrostephanus rodgersii	138	351163.53	-5202245.5	94	68	479.06	301.72	1672	0.18	0.82	-0.15	1
Centrostephanus rodgersii	139	333767.72	-5257974.5	90	51	459.37	271.65	0	0.17	0.8	0.28	1
Centrostephanus rodgersii	140	340737.41	-5239262.5	92	60	468.32	298.19	0	0.18	0.8	0.18	1
Centrostephanus rodgersii	141	600522.06	-4220650	109	33	571.73	196.93	642	0.19	0.96	-0.16	1
Centrostephanus rodgersii	142	296386.75	-5303450.5	61	50	297.06	250.75	0	0.18	0.63	-0.51	1
Centrostephanus rodgersii	143	280601.03	-5289808	58	44	283.43	231.93	0	0.19	0.62	0.01	1
Centrostephanus rodgersii	144	309958.19	-4883093.5	45	108	214.7	565.14	52	0.22	0.17	-0.01	1
Centrostephanus rodgersii	145	-109898.96	-4885808	29	155	122.27	617.75	2416	0.26	0.07	-0.05	1
Centrostephanus rodgersii	146	650177.94	-4160346.25	109	14	568.18	88.05	0	0.19	0.96	-0.13	1
Centrostephanus rodgersii	147	70434.38	-4655474.5	26	29	109.38	190.01	0	0.21	0.02	0.01	1
Centrostephanus rodgersii	148	-58808.05	-4962217	27	155	109.75	447.76	793	0.35	0.08	-0.02	1
Centrostephanus rodgersii	149	157101.05	-5373808	62	60	298.77	276.09	0	0.18	0.64	0.17	1
Centrostephanus rodgersii	150	369878.81	-4964919	107	75	547.44	399.88	53	0.19	0.95	0.01	1
Centrostephanus rodgersii	151	94601.04	-5336308	67	46	334.95	232.02	0	0.19	0.67	-0.01	1

Centrostephanus rodgersii	152	-12898.96	-4926308	29	115	125.95	621.49	0	0.22	0.07	-0.06	1
Centrostephanus rodgersii	153	586101.06	-4256308	105	12	551.87	76.31	0	0.2	0.93	0.26	1
Centrostephanus rodgersii	154	284243.91	-4779522	45	47	216.58	285.47	0	0.22	0.18	0.21	1
Centrostephanus rodgersii	155	316601.03	-4842808	45	60	214.35	383.19	0	0.21	0.17	0.01	1
Heliocidaris erythrogramma	1	-792898.94	-3893808	12	3	48.5	15.13	0	0.24	1	-0.8	1
Heliocidaris erythrogramma	2	-794565.63	-3920474.5	8	5	27.02	28.13	0	0.3	0.58	-0.76	1
Heliocidaris erythrogramma	3	-877898.94	-3968808	4	2	12.87	3.8	0	0.15	0.24	-0.47	1
Heliocidaris erythrogramma	4	-811961.44	-3882245.5	10	7	38.07	18.52	29	0.2	0.83	0.33	1
Heliocidaris erythrogramma	5	-841232.31	-4055474.5	1	1	0	0	0	0	1	1	2
Heliocidaris erythrogramma	6	-764010.06	-4056030	6	6	18.41	22.52	1	0.1	0.01	0.87	3
Heliocidaris erythrogramma	7	-752898.94	-4071308	6	5	12.05	21.36	0	0.1	0.01	-3.31	3
Heliocidaris erythrogramma	8	-841232.31	-4082141.25	2	1	2.8	0.07	0	0.37	1	2.45	4
Heliocidaris erythrogramma	9	-782898.94	-4094141.25	7	7	23.91	18.44	178	0.12	0.02	-4.51	3
Heliocidaris erythrogramma	10	-749461.44	-4096620.5	6	8	21.21	17.23	50	0.1	0.01	-1.69	3
Heliocidaris erythrogramma	11	-849148.94	-4122558	1	2	0	2.74	0	0.37	0	1	4

Heliocidaris erythrogramma	12	-732898.94	-4123808	5	2	13.77	6.08	0	0.08	0.05	-3.65	3
Heliocidaris erythrogramma	13	644958.19	-4120236.5	2	1	2.96	0.06	0	0.02	0	8.69	5
Heliocidaris erythrogramma	14	-794214.75	-4135123.75	3	5	11.19	11.73	208	0.13	0.17	-5.96	3
Heliocidaris erythrogramma	15	-815398.94	-4163808	6	2	20.79	6.94	216	0.14	0.62	1.17	3
Heliocidaris erythrogramma	16	-875398.94	-4176308	2	3	1.45	9.54	0	0.07	0	0.59	3
Heliocidaris erythrogramma	17	623976.06	-4174120.5	5	9	21.93	28.81	73	0.02	0	5.13	5
Heliocidaris erythrogramma	18	-902148.94	-4183808	3	5	7.38	16.87	53	0.08	0.09	-1.12	3
Heliocidaris erythrogramma	19	605851.06	-4205058	7	8	21.4	32.9	0	0.02	0	-5.03	5
Heliocidaris erythrogramma	20	-855398.94	-4213808	9	4	31.06	16.71	29	0.13	0.7	-0.46	3
Heliocidaris erythrogramma	21	-836648.94	-4212558	8	7	31.48	29.46	212	0.15	0.84	-0.4	3
Heliocidaris erythrogramma	22	-807898.94	-4213808	7	6	24.74	33.3	0	0.16	0.7	0.59	3
Heliocidaris erythrogramma	23	-867898.94	-4218808	8	3	27.64	10.68	0	0.12	0.55	1.27	3
Heliocidaris erythrogramma	24	-896232.31	-4221030	5	5	19.45	13.69	101	0.12	0.46	-1.12	3
Heliocidaris erythrogramma	25	-797898.94	-4226308	9	12	37.13	31.1	300	0.18	1	0.12	3
Heliocidaris erythrogramma	26	-752898.94	-4231308	9	4	28.18	19.24	0	0.16	0.57	0.63	3

Heliocidaris erythrogramma	27	-771565.63	-4226141	8	12	23.3	41.2	140	0.16	0.58	-0.1	3
Heliocidaris erythrogramma	28	-685756.13	-4233808	6	10	22.22	24.76	197	0.13	0.43	-0.43	3
Heliocidaris erythrogramma	29	-748732.31	-4245474.5	11	10	39.66	31.17	283	0.16	0.62	0.67	3
Heliocidaris erythrogramma	30	-641232.31	-4252141	4	3	6.42	6.68	54	0.1	0.05	-0.86	3
Heliocidaris erythrogramma	31	-731232.31	-4257141	9	6	32.56	22.34	0	0.14	0.5	-0.8	3
Heliocidaris erythrogramma	32	594878.81	-4234919	11	13	39.64	42.75	224	0.02	0	2.28	5
Heliocidaris erythrogramma	33	-632898.94	-4261308	4	2	7.26	2.79	0	0.09	0.07	-0.84	3
Heliocidaris erythrogramma	34	-793732.31	-4265891	4	7	13.52	22.87	192	0.12	0.12	-0.33	3
Heliocidaris erythrogramma	35	-817898.94	-4278808	6	4	18	14.25	0	0.12	0.16	0.79	3
Heliocidaris erythrogramma	36	-887398.94	-4285808	3	4	5.96	13.56	0	0.08	0.04	0.11	3
Heliocidaris erythrogramma	37	-859565.63	-4282141	5	4	17.91	4.81	23	0.09	0.09	1.34	3
Heliocidaris erythrogramma	38	-833613.25	-4285236.5	6	5	15.65	17.19	102	0.1	0.18	-0.76	3
Heliocidaris erythrogramma	39	577101.06	-4294879.5	16	16	61.35	47.38	572	0.02	0	1.23	5
Heliocidaris erythrogramma	40	-577648.94	-4374308	2	2	6.44	6.28	0	0.01	0	0.47	5
Heliocidaris erythrogramma	41	567101.06	-4413808	20	12	73.61	59.65	0	0.02	0	4.58	5

Heliocidaris erythrogramma	42	563351.06	-4377558	18	15	68.14	41.26	765	0.02	0	5.18	5
Heliocidaris erythrogramma	43	-596113.25	-4416308	4	8	13.87	34.67	170	0.01	0	-0.17	5
Heliocidaris erythrogramma	44	589601.06	-4448808	23	12	85.13	58.25	210	0.02	0	5.82	5
Heliocidaris erythrogramma	45	-572398.94	-4469808	5	10	13.61	32.34	120	0.01	0	-0.81	5
Heliocidaris erythrogramma	46	-552273.94	-4490058	8	9	30.9	21.32	159	0.02	0	-0.1	5
Heliocidaris erythrogramma	47	532101.06	-4498808	9	9	28.07	44.21	0	0.03	0	2.93	5
Heliocidaris erythrogramma	48	558919.25	-4470171.5	18	16	72.23	56.37	1716	0.03	0	-0.13	5
Heliocidaris erythrogramma	49	-537898.94	-4503808	9	5	30.85	27.74	0	0.02	0	-0.02	5
Heliocidaris erythrogramma	50	527101.06	-4511308	10	13	31.21	56.46	0	0.03	0	5.45	5
Heliocidaris erythrogramma	51	-534148.94	-4517558	11	9	38.11	25.57	939	0.02	0	-0.34	5
Heliocidaris erythrogramma	52	-526232.31	-4530474.5	12	8	42.99	27.28	0	0.02	0	0.41	5
Heliocidaris erythrogramma	53	337101.03	-4538808	8	6	25.17	29.77	0	0.03	0	5.77	5
Heliocidaris erythrogramma	54	493277.5	-4532043	13	14	52.19	40.29	2075	0.03	0	-2.2	5
Heliocidaris erythrogramma	55	-516232.28	-4540474.5	11	9	37.12	29.39	245	0.02	0	0	5
Heliocidaris erythrogramma	56	405017.72	-4530891	10	14	36.34	54.12	1342	0.03	0	2.55	5

Heliocidaris erythrogramma	57	-502898.97	-4551308	9	8	24.14	30.25	0	0.02	0	0.22	5
Heliocidaris erythrogramma	58	337101.03	-4551308	9	8	28.11	45.48	0	0.03	0	-0.39	5
Heliocidaris erythrogramma	59	-495398.97	-4558808	9	6	24.06	22.43	0	0.02	0	-0.1	5
Heliocidaris erythrogramma	60	-449148.97	-4578183	8	10	36.46	26.69	1650	0.02	0	0.09	5
Heliocidaris erythrogramma	61	288464.69	-4584717	7	11	27.23	36.87	2915	0.03	0	-1.54	5
Heliocidaris erythrogramma	62	-51583.17	-4599334	4	4	14.22	9.2	3306	0.02	0	1.19	5
Heliocidaris erythrogramma	63	-407898.97	-4611308	5	5	14.77	22.05	390	0.02	0	-0.69	5
Heliocidaris erythrogramma	64	-367898.97	-4611308	7	4	19.31	16.62	406	0.02	0	-0.69	5
Heliocidaris erythrogramma	65	-335398.97	-4611308	8	6	29.37	17.57	2130	0.02	0	0.24	5
Heliocidaris erythrogramma	66	-303898.97	-4610808	5	6	13.42	17.41	432	0.02	0	-0.31	5
Heliocidaris erythrogramma	67	-83898.96	-4610808	5	6	16.16	24.92	3248	0.02	0	-0.57	5
Heliocidaris erythrogramma	68	-96898.96	-4621808	5	5	16.24	11.58	3186	0.02	0	0.77	5
Heliocidaris erythrogramma	69	-24148.96	-4614433	4	4	11.66	14.68	3360	0.02	0	-0.44	5
Heliocidaris erythrogramma	70	-111232.3	-4635474.5	7	4	25.4	11.65	0	0.02	0	-0.73	5
Heliocidaris erythrogramma	71	-255711.45	-4631620.5	5	7	12.78	18.32	2448	0.02	0	0.66	5

Heliocidaris erythrogramma	72	-114565.63	-4652141	7	6	19.11	23.49	3050	0.02	0	-0.59	5
Heliocidaris erythrogramma	73	-136232.3	-4655474.5	4	5	7.89	11.94	0	0.02	0	-0.29	5
Heliocidaris erythrogramma	74	-187898.95	-4663808	5	4	13.98	16.8	460	0.02	0	-0.16	5
Heliocidaris erythrogramma	75	-142898.95	-4663808	5	5	15.14	12.43	0	0.02	0	1.11	5
Heliocidaris erythrogramma	76	-172898.95	-4671308	5	4	14.45	12.24	570	0.02	0	0.6	5
Heliocidaris erythrogramma	77	58172.47	-4655593.5	5	8	11.18	27.57	339	0.03	0	0.2	5
Heliocidaris erythrogramma	78	-154565.63	-4677141	7	7	29.22	23.38	2816	0.02	0	-0.77	5
Heliocidaris erythrogramma	79	188351.05	-4681808	4	7	8.95	18.55	3747	0.03	0	0.32	5
Heliocidaris erythrogramma	80	167101.05	-4708808	7	3	20.16	13.74	0	0.03	0	-0.24	5
Heliocidaris erythrogramma	81	135177.97	-4694577	6	6	20.19	16.12	5	0.03	0	-0.23	5
Heliocidaris erythrogramma	82	221646.5	-4730626	8	6	34.41	18.2	3996	0.03	0.02	286.54	5
Heliocidaris erythrogramma	83	251267.7	-4758808	8	8	25.07	22.55	3758	0.03	0.02	-40.5	5
Heliocidaris erythrogramma	84	238767.7	-4767141	8	6	26.7	23.06	75	0.03	0.02	-110.57	5
Heliocidaris erythrogramma	85	332101.03	-4783808	12	8	42.65	35.32	1384	0.03	0.14	-6.77	5
Heliocidaris erythrogramma	86	-132898.95	-4783808	10	5	35.52	18.69	4	0.02	0	0.46	5

Heliocidaris erythrogramma	87	257101.05	-4793808	9	5	29.07	27.26	0	0.03	0.03	-461.55	5
Heliocidaris erythrogramma	88	322101.03	-4791308	12	5	41.71	21.25	0	0.03	0.14	-75.76	5
Heliocidaris erythrogramma	89	383639.5	-4783423.5	8	8	35.97	15.56	1497	0.03	0.11	-198.34	5
Heliocidaris erythrogramma	90	387101.03	-4793808	7	6	29.14	25.02	0	0.03	0.19	5.14	5
Heliocidaris erythrogramma	91	262101.05	-4798808	10	5	36.91	28.57	0	0.03	0.05	309.72	5
Heliocidaris erythrogramma	92	392101.03	-4798808	8	4	33.28	18.83	0	0.03	0.27	-46.38	5
Heliocidaris erythrogramma	93	290712.16	-4784919	8	16	29.78	47.46	4252	0.03	0.08	15.47	5
Heliocidaris erythrogramma	94	413767.72	-4802141	7	5	21.26	20.25	700	0.03	0.18	-38.03	5
Heliocidaris erythrogramma	95	-137898.95	-4806308	9	5	31.03	15.48	23	0.02	0	0.32	5
Heliocidaris erythrogramma	96	315434.38	-4805474.5	13	6	47.53	26.1	0	0.03	0.12	-210.29	5
Heliocidaris erythrogramma	97	-132898.95	-4816308	6	5	21.95	13.25	0	0.02	0	0.68	5
Heliocidaris erythrogramma	98	-127898.96	-4833808	9	2	33.9	6.06	0	0.02	0	-0.77	5
Heliocidaris erythrogramma	99	312101.03	-4838808	10	5	33.05	24.94	0	0.03	0.07	-167.17	5
Heliocidaris erythrogramma	100	317101.03	-4843808	8	6	21.59	30.47	0	0.03	0.05	13.96	5
Heliocidaris erythrogramma	101	-127898.96	-4848808	8	8	25.69	30.76	112	0.02	0	-0.85	5

Heliocidaris erythrogramma	102	-96648.96	-4854224.5	10	13	31.86	42.53	36	0.02	0	-1.19	5
Heliocidaris erythrogramma	103	299828.31	-4860171.5	17	17	77.08	60.31	3079	0.03	0.25	190.01	5
Heliocidaris erythrogramma	104	-112343.41	-4882141	11	12	39.89	41.68	328	0.02	0	0.23	5
Heliocidaris erythrogramma	105	376767.72	-4872141	6	11	27.58	39.31	34	0.03	0.42	90.05	5
Heliocidaris erythrogramma	106	-37898.96	-4891308	11	9	37.2	39.69	0	0.02	0	0.21	5
Heliocidaris erythrogramma	107	387101.03	-4893808	20	5	83.79	22.89	0	0.03	0.97	-90.98	5
Heliocidaris erythrogramma	108	-120398.96	-4896308	10	9	36.67	39.09	0	0.02	0	-0.26	5
Heliocidaris erythrogramma	109	-20398.96	-4896308	11	12	35.85	45.96	350	0.02	0	0.72	5
Heliocidaris erythrogramma	110	2101.04	-4898808	13	3	52.92	15.01	0	0.02	0	0.29	5
Heliocidaris erythrogramma	111	27101.04	-4898808	14	5	47.11	24.51	235	0.02	0	0.04	5
Heliocidaris erythrogramma	112	315562.59	-4876885	11	15	47.03	48.68	25	0.03	0.31	-17.57	5
Heliocidaris erythrogramma	113	409601.03	-4898808	25	13	106.03	55.54	1571	0.03	0.98	15.26	5
Heliocidaris erythrogramma	114	387101.03	-4906308	25	7	102.2	35.44	0	0.03	0.98	38.01	5
Heliocidaris erythrogramma	115	315434.38	-4910474.5	20	14	82.62	75.99	0	0.03	0.69	56.49	5
Heliocidaris erythrogramma	116	337101.03	-4911308	21	17	94.86	76.42	944	0.03	0.82	-124.5	5

Heliocidaris erythrogramma	117	292101.03	-4921308	17	19	65.09	101.49	1562	0.03	0.56	22.3	5
Heliocidaris erythrogramma	118	382101.03	-4920808	27	16	111.99	68.57	297	0.03	1	-7.83	5
Heliocidaris erythrogramma	119	357101.03	-4928808	25	14	97.72	65.09	1	0.03	0.96	-127.24	5
Heliocidaris erythrogramma	120	-39898.96	-4926308	12	15	40.35	50.22	522	0.02	0	0.48	5
Heliocidaris erythrogramma	121	-148732.3	-4932974.5	3	3	9.28	9.25	0	0.02	0	1.01	5
Heliocidaris erythrogramma	122	118767.7	-4939363.5	1	2	0	4.94	0	0.02	0	1	5
Heliocidaris erythrogramma	123	369601.03	-4943808	23	17	94.16	65.94	7	0.03	0.85	107.25	5
Heliocidaris erythrogramma	124	380434.38	-4940474.5	25	14	105.16	61.41	1	0.03	0.92	514.84	5
Heliocidaris erythrogramma	125	2101.04	-4926308	11	14	44.6	37.25	282	0.02	0	1.04	5
Heliocidaris erythrogramma	126	377101.03	-4948808	20	14	80.79	69.69	0	0.03	0.78	-405.13	5
Heliocidaris erythrogramma	127	40851.04	-4957558	4	3	9.83	11.16	0	0.02	0	0.29	5
Heliocidaris erythrogramma	128	315101.03	-4954808	20	18	91.8	76.01	0	0.03	0.86	-88.77	5
Heliocidaris erythrogramma	129	384601.03	-4976308	12	16	50.46	65.27	836	0.03	0.56	-233.11	5
Heliocidaris erythrogramma	130	277101.03	-4968808	12	26	48.79	92.93	0	0.03	0.38	-14.16	5
Heliocidaris erythrogramma	131	242101.05	-4983808	11	1	34.66	4.72	0	0.03	0.11	67.11	5

Heliocidaris erythrogramma	132	370226.03	-4971933	10	17	39.89	56.21	1523	0.03	0.44	311	5
Heliocidaris erythrogramma	133	-51898.96	-4964808	11	16	37.73	54.4	288	0.02	0	-0.28	5
Heliocidaris erythrogramma	134	195101.05	-4991808	9	11	24.66	52.94	0	0.03	0.1	-55.56	5
Heliocidaris erythrogramma	135	144601.05	-5002558	5	8	19.71	25.51	0	0.03	0.03	-161.84	5
Heliocidaris erythrogramma	136	177101.05	-5001308	7	8	23.51	36.79	0	0.03	0.06	59.1	5
Heliocidaris erythrogramma	137	-39148.96	-5002558	7	6	19.47	27.49	0	0.02	0	-1.75	5
Heliocidaris erythrogramma	138	371646.5	-5007899	5	12	15.72	50.25	54	0.03	0.06	-65.67	5
Heliocidaris erythrogramma	139	-36961.46	-5035995.5	7	7	20.55	21.07	1518	0.02	0	0.88	5
Heliocidaris erythrogramma	140	371267.72	-5044641	5	10	17.52	44.41	3110	0.03	0.1	85.99	5
Heliocidaris erythrogramma	141	-16080.78	-5098808	7	3	25.99	8.52	1562	0.02	0	1.02	5
Heliocidaris erythrogramma	142	369408.72	-5098423.5	4	5	15.79	17.32	2862	0.03	0.01	-105.45	5
Heliocidaris erythrogramma	143	370434.38	-5132141	6	2	25.64	4.95	2862	0.03	0.01	-22.9	5
Heliocidaris erythrogramma	144	17726.04	-5148808	2	3	3.55	10.08	1602	0.02	0	2.85	5
Heliocidaris erythrogramma	145	357601.03	-5161808	2	2	6.88	5.45	0	0.03	0	388.8	5
Heliocidaris erythrogramma	146	362101.03	-5188808	6	3	20.3	16.22	86	0.03	0	377.08	5

Heliocidaris erythrogramma	147	38172.47	-5248808	2	7	5.74	16.07	1672	0.02	0	9.18	5
Heliocidaris erythrogramma	148	341716.44	-5210346.5	5	6	18.46	18.64	2863	0.03	0	112.7	5
Heliocidaris erythrogramma	149	52101.04	-5273808	6	4	19.49	12.63	0	0.02	0	-1.98	5
Heliocidaris erythrogramma	150	59601.04	-5283808	6	5	15.43	12.71	0	0.02	0	7.52	5
Heliocidaris erythrogramma	151	67101.04	-5291308	7	7	20.74	20.57	199	0.02	0	-11.65	5
Heliocidaris erythrogramma	152	72101.04	-5298808	7	6	19.08	23.43	0	0.02	0	-5.05	5
Heliocidaris erythrogramma	153	342101.03	-5292558	12	8	47.93	24.31	2955	0.03	0	-291.41	5
Heliocidaris erythrogramma	154	287101.03	-5288808	4	8	8.56	24.68	0	0.03	0	-45.21	5
Heliocidaris erythrogramma	155	302101.03	-5318808	11	6	42	30.21	0	0.03	0	68.74	5
Heliocidaris erythrogramma	156	334601.03	-5313808	18	5	82.5	19.02	0	0.03	0	140.75	5
Heliocidaris erythrogramma	157	332101.03	-5323808	19	4	79.74	15.14	0	0.03	0	53.95	5
Heliocidaris erythrogramma	158	314601.03	-5326308	19	10	74.32	37.2	2973	0.03	0	-28.31	5
Heliocidaris erythrogramma	159	272101.03	-5326308	14	11	57.07	37.62	176	0.03	0	-21.4	5
Heliocidaris erythrogramma	160	93767.7	-5344141	9	12	40.9	47	2185	0.02	0	-7.15	5
Heliocidaris erythrogramma	161	263767.72	-5349641	15	9	57.18	38.53	182	0.03	0	20.82	5

Heliocidaris erythrogramma	162	259601.05	-5381308	13	11	40.97	42.79	241	0.03	0	-20.83	5
Heliocidaris erythrogramma	163	234601.05	-5362558	9	11	31.39	38.87	252	0.03	0	13.57	5
Heliocidaris erythrogramma	164	223767.7	-5420474.5	13	7	51.79	33.28	0	0.02	0	-1.63	5
Heliocidaris erythrogramma	165	-805518	-3931665	10	15	35.13	40.2	48	0.34	0.75	-0.15	1
Heliocidaris erythrogramma	166	-825530.56	-3963544.75	10	12	36.57	41.8	35	0.25	0.74	-0.04	1
Heliocidaris erythrogramma	167	-843836.44	-3937870.5	11	11	36.45	37.2	36	0.27	0.69	-0.1	1
Heliocidaris erythrogramma	168	-792898.94	-3875308	7	4	24.52	13.13	0	0.19	0.55	-0.03	1
Heliocidaris erythrogramma	169	-831722.5	-3925572.5	11	15	34.63	50.28	63	0.31	0.72	0.31	1
Heliocidaris erythrogramma	170	-827343.38	-3897696.75	9	9	25.79	31.43	26	0.25	0.54	0.43	1
Heliocidaris erythrogramma	171	110101.04	-5365808	8	9	27.96	38.85	0	0.02	0	3.52	5
Heliocidaris erythrogramma	172	125434.38	-5375474.5	8	12	23.35	41.22	2129	0.03	0	-26.93	5
Heliocidaris erythrogramma	173	142458.19	-5379879.5	9	14	29.15	47.5	42	0.03	0	12.24	5
Heliocidaris erythrogramma	174	153976.05	-5390683	9	16	27.22	57.29	29	0.03	0	3.71	5
Heliocidaris erythrogramma	175	165336.33	-5380866.5	9	17	29.33	54.68	2312	0.03	0	9.22	5
Heliocidaris erythrogramma	176	180737.41	-5381080.5	8	16	23.81	59.93	0	0.03	0	-20.82	5

Heliocidaris erythrogramma	177	199601.05	-5386308	9	16	28.8	62.29	240	0.03	0	12.26	5
Heliocidaris erythrogramma	178	218976.05	-5375058	9	11	24.78	45.23	247	0.02	0	22.04	5
Heliocidaris erythrogramma	179	251101.05	-5368808	12	12	45.72	45.43	254	0.03	0	9.37	5
Heliocidaris erythrogramma	180	-107898.96	-4773093.5	8	6	23.41	22.17	7	0.02	0	0.06	5
Heliocidaris erythrogramma	181	-90756.1	-4779879.5	8	10	23.69	29.46	50	0.02	0	0.18	5
Heliocidaris erythrogramma	182	-86320.02	-4802492	9	12	31.31	29.33	40	0.02	0	0.23	5
Heliocidaris erythrogramma	183	-76846.33	-4823281.5	9	12	29.56	31.77	44	0.02	0	-0.32	5
Heliocidaris erythrogramma	184	-84398.96	-4839308	9	11	27.93	34.06	0	0.02	0	0.27	5
Heliocidaris erythrogramma	185	-117898.96	-4861308	9	10	28.46	40.96	11	0.02	0	-0.06	5
Heliocidaris erythrogramma	186	210156.59	-4971030	10	23	33.39	93.34	380	0.03	0.13	48.74	5
Heliocidaris erythrogramma	187	232767.7	-4961141	11	26	41.53	104.35	15	0.03	0.18	-47.97	5
Heliocidaris erythrogramma	188	248351.05	-4962245.5	13	27	50.38	91.96	1236	0.03	0.32	123.27	5
Heliocidaris erythrogramma	189	289601.03	-4953808	15	24	59.15	94.06	9	0.03	0.5	93.9	5
Heliocidaris erythrogramma	190	6574.72	-4627492	4	6	12.41	20.22	3410	0.03	0	-0.18	5
Heliocidaris erythrogramma	191	30562.58	-4637654	5	6	14.08	15.43	3456	0.03	0	-0.03	5

Heliocidaris erythrogramma	192	86684.38	-4661724.5	6	8	20.21	27.47	3536	0.03	0	-0.36	5
Heliocidaris erythrogramma	193	269288.53	-4762870.5	10	13	44.42	36.38	3978	0.03	0.06	145.98	5
Heliocidaris erythrogramma	194	317434.38	-4552808	8	10	29.57	21.65	184	0.03	0	11.96	5
Heliocidaris erythrogramma	195	183767.7	-4664808	3	6	5.06	18.33	0	0.03	0	0.4	5
Heliocidaris erythrogramma	196	177101.05	-4697558	6	5	18.34	12.59	88	0.03	0	-0.51	5
Heliocidaris erythrogramma	197	-52541.82	-4983093.5	11	14	38.56	44.98	1071	0.02	0	0.4	5
Heliocidaris erythrogramma	198	-691898.94	-4217308	3	6	4.41	25.19	0	0.12	0.02	0.47	3
Heliocidaris erythrogramma	199	-16898.96	-4931808	10	13	39.53	49.37	0	0.02	0	-0.79	5
Heliocidaris erythrogramma	200	-6648.96	-4907558	11	10	44.95	46.9	13	0.02	0	-0.5	5
Heliocidaris erythrogramma	201	-18898.96	-4919308	11	15	36.38	43.25	81	0.02	0	-0.62	5
Heliocidaris erythrogramma	202	18976.04	-4945683	7	9	27.93	29.6	138	0.02	0	-1.04	5
Heliocidaris erythrogramma	203	449913.53	-4530995.5	11	16	42.66	57.26	1631	0.03	0	-4.9	5
Heliocidaris erythrogramma	204	516101.03	-4520808	11	13	39.21	47.71	0	0.03	0	-5.37	5
Heliocidaris erythrogramma	205	107101.04	-4686808	8	5	22.47	19.01	252	0.03	0	-0.23	5
Heliocidaris erythrogramma	206	143767.7	-4720474.5	10	7	38.53	25.55	3666	0.03	0	-0.17	5

Heliocidaris erythrogramma	207	123529.61	-4680950.5	6	5	20.99	11.95	0	0.03	0	-0.28	5
Heliocidaris erythrogramma	208	331684.38	-4869224.5	6	9	20.37	27.57	0	0.03	0.05	44.56	5
Heliocidaris erythrogramma	209	318767.72	-4892974.5	15	21	68.62	79.68	1452	0.03	0.38	231.62	5
Heliocidaris erythrogramma	210	-225756.11	-4651665	5	6	19.18	19.7	2546	0.02	0	-0.44	5
Heliocidaris erythrogramma	211	-283808.06	-4614717	5	6	13.49	16.7	442	0.02	0	-0.01	5
Heliocidaris erythrogramma	212	562726.06	-4436933	18	15	65.42	57.6	0	0.02	0	0.61	5
Heliocidaris erythrogramma	213	-735756.13	-4107379.25	4	4	8.79	9.48	14	0.09	0.01	5.91	3
Heliocidaris erythrogramma	214	569601.06	-4328808	15	14	54.99	54.49	0	0.02	0	0.31	5
Heliocidaris erythrogramma	215	354101.03	-4537308	9	11	28.72	34.58	26	0.03	0	-4.31	5
Heliocidaris erythrogramma	216	333767.72	-5257974.5	6	6	19.31	18.35	112	0.03	0	42.8	5
Heliocidaris erythrogramma	217	338639.5	-5236885	5	6	13	16.3	2881	0.03	0	-496.94	5
Heliocidaris erythrogramma	218	82101.04	-5318808	6	11	18.2	38.71	2104	0.02	0	7.74	5
Heliocidaris erythrogramma	219	-782065.63	-4069224.5	6	5	17.63	14.69	0	0.11	0.04	0.21	3
Heliocidaris erythrogramma	220	-424262.59	-4591080.5	5	9	19.08	24.46	1764	0.02	0	0.62	5
Heliocidaris erythrogramma	221	274323.25	-5297697	4	9	6.65	26.47	60	0.03	0	-33.27	5

Heliocidaris erythrogramma	222	290434.38	-5304919	6	10	19.96	23.69	153	0.03	0	50.01	5
Heliocidaris erythrogramma	223	-588315.63	-4440474.5	4	8	9.32	24.95	336	0.01	0	-0.32	5
Heliocidaris erythrogramma	224	-814437.44	-4224961.5	7	10	28.65	23.86	16	0.15	0.82	0.52	3
Heliocidaris erythrogramma	225	-818565.63	-3950808	10	14	36.91	44.69	42	0.31	0.73	-0.36	1
Heliocidaris erythrogramma	226	-817343.38	-3914363.5	12	15	40.28	54.79	17	0.32	0.83	-0.09	1
Heliocidaris erythrogramma	227	289601.03	-4761308	6	14	19.4	33.64	112	0.03	0.04	93.12	5
Heliocidaris erythrogramma	228	-860041.81	-3960236.5	7	6	21.54	20.2	30	0.19	0.4	-0.6	1
Heliocidaris erythrogramma	229	-804262.63	-3944717	8	14	26.2	49.59	0	0.27	0.56	-0.35	1
Heliocidaris erythrogramma	230	-661787.88	-4236030	4	7	11.8	21.05	104	0.11	0.03	-0.35	3
Heliocidaris erythrogramma	231	301476.03	-4564433	6	10	20.69	32.85	0	0.03	0	-8.03	5
Heliocidaris erythrogramma	232	-46360.5	-4952654	11	15	35.69	46.23	93	0.02	0	-0.54	5
Heliocidaris erythrogramma	233	48254.89	-4644961.5	5	6	12.54	13.68	330	0.03	0	-0.05	5
Heliocidaris erythrogramma	234	-809010.06	-3901030	12	10	43.35	28.41	44	0.29	0.86	-0.16	1
Heliocidaris erythrogramma	235	-751787.88	-4084363.5	7	8	22.24	22.31	16	0.1	0.02	6.9	3
Heliocidaris erythrogramma	236	-835398.94	-3911308	11	12	37.29	52.33	0	0.27	0.79	0.68	1

Heliocidaris erythrogramma	237	-847898.94	-3950683	10	8	34.73	30.23	28	0.23	0.71	-0.26	1
Heliocidaris erythrogramma	238	-82898.96	-4813808	8	12	23.93	42.82	0	0.02	0	0.25	5
Heliocidaris erythrogramma	239	223976.05	-4970683	10	23	32.41	98.48	0	0.03	0.11	-65.1	5
Heliocidaris erythrogramma	240	377101.03	-4531308	9	13	29.81	50.9	1334	0.03	0	0.41	5
Heliocidaris erythrogramma	241	-765676.75	-4261030	7	12	22.46	45.22	230	0.14	0.58	-0.91	3
Heliocidaris erythrogramma	242	548601.06	-4494308	15	15	61.65	47.71	48	0.03	0	-3.21	5
Heliocidaris erythrogramma	243	576101.06	-4315808	17	15	63.91	49.61	0	0.02	0	-5.73	5
Heliocidaris erythrogramma	244	567101.06	-4346308	15	14	52.02	45.2	0	0.02	0	3.96	5
Heliocidaris erythrogramma	245	578101.06	-4272808	11	14	35.83	52.42	0	0.02	0	1.82	5
Heliocidaris erythrogramma	246	586267.69	-4253808	11	13	37.05	50.94	0	0.02	0	1.55	5
Heliocidaris erythrogramma	247	562101.06	-4392558	19	15	73.93	51.61	0	0.02	0	-6.4	5
Heliocidaris erythrogramma	248	557101.06	-4413808	17	12	67.27	43.01	0	0.02	0	-13.14	5
Heliocidaris erythrogramma	249	298601.03	-4838808	14	17	53.52	66.93	321	0.03	0.14	-199.18	5
Heliocidaris erythrogramma	250	340434.38	-4943252.5	22	22	86.24	78.3	1935	0.03	0.83	59.38	5
Heliocidaris erythrogramma	251	365101.03	-4955808	19	16	85.33	54.63	192	0.03	0.81	-389.42	5

Heliocidaris erythrogramma	252	264958.19	-4970236.5	12	23	49.07	89.38	0	0.03	0.41	15.33	5
Heliocidaris erythrogramma	253	324601.03	-4946308	22	20	92.18	71.27	0	0.03	0.92	30.19	5
Chrysophrys auratus	1	-837898.94	-3913808	16	17	52.97	64.72	41	0.29	0.9	3.45	1
Chrysophrys auratus	2	-797898.94	-3923808	17	15	60.57	38.24	2	0.42	0.99	19.63	1
Chrysophrys auratus	3	-792898.94	-3948808	15	15	58.62	37.75	37	0.42	1	-23.05	1
Chrysophrys auratus	4	-892184.69	-3972379.25	4	5	9.18	15.47	0	0.17	0.14	-0.01	1
Chrysophrys auratus	5	-825398.94	-3993808	10	15	39.7	52.17	56	0.32	0.71	-7.74	1
Chrysophrys auratus	6	-839898.94	-4014808	5	8	15.13	29.09	0	0.21	0.23	-4.61	1
Chrysophrys auratus	7	528767.69	-4495474.5	11	3	33.72	10.6	0	0.08	0.02	-0.04	2
Chrysophrys auratus	8	394601.03	-4528808	11	7	37.4	27.09	16	0.09	0.02	-0.25	2
Chrysophrys auratus	9	313101.03	-4549808	9	11	24.56	40.61	0	0.09	0.02	-0.07	2
Chrysophrys auratus	10	289601.03	-4575474.5	9	11	23.12	26.54	82	0.1	0.01	-0.12	2
Chrysophrys auratus	11	-39898.96	-4597808	16	17	62.17	42.15	137	0.15	1	-0.33	2
Chrysophrys auratus	12	-72898.96	-4608808	14	17	45.99	59.82	0	0.13	0.73	0.18	2
Chrysophrys auratus	13	-295398.97	-4611308	3	8	7.54	24.45	0	0.08	0.03	0.47	2

Chrysophrys auratus	14	-87898.96	-4613808	13	17	39.46	65.02	0	0.13	0.61	-0.21	2
Chrysophrys auratus	15	-102898.96	-4621308	13	16	40.03	59.8	0	0.13	0.53	-0.21	2
Chrysophrys auratus	16	17101.04	-4621308	15	7	63.33	21.5	0	0.14	0.97	-0.07	2
Chrysophrys auratus	17	27101.04	-4628808	15	6	62.37	15.67	0	0.14	0.95	-0.03	2
Chrysophrys auratus	18	-112898.96	-4636308	15	16	53.6	54.01	0	0.12	0.61	0.08	2
Chrysophrys auratus	19	-234565.63	-4640474.5	5	8	18.03	34.07	0	0.08	0.17	-0.34	2
Chrysophrys auratus	20	-112898.96	-4648808	15	18	53.9	64.75	146	0.12	0.65	-0.03	2
Chrysophrys auratus	21	79601.04	-4653808	12	6	47.67	29.71	209	0.14	0.79	-0.12	2
Chrysophrys auratus	22	-209565.63	-4655474.5	6	9	19.54	36.91	18	0.09	0.21	0	2
Chrysophrys auratus	23	-137898.95	-4656308	13	15	49.47	54.04	0	0.11	0.6	0.01	2
Chrysophrys auratus	24	-147898.95	-4666308	12	14	42.8	50.99	123	0.11	0.52	-0.35	2
Chrysophrys auratus	25	182101.05	-4656308	8	11	27.83	22.62	0	0.11	0.01	0.06	2
Chrysophrys auratus	26	-790676.75	-3862696.75	14	13	42.56	49.42	0	0.28	0.81	7.01	1
Chrysophrys auratus	27	-790041.81	-3882379.25	15	14	46.31	41.9	0	0.32	0.86	-4.28	1
Chrysophrys auratus	28	-796470.38	-3895950.75	15	14	45.21	34.71	0	0.38	0.84	5.91	1

Chrysophrys auratus	29	-805121.19	-3878808	15	14	46.69	33.7	0	0.36	0.86	-4.72	1
Chrysophrys auratus	30	-820398.94	-3886308	15	15	46.47	37.46	0	0.35	0.86	-4.43	1
Chrysophrys auratus	31	-830398.94	-3896308	15	15	45.17	55.01	0	0.3	0.84	4.89	1
Chrysophrys auratus	32	-110398.96	-4628808	15	16	54.03	58.93	0	0.12	0.59	0.14	2
Chrysophrys auratus	33	-65398.96	-4593808	14	15	49.12	63.14	0	0.14	0.76	0.08	2
Chrysophrys auratus	34	-55398.96	-4593808	14	16	49.47	57.31	0	0.13	0.76	0.06	2
Chrysophrys auratus	35	-47898.96	-4593808	15	15	56.85	67.76	0	0.13	0.9	-0.21	2
Chrysophrys auratus	36	2101.04	-4621308	16	10	62.99	44.82	0	0.13	0.95	0.11	2
Chrysophrys auratus	37	9601.04	-4621308	15	11	59.93	39.74	123	0.14	0.92	-0.01	2
Chrysophrys auratus	38	172101.05	-4676308	9	11	34.29	34.93	200	0.11	0.12	-0.33	2
Chrysophrys auratus	39	172101.05	-4661308	8	11	28.66	31.53	0	0.1	0.01	0.02	2
Chrysophrys auratus	40	194601.05	-4653808	8	11	26.05	39.25	0	0.09	0.01	0.14	2
Chrysophrys auratus	41	299101.03	-4562808	9	11	23.6	26.74	0	0.09	0.01	-0.09	2
Chrysophrys auratus	42	324601.03	-4541308	9	11	25	41.47	0	0.09	0.02	-0.07	2
Chrysophrys auratus	43	540434.38	-4495474.5	11	3	33.39	9.95	0	0.08	0.02	-0.04	2

Chrysophrys auratus	44	-797898.94	-3861308	14	13	42.7	58.45	0	0.27	0.81	6.42	1
Chrysophrys auratus	45	-813898.94	-3880808	15	14	46.79	37.82	0	0.33	0.87	-4.84	1
Chrysophrys auratus	46	-829565.63	-3905474.5	16	16	51.62	59.22	0	0.31	0.87	-2.53	1
Chrysophrys auratus	47	-801232.31	-3902141.25	16	14	50.84	43.05	0	0.32	0.86	-1.82	1
Chrysophrys auratus	48	-820398.94	-3892558	15	15	45.39	57.74	0	0.31	0.84	1.77	1
Sillaginodes punctatus	1	-865398.94	-3965474.5	5	0	13.73	0	0	0.16	0	7.86	1
Sillaginodes punctatus	2	-802898.94	-3948808	4	0	10.03	0	0	0.17	0	6.01	1
Sillaginodes punctatus	3	-969898.94	-4073808	7	0	16.95	0	0	0.16	0	9.47	1
Sillaginodes punctatus	4	-837898.94	-4093808	6	0	17.36	0	0	0.16	0	9.68	1
Sillaginodes punctatus	5	-878523.94	-4119433	6	0	14.73	0	0	0.16	0	8.36	1
Sillaginodes punctatus	6	-894565.63	-4137141.25	7	0	20.64	0	0	0.16	0	11.32	1
Sillaginodes punctatus	7	-732898.94	-4158808	3	0	9.03	0	0	0.19	0	5.51	1
Sillaginodes punctatus	8	-728523.94	-4134433	3	0	9.22	0	0	0.19	0	5.61	1
Sillaginodes punctatus	9	-732898.94	-4171308	3	0	9.12	0	0	0.19	0	5.56	1
Sillaginodes punctatus	10	-842273.94	-4168183	7	0	16.8	0	0	0.2	0	9.4	1

Sillaginodes punctatus	11	-876232.31	-4175474.5	7	0	14.51	0	0	0.21	0	8.26	1
Sillaginodes punctatus	12	-751787.88	-4194919	5	0	18.31	0	0	0.19	0	10.15	1
Sillaginodes punctatus	13	-769565.63	-4212141	7	0	20.93	0	0	0.18	0	11.47	1
Sillaginodes punctatus	14	-705398.94	-4218808	7	0	19.51	0	0	0.19	0	10.75	1
Sillaginodes punctatus	15	-805398.94	-4231308	7	0	15.99	0	0	0.2	0	8.99	1
Sillaginodes punctatus	16	-575756.13	-4367379.5	7	0	24.51	0	0	0.2	0	13.26	1
Sillaginodes punctatus	17	-547898.94	-4483808	8	0	20.87	0	0	0.22	0	11.43	1
Sillaginodes punctatus	18	532101.06	-4496308	8	0	19.04	0	0	0.13	0	10.52	1
Sillaginodes punctatus	19	444601.03	-4528808	10	0	32.52	0	0	0.14	0	17.26	1
Sillaginodes punctatus	20	459601.03	-4528808	9	0	25.7	0	0	0.13	0	13.85	1
Sillaginodes punctatus	21	332934.38	-4545474.5	10	0	32.61	0	0	0.14	0	17.3	1
Sillaginodes punctatus	22	-432898.97	-4578808	8	0	25.41	0	0	0.19	0	13.71	1
Sillaginodes punctatus	23	-407898.97	-4593808	8	0	29.14	0	0	0.18	0	15.57	1
Sillaginodes punctatus	24	-360398.97	-4593808	5	0	15.67	0	0	0.19	0	8.84	1
Sillaginodes punctatus	25	-402898.97	-4598808	8	0	29.72	0	0	0.18	0	15.86	1

Sillaginodes punctatus	26	-67898.96	-4598808	8	0	29.47	0	0	0.18	0	15.74	1
Sillaginodes punctatus	27	-40398.96	-4598808	8	0	28.36	0	0	0.18	0	15.18	1
Sillaginodes punctatus	28	-322898.97	-4608808	6	0	21.41	0	0	0.19	0	11.71	1
Sillaginodes punctatus	29	-295398.97	-4608808	6	0	21.68	0	0	0.19	0	11.84	1
Sillaginodes punctatus	30	-282898.97	-4608808	5	0	14.8	0	0	0.19	0	8.4	1
Sillaginodes punctatus	31	-80398.96	-4608808	8	0	30.01	0	0	0.18	0	16.01	1
Sillaginodes punctatus	32	-27898.96	-4608808	8	0	27.66	0	0	0.18	0	14.83	1
Sillaginodes punctatus	33	-377898.97	-4608808	8	0	32.47	0	0	0.19	0	17.24	1
Sillaginodes punctatus	34	-20398.96	-4613808	8	0	27.24	0	0	0.18	0	14.62	1
Sillaginodes punctatus	35	-97898.96	-4618808	7	0	23.96	0	0	0.18	0	12.98	1
Sillaginodes punctatus	36	-112898.96	-4628808	7	0	25.3	0	0	0.18	0	13.65	1
Sillaginodes punctatus	37	29601.04	-4628808	10	0	34.92	0	0	0.18	0	18.46	1
Sillaginodes punctatus	38	14958.18	-4627379.5	10	0	36.48	0	0	0.18	0	19.24	1
Sillaginodes punctatus	39	-112898.96	-4643808	5	0	11.95	0	0	0.18	0	6.97	1
Sillaginodes punctatus	40	40434.38	-4642141	10	0	33.35	0	0	0.17	0	17.67	1

Sillaginodes punctatus	41	62101.04	-4641308	10	0	31.94	0	0	0.17	0	16.97	1
Sillaginodes punctatus	42	-207898.95	-4653808	5	0	15.11	0	0	0.18	0	8.55	1
Sillaginodes punctatus	43	-117898.96	-4653808	5	0	12.39	0	0	0.18	0	7.19	1
Sillaginodes punctatus	44	72101.04	-4653808	10	0	31.93	0	0	0.17	0	16.97	1
Sillaginodes punctatus	45	178351.05	-4661308	10	0	32.81	0	0	0.14	0	17.4	1
Sillaginodes punctatus	46	97101.04	-4673808	10	0	31.13	0	0	0.17	0	16.57	1
Sillaginodes punctatus	47	132101.05	-4673808	10	0	31.37	0	0	0.15	0	16.69	1
Sillaginodes punctatus	48	107101.04	-4683808	10	0	30.78	0	0	0.16	0	16.39	1
Sillaginodes punctatus	49	192101.05	-4683808	10	0	30.1	0	0	0.14	0	16.05	1
Sillaginodes punctatus	50	167101.05	-4686308	10	0	31.56	0	0	0.14	0	16.78	1
Sillaginodes punctatus	51	-5398.96	-4923808	10	0	26.59	0	0	0.15	0	14.3	1
Sillaginodes punctatus	52	8351.04	-4935058	10	0	28.5	0	0	0.14	0	15.25	1
Sillaginodes punctatus	53	332101.03	-4943808	8	0	28.97	0	0	0.13	0	15.48	1
Sillaginodes punctatus	54	27101.04	-4946308	10	0	30.62	0	0	0.14	0	16.31	1
Sillaginodes punctatus	55	337101.03	-4948808	8	0	29.39	0	0	0.13	0	15.7	1

Sillaginodes punctatus	56	310101.03	-4955808	8	0	28.04	0	0	0.13	0	15.02	1
Sillaginodes punctatus	57	257101.05	-4968808	8	0	25.2	0	0	0.13	0	13.6	1
Sillaginodes punctatus	58	262101.05	-4978808	8	0	27.18	0	0	0.13	0	14.59	1
Sillaginodes punctatus	59	199601.05	-4993808	8	0	25.59	0	0	0.13	0	13.8	1
Sillaginodes punctatus	60	377101.03	-5026308	10	0	40.37	0	0	0.14	0	21.19	1
Sillaginodes punctatus	61	369601.03	-5033808	10	0	41.24	0	0	0.14	0	21.62	1
Sillaginodes punctatus	62	-792898.94	-3856308	2	0	2.21	0	0	0.17	0	2.11	1
Sillaginodes punctatus	63	-795398.94	-3866308	2	0	2.13	0	0	0.17	0	2.06	1
Sillaginodes punctatus	64	-787898.94	-3868808	2	0	2.16	0	0	0.17	0	2.08	1
Sillaginodes punctatus	65	-787898.94	-3883808	2	0	2	0	0	0.17	0	2	1
Sillaginodes punctatus	66	-805398.94	-3873808	2	0	2.06	0	0	0.17	0	2.03	1
Sillaginodes punctatus	67	-817898.94	-3876308	3	0	8.57	0	0	0.17	0	5.29	1
Sillaginodes punctatus	68	-822898.94	-3883808	3	0	8.11	0	0	0.17	0	5.06	1
Sillaginodes punctatus	69	-825398.94	-3891308	3	0	7.48	0	0	0.17	0	4.74	1
Sillaginodes punctatus	70	-831648.94	-3902558	4	0	13.12	0	0	0.17	0	7.56	1

Sillaginodes punctatus	71	-841898.94	-3914808	4	0	12.6	0	0	0.17	0	7.3	1
Sillaginodes punctatus	72	-845398.94	-3931308	4	0	11.05	0	0	0.17	0	6.53	1
Sillaginodes punctatus	73	-850898.94	-3939808	4	0	10.25	0	0	0.17	0	6.12	1
Sillaginodes punctatus	74	-840398.94	-4016308	5	0	11.33	0	0	0.16	0	6.66	1
Sillaginodes punctatus	75	-834565.63	-4005474.5	5	0	12.27	0	0	0.16	0	7.13	1
Sillaginodes punctatus	76	-829565.63	-3997141.25	5	0	12.77	0	0	0.16	0	7.39	1
Sillaginodes punctatus	77	-824565.63	-3990474.5	5	0	13.28	0	0	0.16	0	7.64	1
Sillaginodes punctatus	78	-819898.94	-3976808	5	0	14.08	0	0	0.16	0	8.04	1
Sillaginodes punctatus	79	-814148.94	-3962558	5	0	15.45	0	0	0.16	0	8.72	1
Sillaginodes punctatus	80	-799327.5	-3888808	3	0	8.61	0	0	0.17	0	5.31	1
Sillaginodes punctatus	81	-804565.63	-3897141.25	3	0	8.02	0	0	0.17	0	5.01	1
Sillaginodes punctatus	82	-812898.94	-3903808	3	0	7.27	0	0	0.17	0	4.63	1
Sillaginodes punctatus	83	-795398.94	-3941308	4	0	11.98	0	0	0.17	0	6.99	1
Sillaginodes punctatus	84	-802898.94	-3931308	4	0	11.94	0	0	0.17	0	6.97	1
Sillaginodes punctatus	85	-808732.31	-3917141.25	4	0	13.12	0	0	0.17	0	7.56	1

Sillaginodes punctatus	86	-889327.5	-3970950.75	6	0	17.31	0	0	0.17	0	9.66	1
Sillaginodes punctatus	87	-837898.94	-4041308	5	0	11.15	0	0	0.16	0	6.57	1
Sillaginodes punctatus	88	-840398.94	-4058808	5	0	11.2	0	0	0.16	0	6.6	1
Sillaginodes punctatus	89	-855398.94	-4068808	6	0	16.16	0	0	0.16	0	9.08	1
Sillaginodes punctatus	90	-845398.94	-4078808	6	0	16.52	0	0	0.16	0	9.26	1
Sillaginodes punctatus	91	-842898.94	-4118808	5	0	10.89	0	0	0.16	0	6.44	1
Sillaginodes punctatus	92	-858454.5	-4173252.25	7	0	15.62	0	0	0.2	0	8.81	1
Sillaginodes punctatus	93	-794327.5	-4140950.75	7	0	26.76	0	0	0.19	0	14.38	1
Sillaginodes punctatus	94	-793523.94	-4124433	6	0	23.47	0	0	0.19	0	12.74	1
Sillaginodes punctatus	95	-782898.94	-4096308	3	0	7.43	0	0	0.19	0	4.72	1
Sillaginodes punctatus	96	-785676.75	-4079919	3	0	7.52	0	0	0.19	0	4.76	1
Sillaginodes punctatus	97	-765398.94	-4046308	3	0	9.36	0	0	0.19	0	5.68	1
Sillaginodes punctatus	98	-775398.94	-4055474.5	3	0	8.59	0	0	0.19	0	5.29	1
Sillaginodes punctatus	99	-765121.19	-4060474.5	3	0	9.19	0	0	0.19	0	5.59	1
Sillaginodes punctatus	100	-759327.5	-4082379.25	3	0	9.69	0	0	0.19	0	5.85	1

Sillaginodes punctatus	101	-739148.94	-4094433	3	0	9.93	0	0	0.19	0	5.97	1
Sillaginodes punctatus	102	-736648.94	-4102558	3	0	9.57	0	0	0.19	0	5.78	1
Sillaginodes punctatus	103	-733898.94	-4117308	3	0	9.19	0	0	0.19	0	5.59	1
Sillaginodes punctatus	104	-807898.94	-4162558	7	0	20.5	0	0	0.19	0	11.25	1
Sillaginodes punctatus	105	-797273.94	-4158183	7	0	22.54	0	0	0.18	0	12.27	1
Sillaginodes punctatus	106	-826232.31	-4168252.25	7	0	18.1	0	0	0.2	0	10.05	1
Sillaginodes punctatus	107	-588523.94	-4393808	8	0	24.18	0	0	0.22	0	13.09	1
Sillaginodes punctatus	108	-391648.97	-4610058	8	0	29.65	0	0	0.18	0	15.83	1
Sillaginodes punctatus	109	-371232.28	-4602141	5	0	13.92	0	0	0.19	0	7.96	1
Sillaginodes punctatus	110	7101.04	-4622141	9	0	30.44	0	0	0.18	0	16.22	1
Sillaginodes punctatus	111	176101.05	-4676808	10	0	31.43	0	0	0.14	0	16.72	1
Sillaginodes punctatus	112	190434.38	-4659641	10	0	32.38	0	0	0.13	0	17.19	1
Sillaginodes punctatus	113	303767.72	-4557141	10	0	32.44	0	0	0.14	0	17.22	1
Sillaginodes punctatus	114	317101.03	-4550058	10	0	32.58	0	0	0.14	0	17.29	1
Sillaginodes punctatus	115	347101.03	-4538808	10	0	32.78	0	0	0.14	0	17.39	1

Sillaginodes punctatus	116	300434.38	-4947141	8	0	27.24	0	0	0.13	0	14.62	1
Sillaginodes punctatus	117	-762898.94	-4076308	3	0	9.57	0	0	0.19	0	5.79	1
Sillaginodes punctatus	118	-750398.94	-4083808	3	0	10.15	0	0	0.19	0	6.07	1
Sillaginodes punctatus	119	-865398.94	-4111308	6	0	15.33	0	0	0.15	0	8.67	1
Sillaginodes punctatus	120	-872898.94	-4111308	6	0	14.64	0	0	0.16	0	8.32	1
Sillaginodes punctatus	121	-890398.94	-4121308	6	0	14.42	0	0	0.17	0	8.21	1
Sillaginodes punctatus	122	-782898.94	-4106308	4	0	13.89	0	0	0.19	0	7.94	1
Sillaginodes punctatus	123	-785398.94	-4116308	5	0	19.26	0	0	0.19	0	10.63	1
Sillaginodes punctatus	124	-767065.63	-4071308	3	0	9.22	0	0	0.19	0	5.61	1
Sillaginodes punctatus	125	-746898.94	-4089808	3	0	10.04	0	0	0.19	0	6.02	1
Sillaginodes punctatus	126	-725398.94	-4146308	3	0	9.3	0	0	0.19	0	5.65	1
Sillaginodes punctatus	127	-854148.94	-4117558	6	0	16.67	0	0	0.16	0	9.33	1
Sillaginodes punctatus	128	-805398.94	-3953808	4	0	9.39	0	0	0.16	0	5.69	1
Sillaginodes punctatus	129	-577184.69	-4382379.5	8	0	30.41	0	0	0.2	0	16.2	1
Sillaginodes punctatus	130	-802898.94	-3923808	4	0	12.61	0	0	0.17	0	7.3	1

Sillaginodes punctatus	131	-796232.31	-3879641.25	2	0	2	0	0	0.17	0	2	1
Sillaginodes punctatus	132	-810398.94	-3911308	4	0	13.76	0	0	0.17	0	7.88	1
Sillaginodes punctatus	133	-873898.94	-3971808	5	0	10.94	0	0	0.16	0	6.47	1
Sillaginodes punctatus	134	-891898.94	-4181808	7	0	13.94	0	0	0.2	0	7.97	1
Sillaginodes punctatus	135	-884565.63	-4175474.5	7	0	14.14	0	0	0.2	0	8.07	1
Sillaginodes punctatus	136	-894148.94	-3977558	6	0	16	0	0	0.17	0	9	1
Sillaginodes punctatus	137	-781648.94	-4063808	3	0	8.09	0	0	0.19	0	5.05	1
Sillaginodes punctatus	138	-966898.94	-4087808	7	0	16.54	0	0	0.17	0	9.27	1
Sillaginodes punctatus	139	179601.05	-4686308	10	0	30.46	0	0	0.14	0	16.23	1
Sillaginodes punctatus	140	-812898.94	-3941308	4	0	10.7	0	0	0.17	0	6.35	1
Sillaginodes punctatus	141	-776947.88	-4156362.25	0	46	0	69.32	0	0.19	0	1	1
Sillaginodes punctatus	142	-440203.94	-4605758	0	57	0	141.84	0	0.19	0	1	1
Sillaginodes punctatus	143	-53502.41	-4809756	0	41	0	137.75	0	0.12	0	1	1
Sillaginodes punctatus	144	-82802.19	-4954066	0	39	0	97.69	0	0.13	0	1	1
Sillaginodes punctatus	145	-867013.56	-4046047.5	0	61	0	125.29	0	0.16	0	1	1

Sillaginodes punctatus	146	-892570.5	-4023443	0	60	0	72.31	0	0.18	0	1	1
Sillaginodes punctatus	147	-929470.38	-4096474.5	0	66	0	242.47	0	0.18	0	1	1
Sillaginodes punctatus	148	-892294.13	-4108687	0	61	0	228.58	0	0.19	0	1	1
Sillaginodes punctatus	149	-922711.44	-4176120.5	0	72	0	311.32	0	0.19	0	1	1
Sillaginodes punctatus	150	-866023.94	-4200599.5	0	60	0	201.15	0	0.22	0	1	1
Sillaginodes punctatus	151	-551535.31	-4512080.5	0	49	0	178.2	0	0.2	0	1	1
Sillaginodes punctatus	152	-509219.72	-4560883.5	0	50	0	178.42	0	0.19	0	1	1
Sillaginodes punctatus	153	-153820.02	-4781044.5	0	47	0	114.2	0	0.16	0	1	1
Sillaginodes punctatus	154	-145220.39	-4857379.5	0	44	0	135.61	0	0.12	0	1	1
Sillaginodes punctatus	155	-70140.34	-4828118	0	41	0	156.24	0	0.11	0	1	1
Sillaginodes punctatus	156	-49850.18	-4857832.5	0	34	0	116.54	0	0.11	0	1	1
Sillaginodes punctatus	157	-24353.51	-4843899	0	33	0	116.04	0	0.11	0	1	1

Appendix 5

Table A5.1: Species distribution model summary for pink ling – Boosted Regression Trees (BRT).

mean total deviance = 0.29
mean residual deviance = 0.094
estimated cv deviance = 0.108; se = 0.004
training data correlation = 0.702
cv correlation = 0.68; se = 0.009
training data AUC score = 0.971
cv AUC score = 0.96; se = 0.003

Table A5.2: SDMs predictive variables relative influence.

Variable	**Relative Influence**
Temperature	76.93%
Oxygen	12.82%
pH	6.80%
Currents velocity	2.38%
Chlorophyll A concentration	1.05%

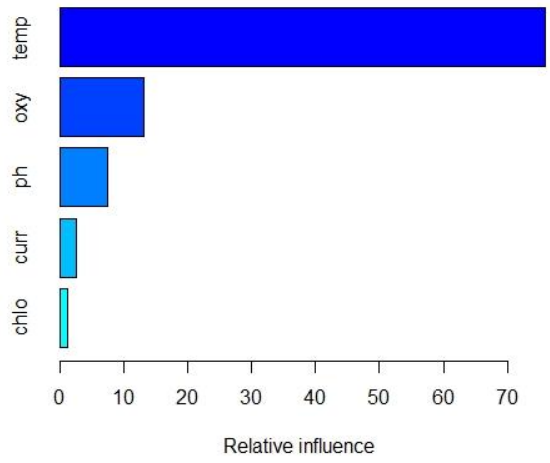


Figure A5.1: SDMs variables relative influence.

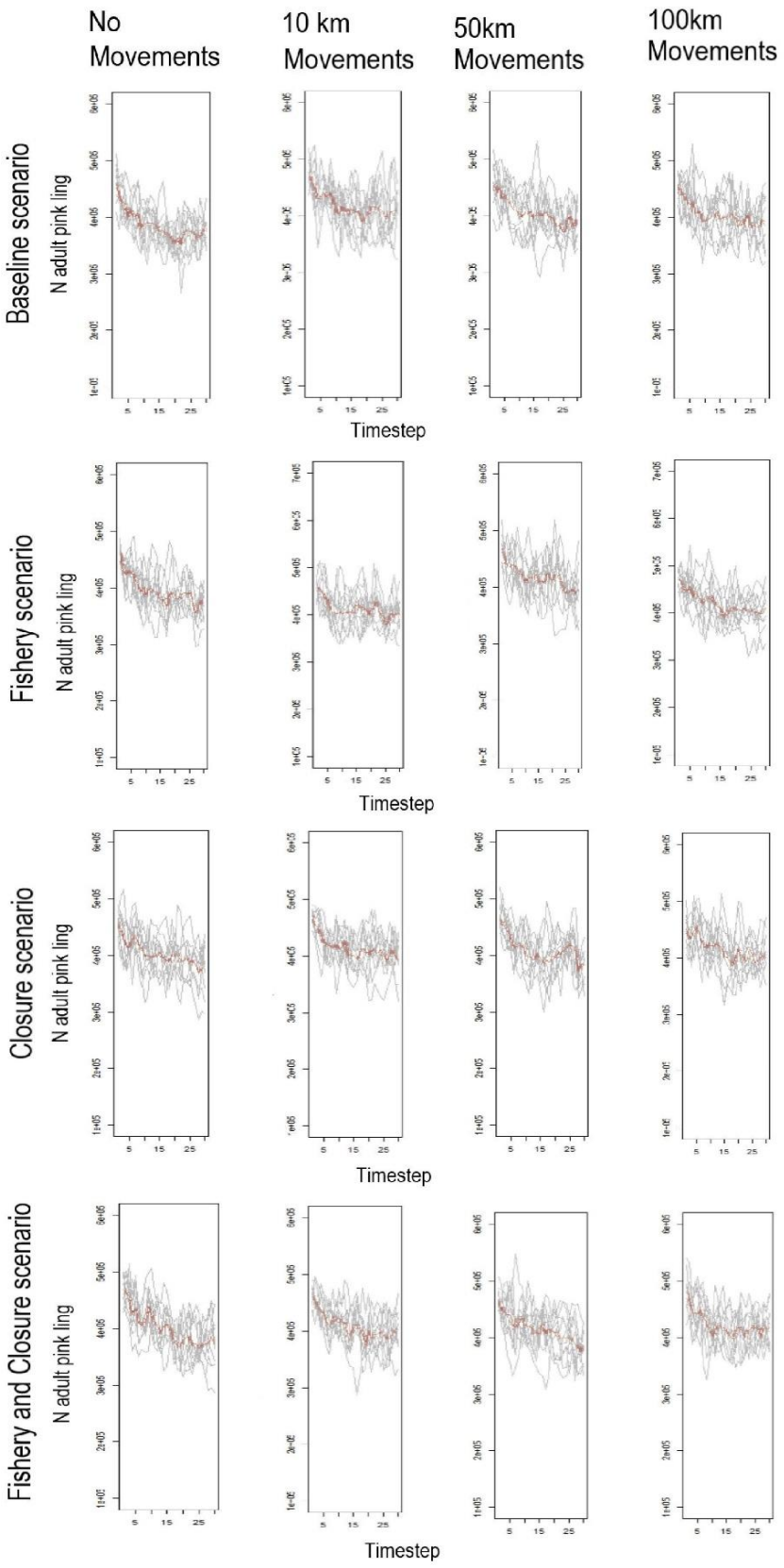


Figure A5.2: Results of pink ling abundance for adult stage, red lines show average number of individuals and grey lines show each replicate results.

Spatial Analysis

Baseline scenario: maps of pink ling abundance for all timesteps for eastern and western stock (Fig. A5.3; A5.4; A5.5; A5.6).

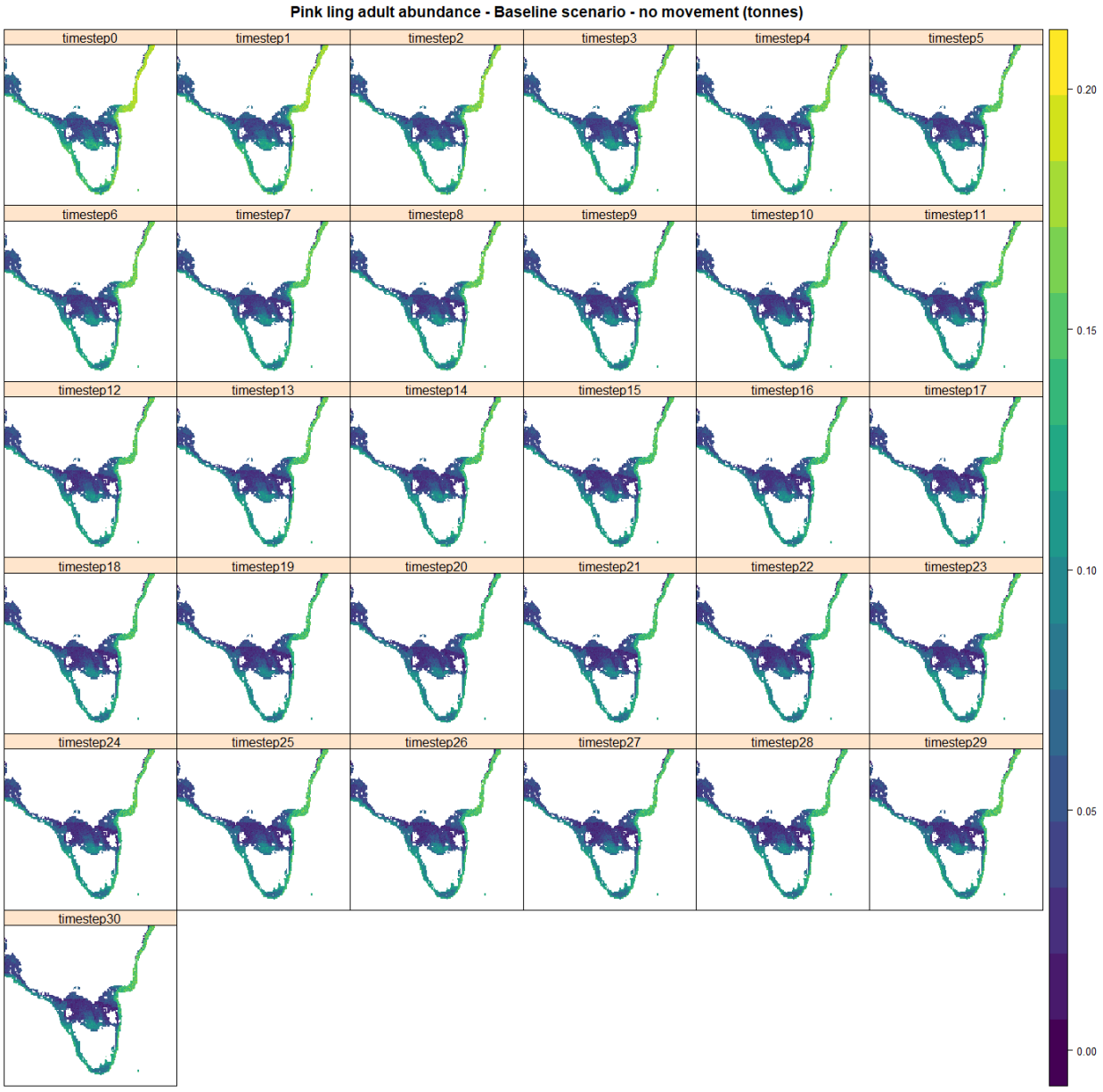


Figure A5.3

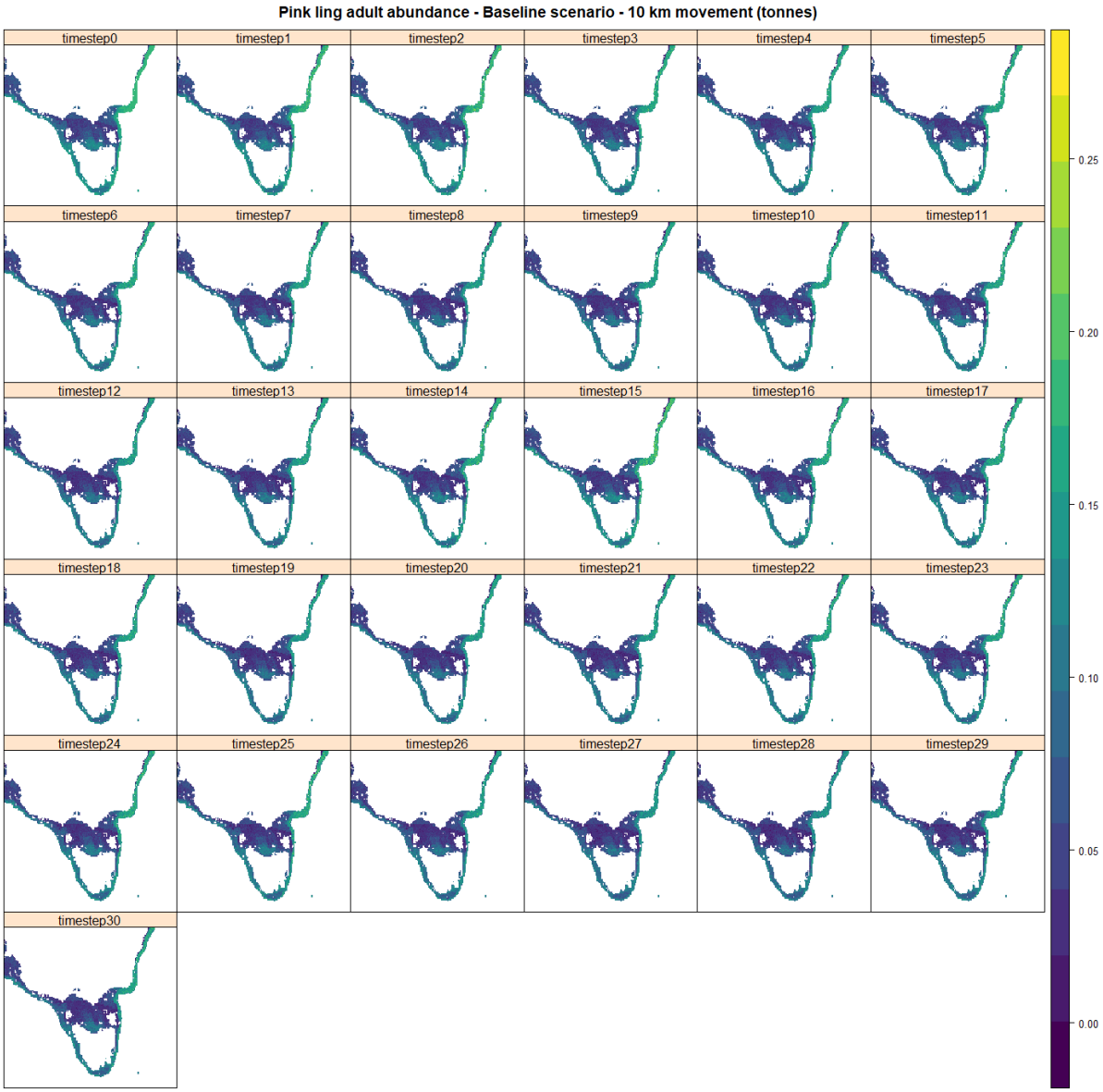

Pink ling adult abundance - Baseline scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.4

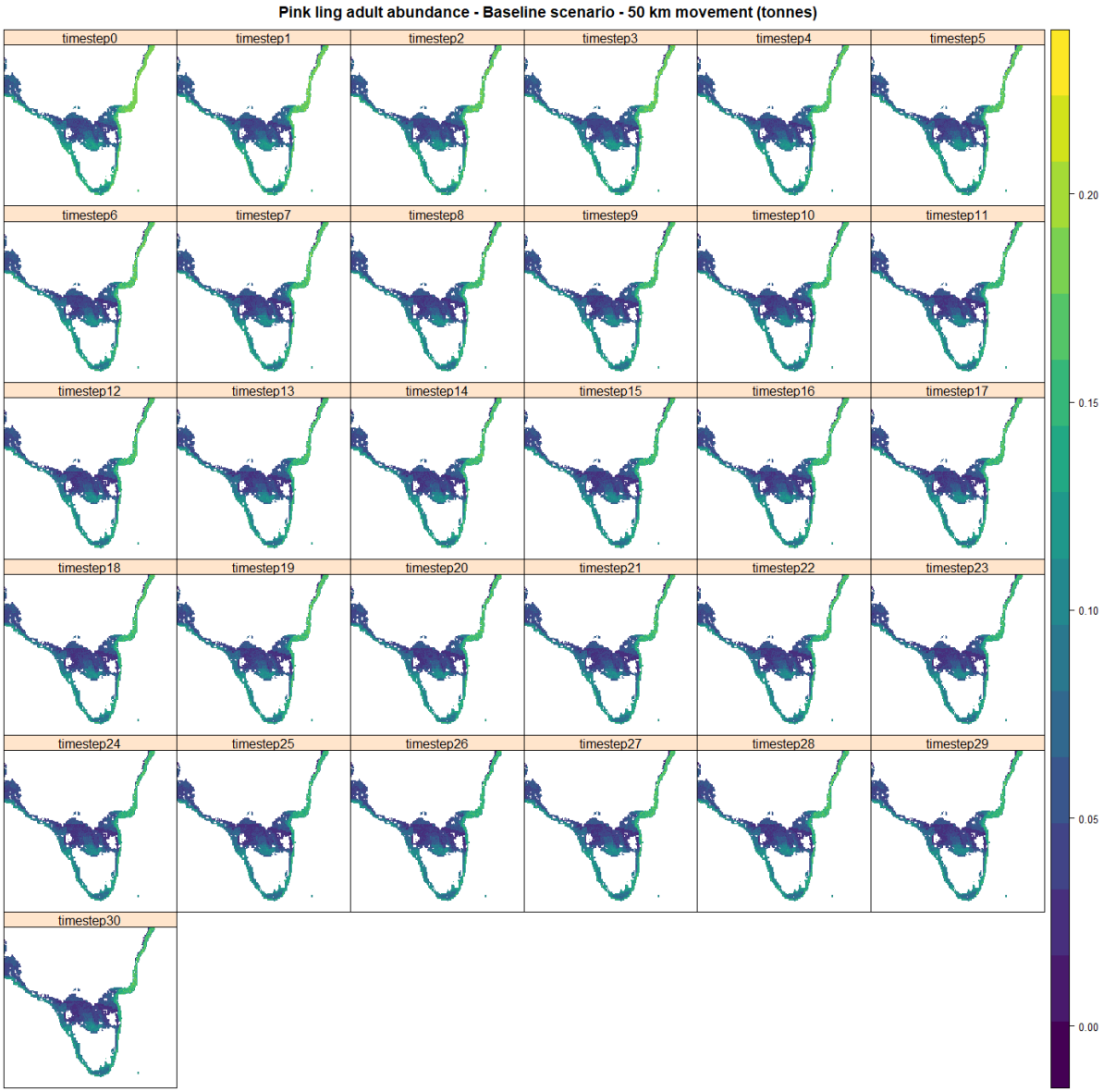

Pink ling adult abundance - Baseline scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.5

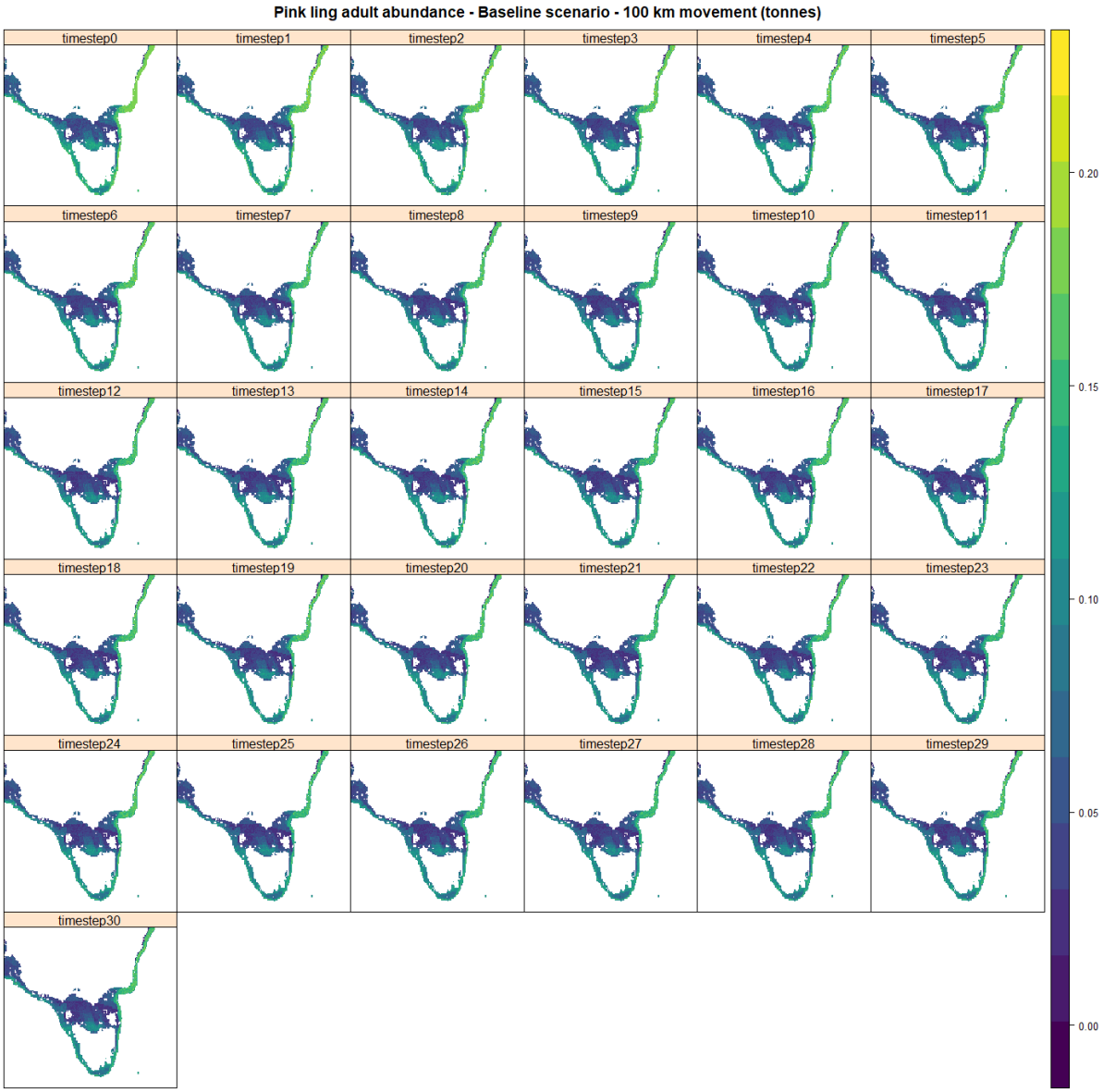

Pink ling adult abundance - Baseline scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.6

Closure scenario: maps of pink ling abundance for all timesteps for eastern and western stock (Fig. A5.7; A5.8; A5.9; A5.10).

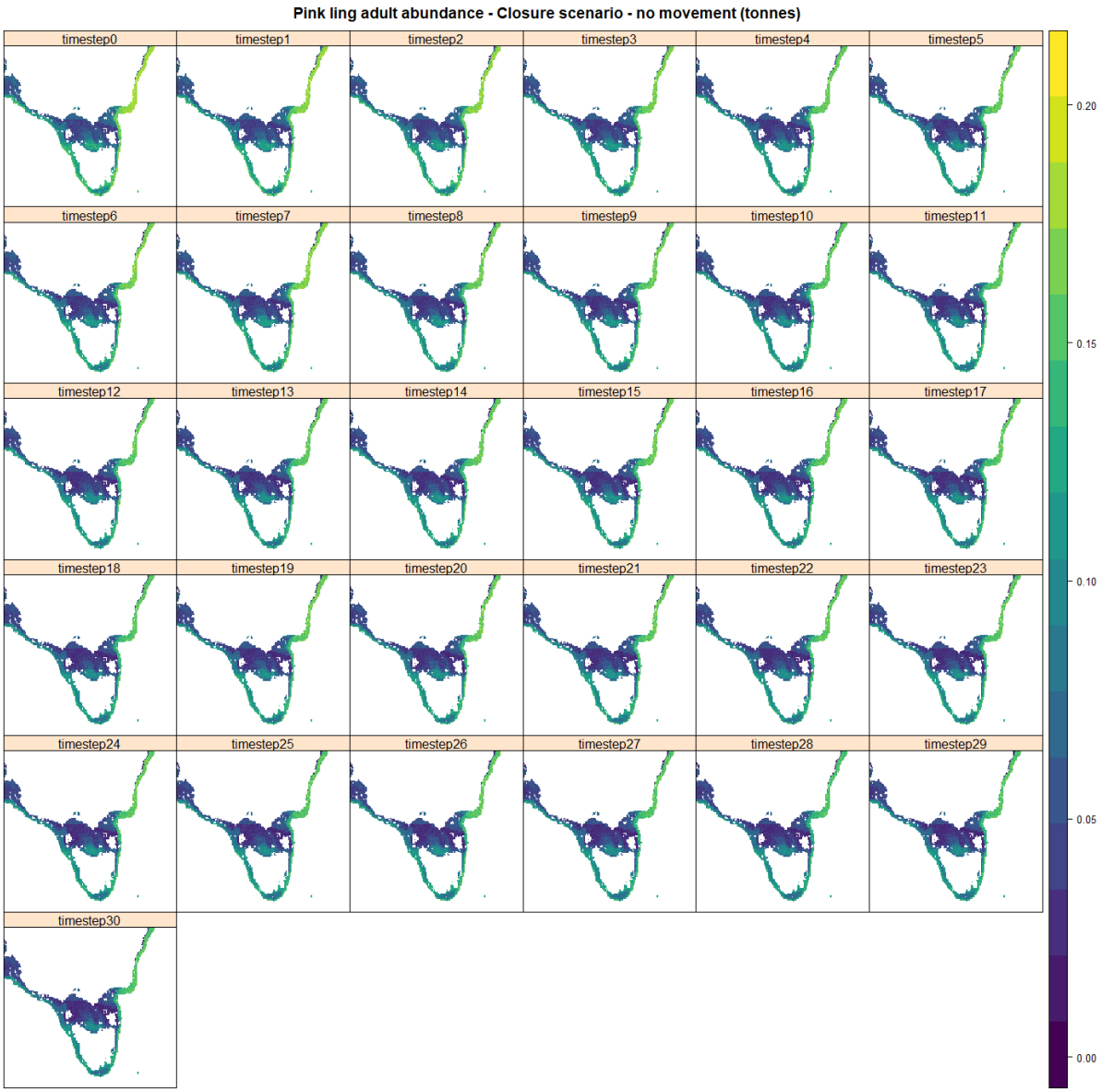
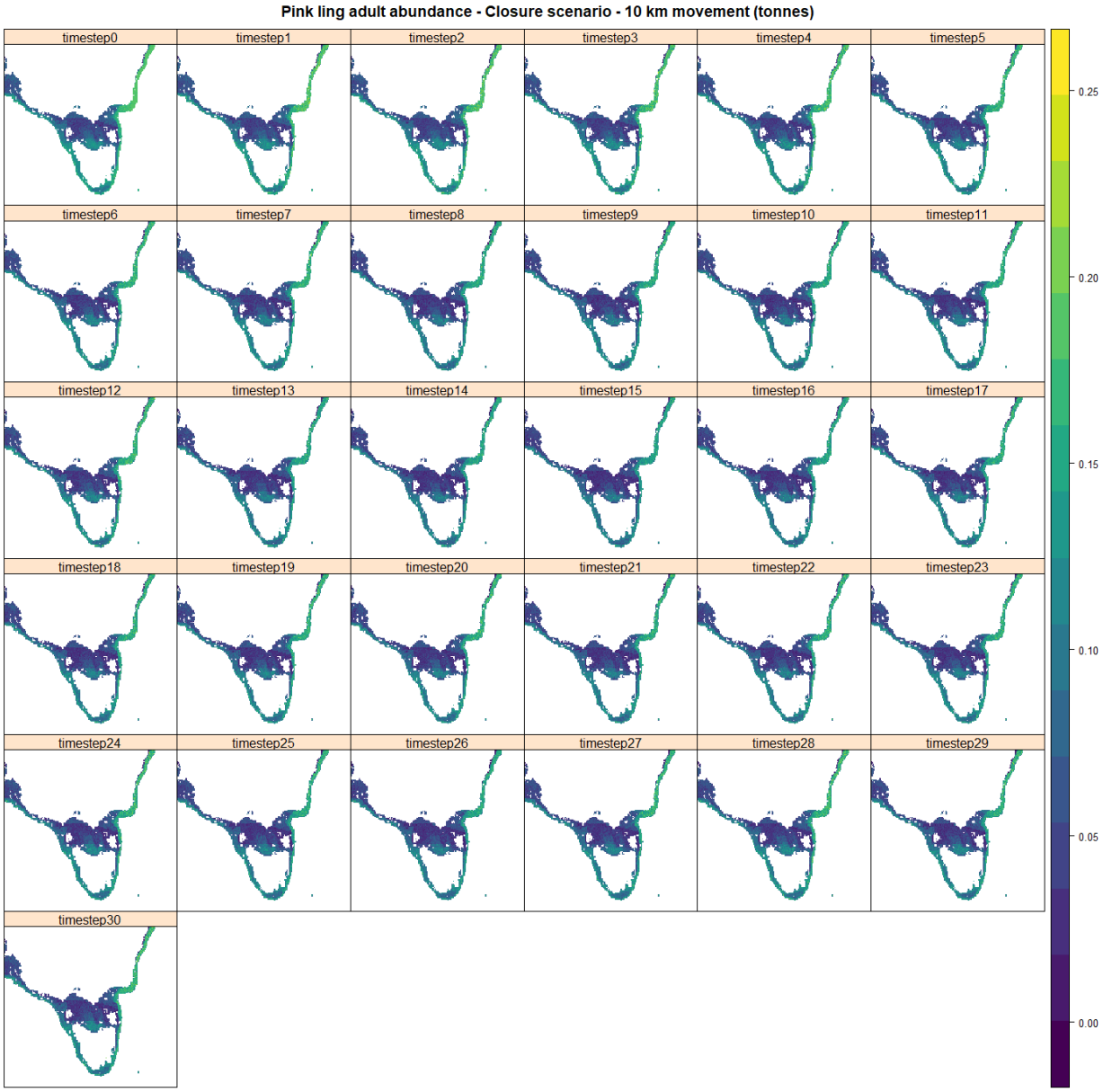


Figure A5.7


Pink ling adult abundance - Closure scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
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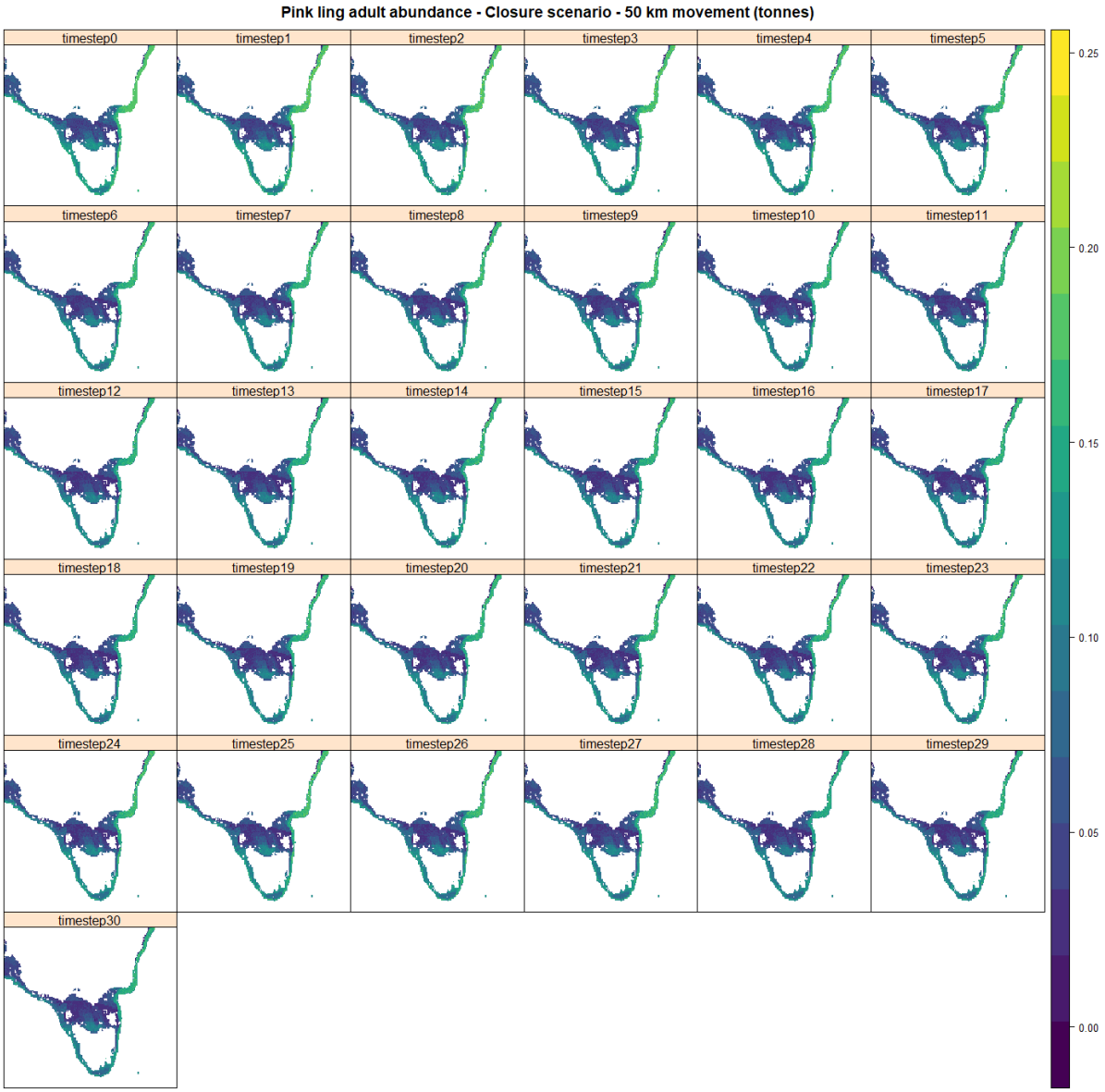
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.8


Pink ling adult abundance - Closure scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
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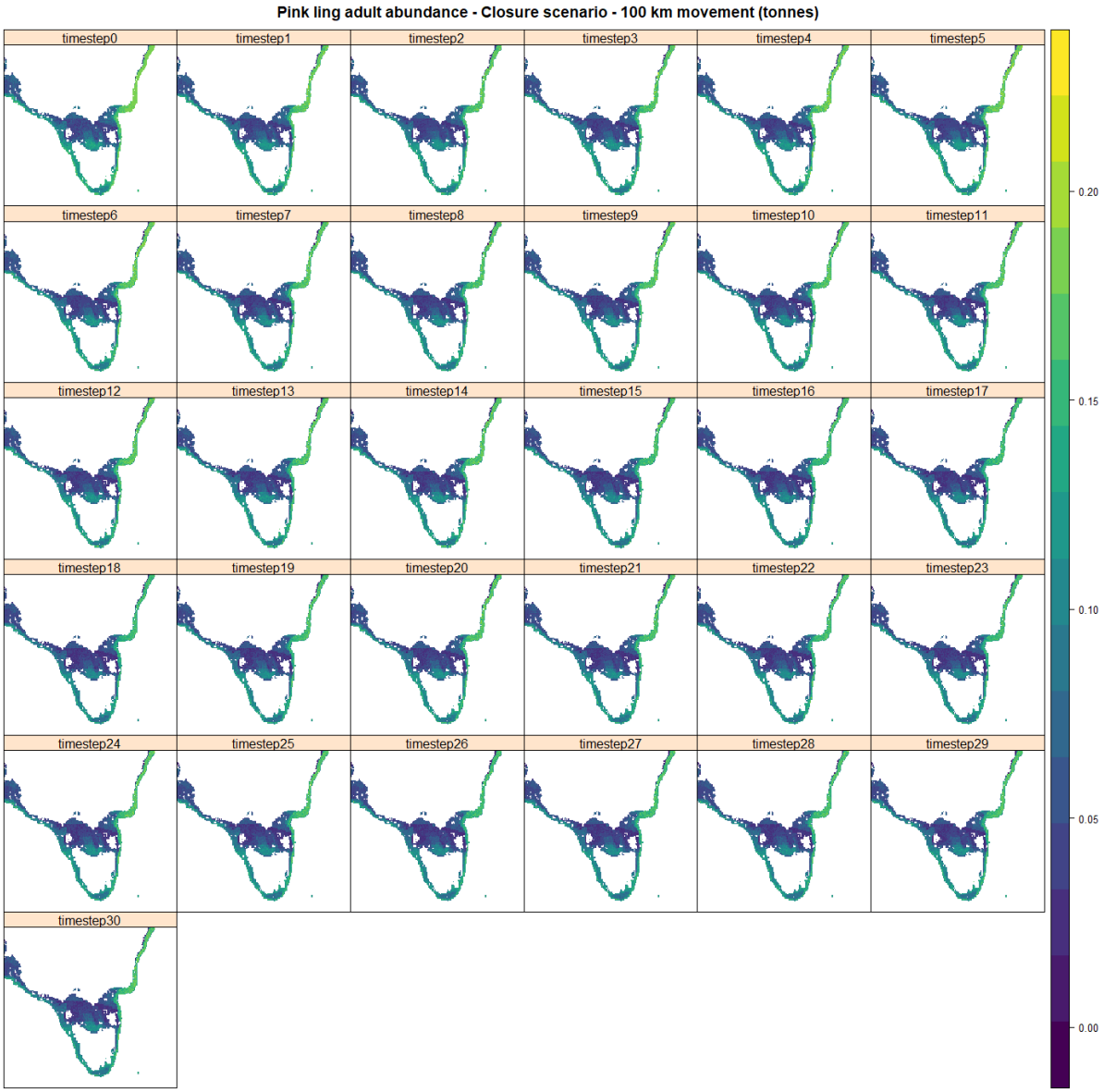
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.9


Pink ling adult abundance - Closure scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
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timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.10

Fishery scenario: maps of pink ling abundance for all timesteps for eastern and western stock (Fig. A5.11; A5.12; A5.13; A5.14).

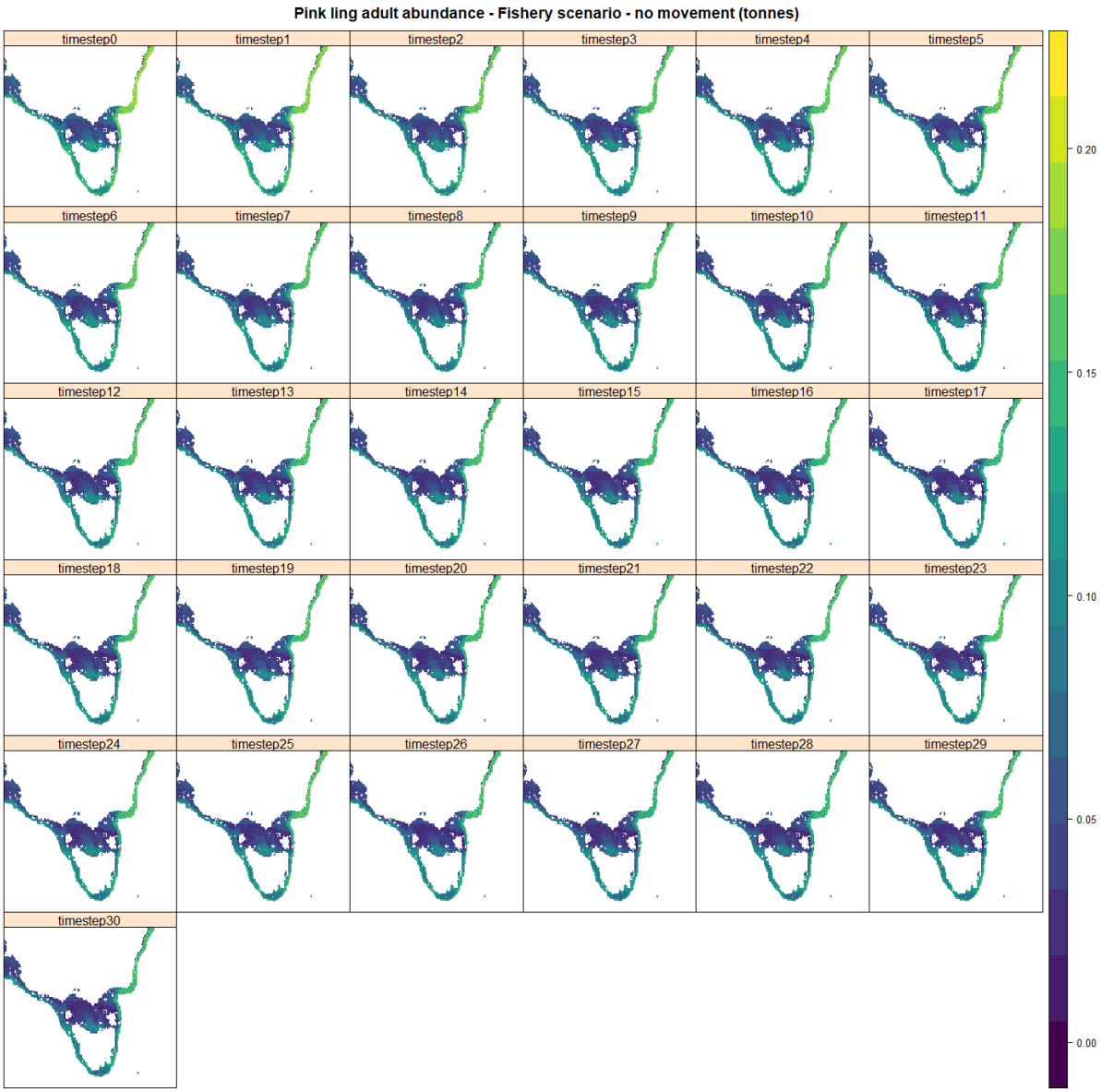
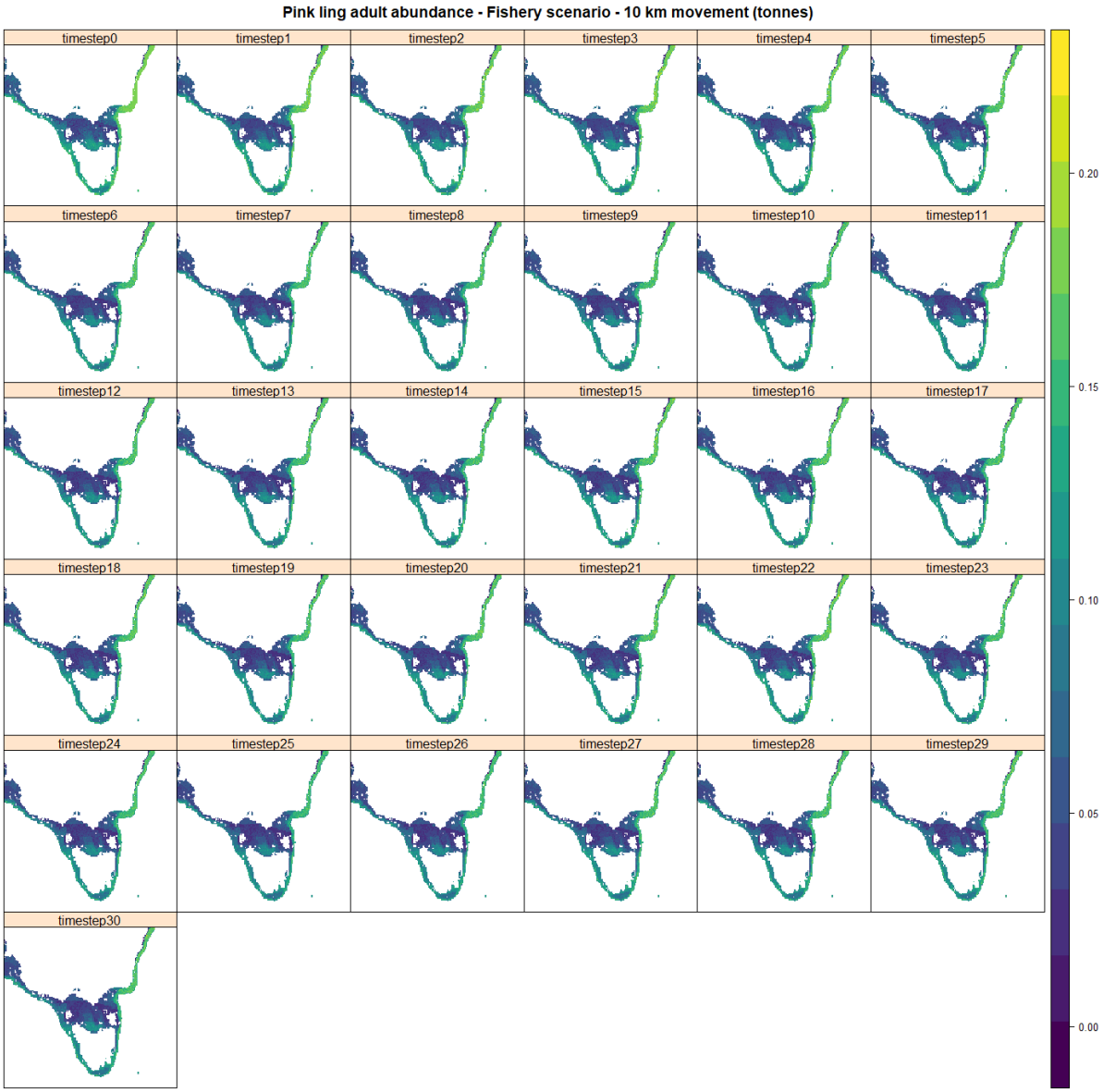


Figure A5.11


Pink ling adult abundance - Fishery scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
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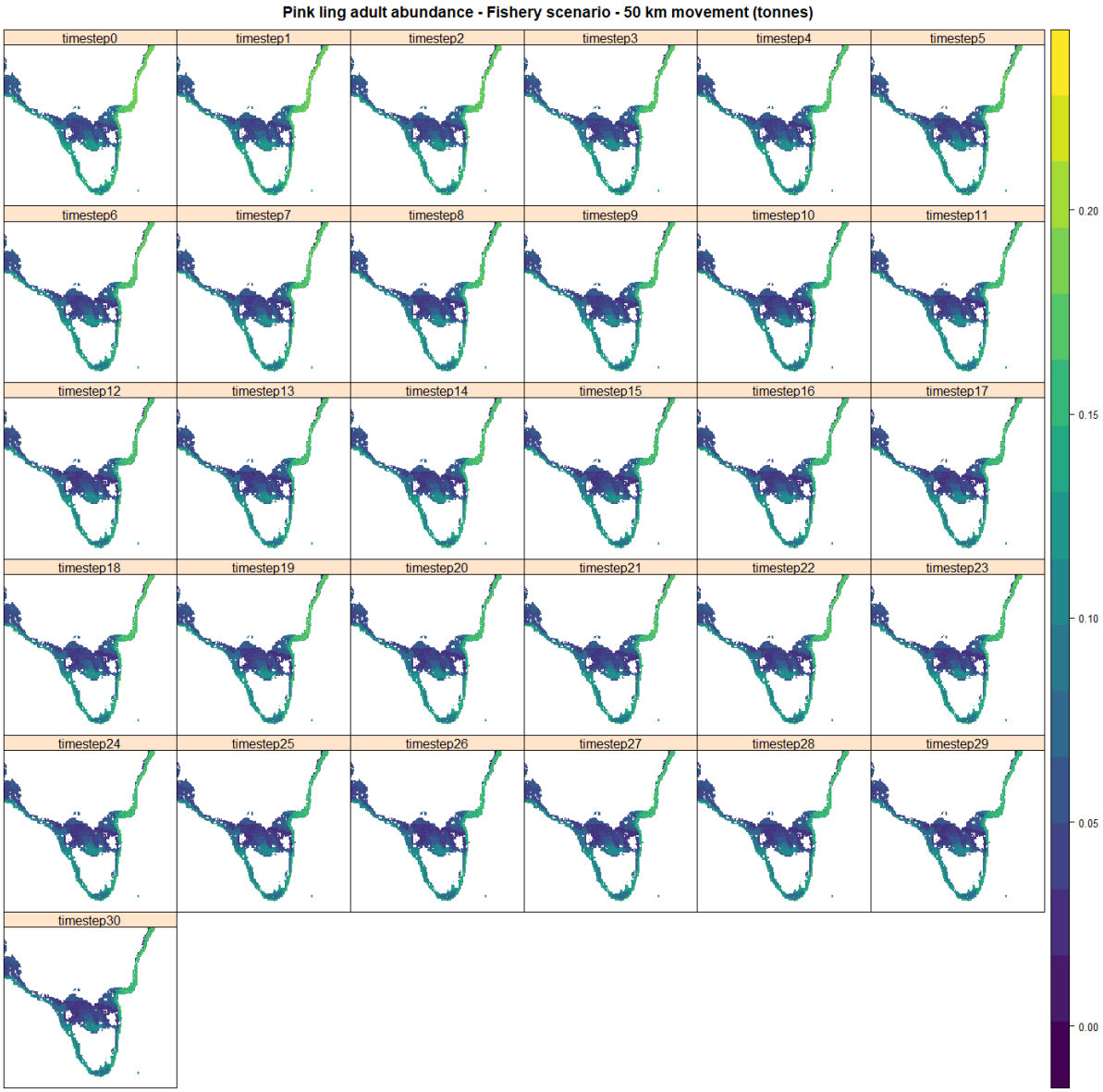
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.12


Pink ling adult abundance - Fishery scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
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timestep21
timestep22
timestep23
timestep24
timestep25
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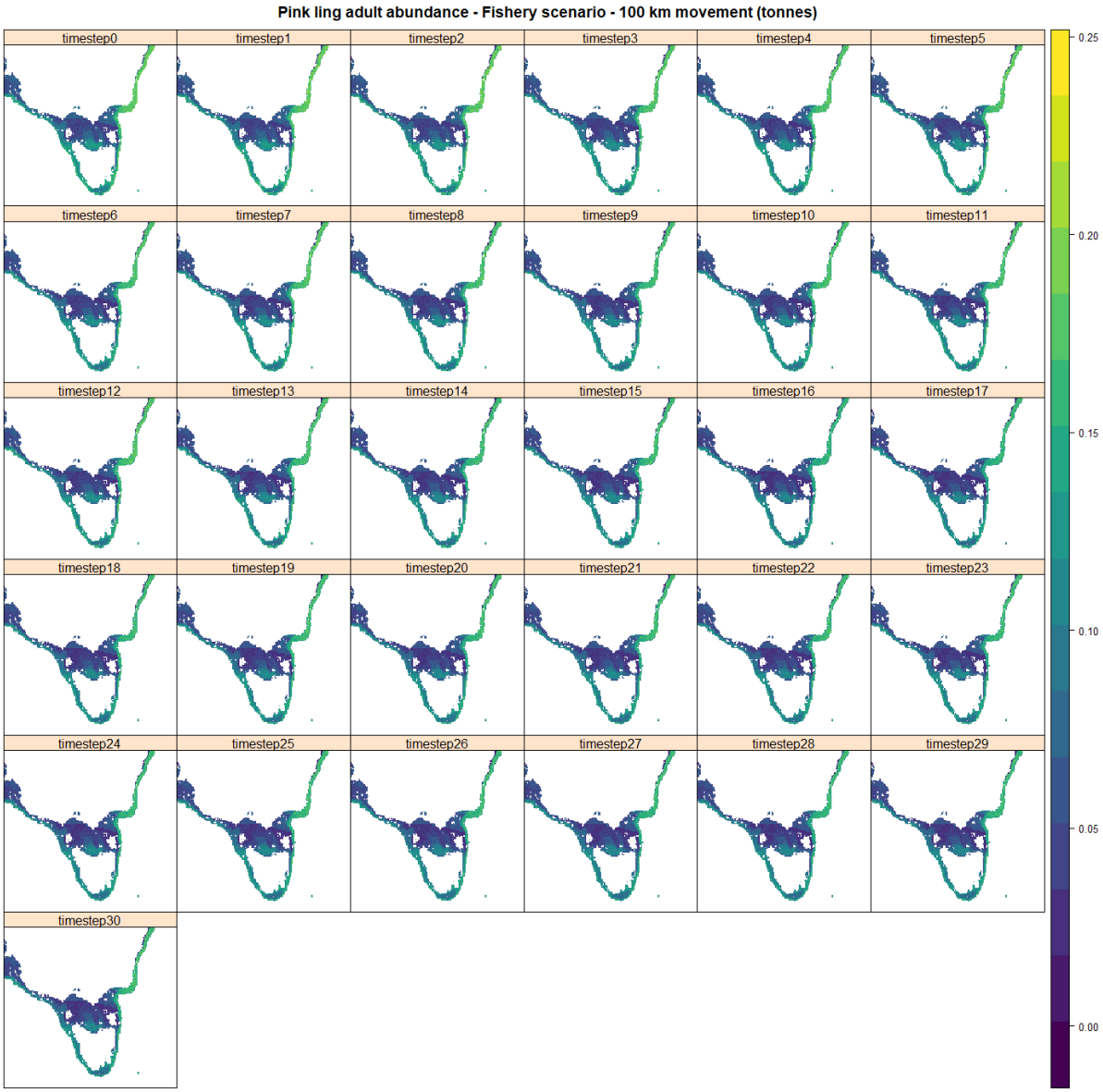
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.13


Pink ling adult abundance - Fishery scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
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timestep14
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timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.14

Fishery and closure scenario: maps of pink ling abundance for all timesteps for eastern and western stock (Fig. A5.15; A5.16; A5.17; A5.18).

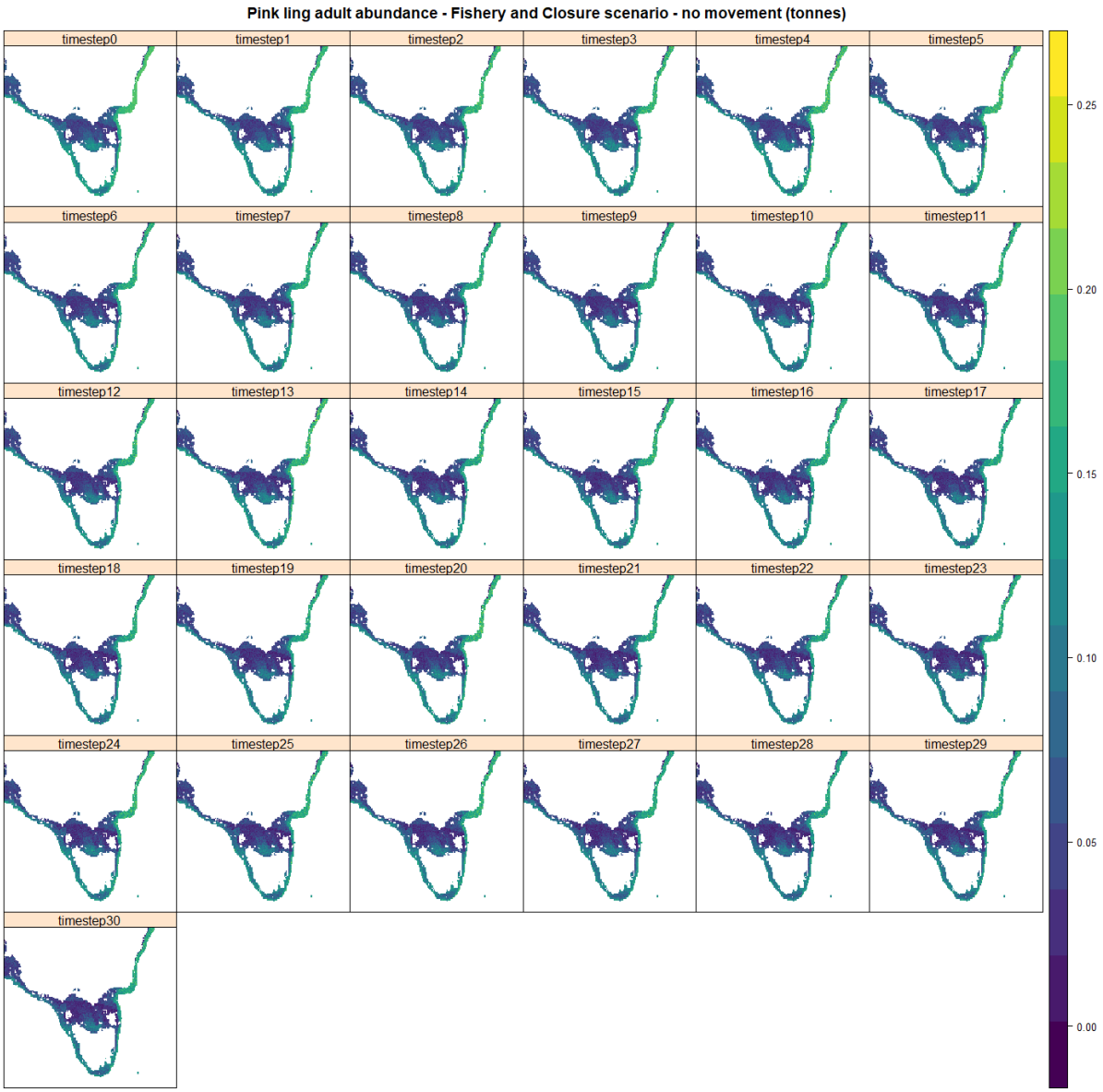
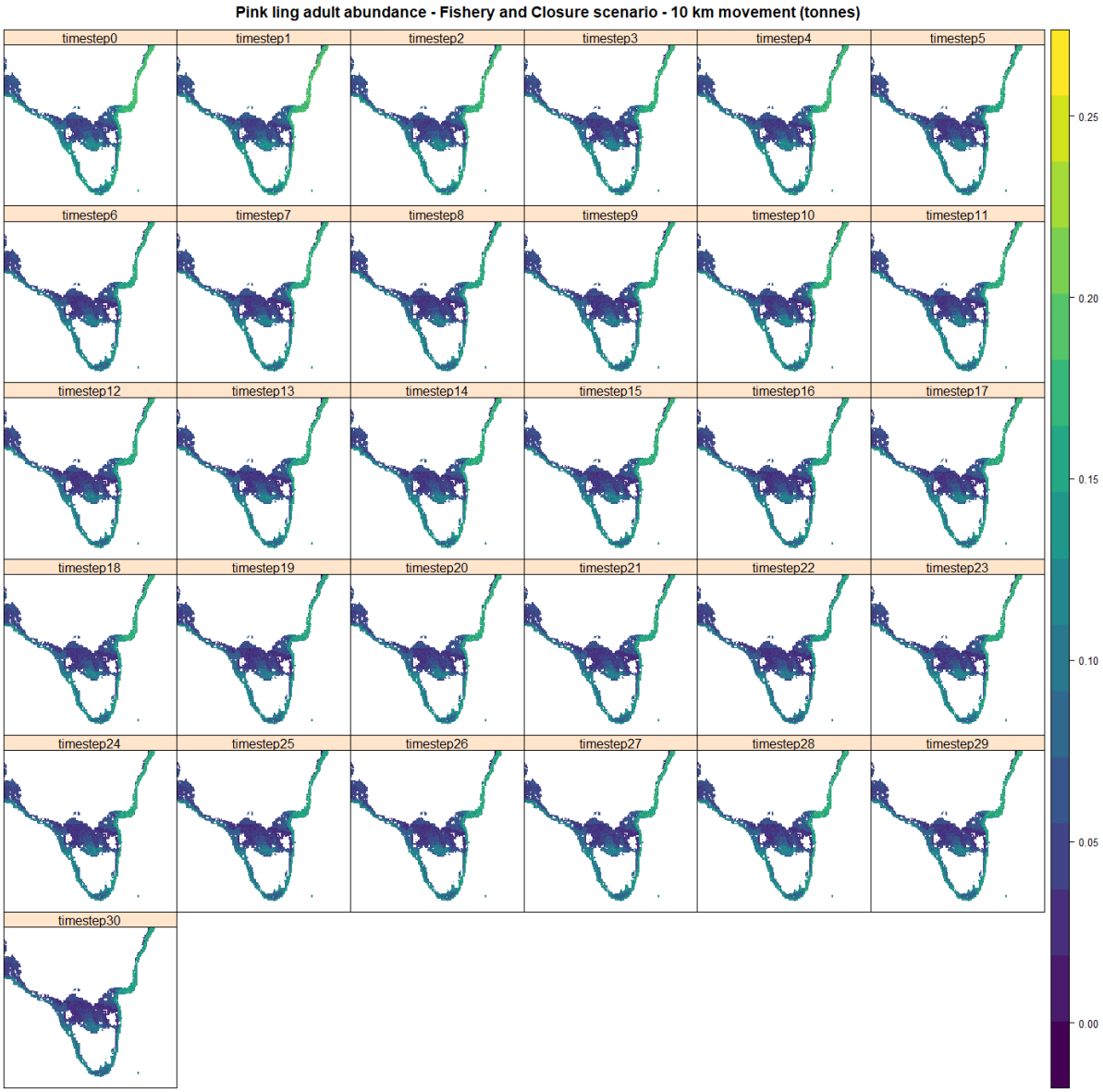


Figure A5.15


Pink ling adult abundance - Fishery and Closure scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
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timestep13
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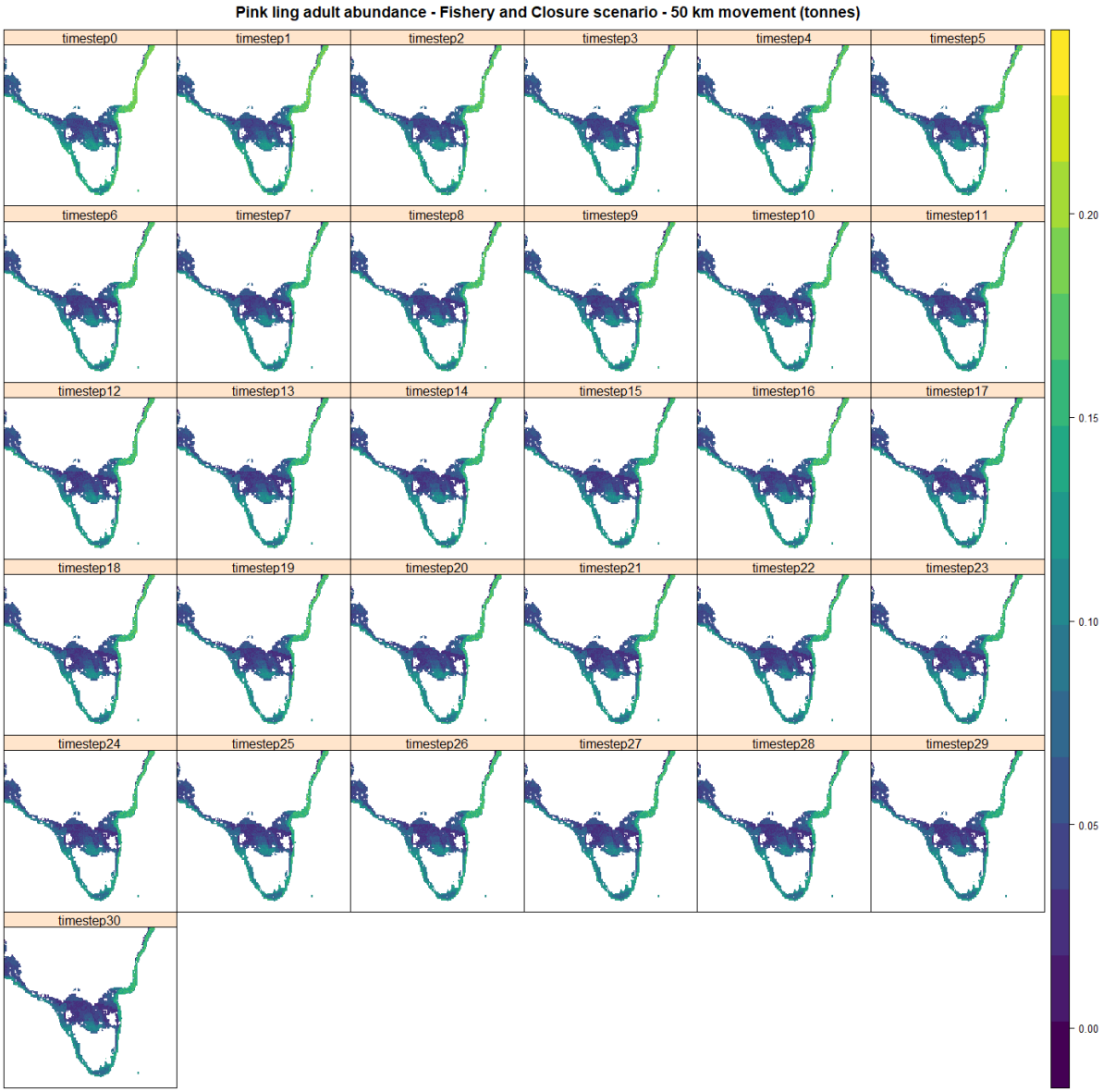
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.16


Pink ling adult abundance - Fishery and Closure scenario - 50 km movement (tonnes)
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timestep3
timestep4
timestep5
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timestep21
timestep22
timestep23
timestep24
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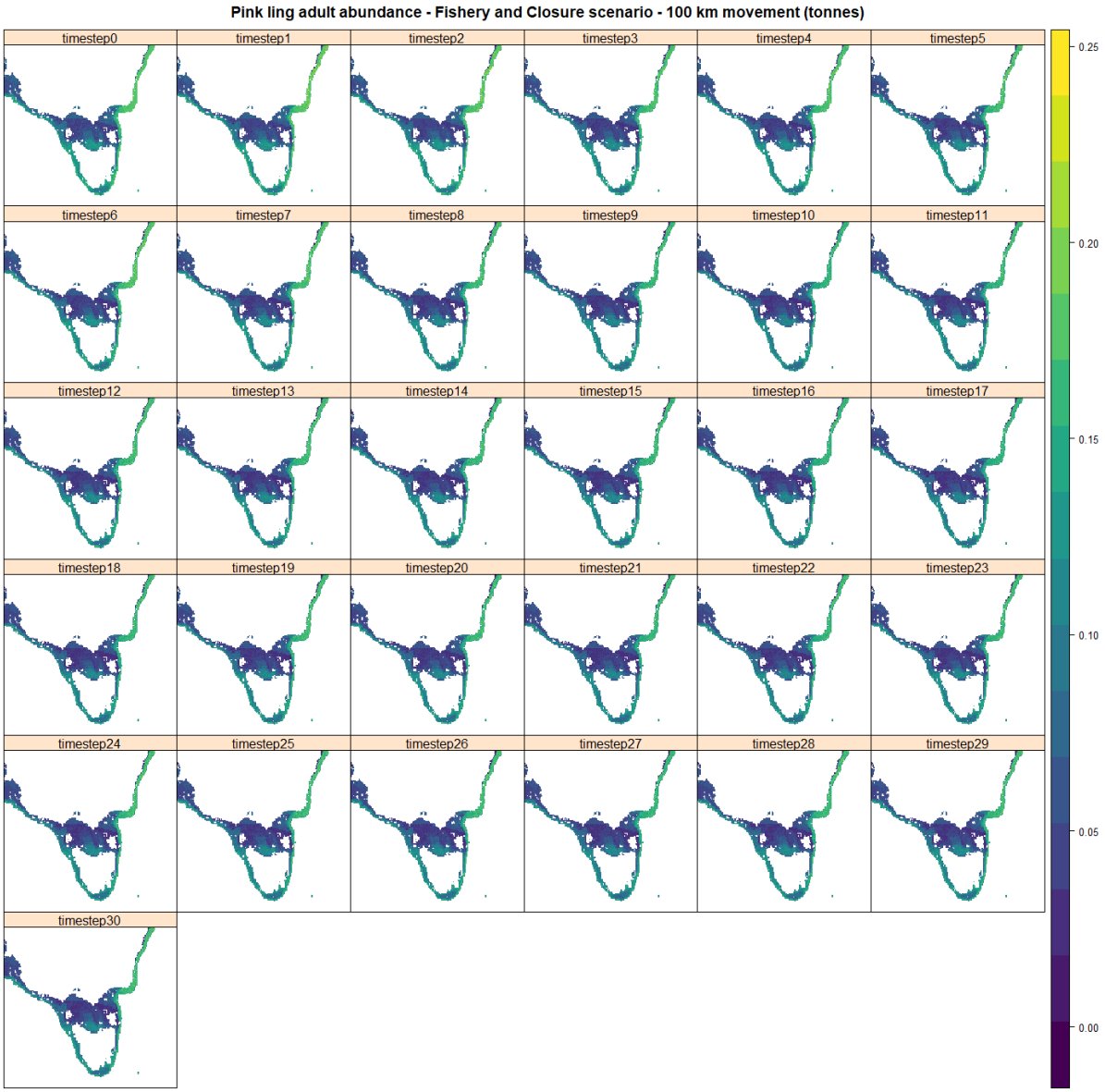
Figure A5.17


Pink ling adult abundance - Fishery and Closure scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
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timestep22
timestep23
timestep24
timestep25
timestep26
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timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.18

Habitat suitability, Carrying capacity and Matrix scenarios for sensitivity analysis (+10%) - maps of pink ling abundance for all timesteps for eastern and western stock (Habitat suitability Fig. A5.19; A5.20; A5.21; A5.22 – Carrying capacity Fig. A.423; A5.24; A5.25; A5.26 – Matrix Fig. A5.27; A5.28; A5.29; A5.30).

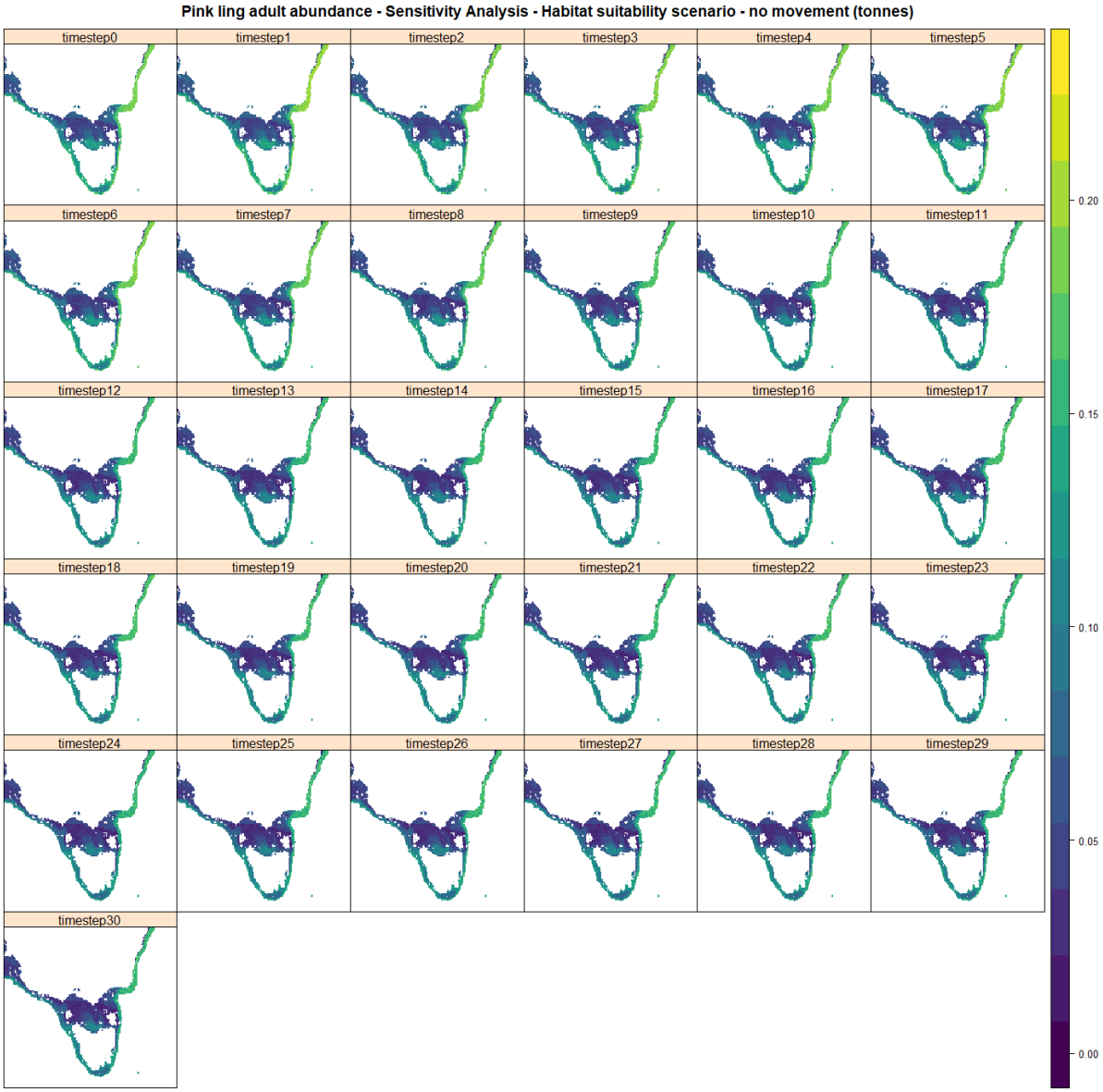


Figure A5.19

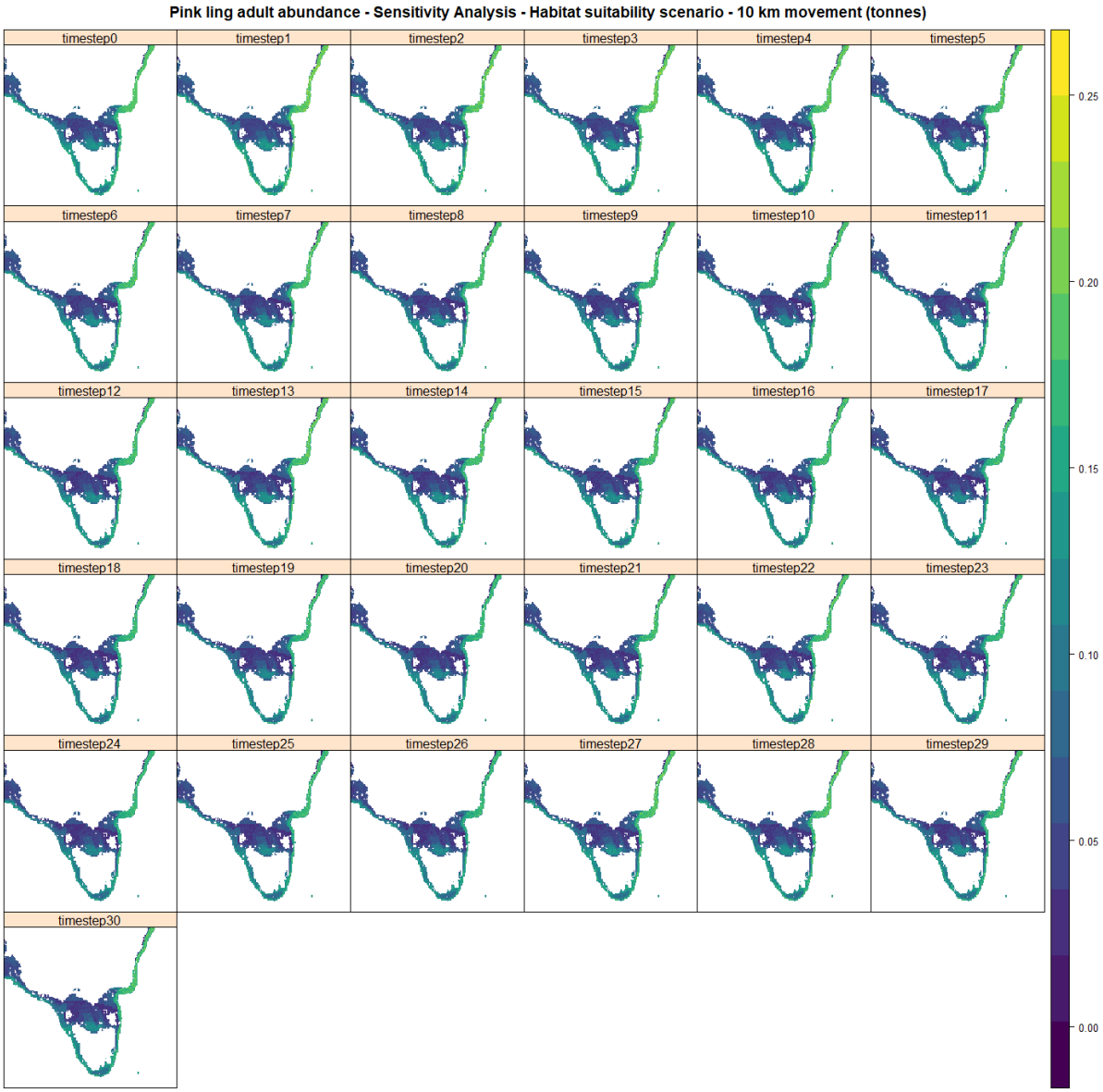

Pink ling adult abundance - Sensitivity Analysis - Habitat suitability scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.20

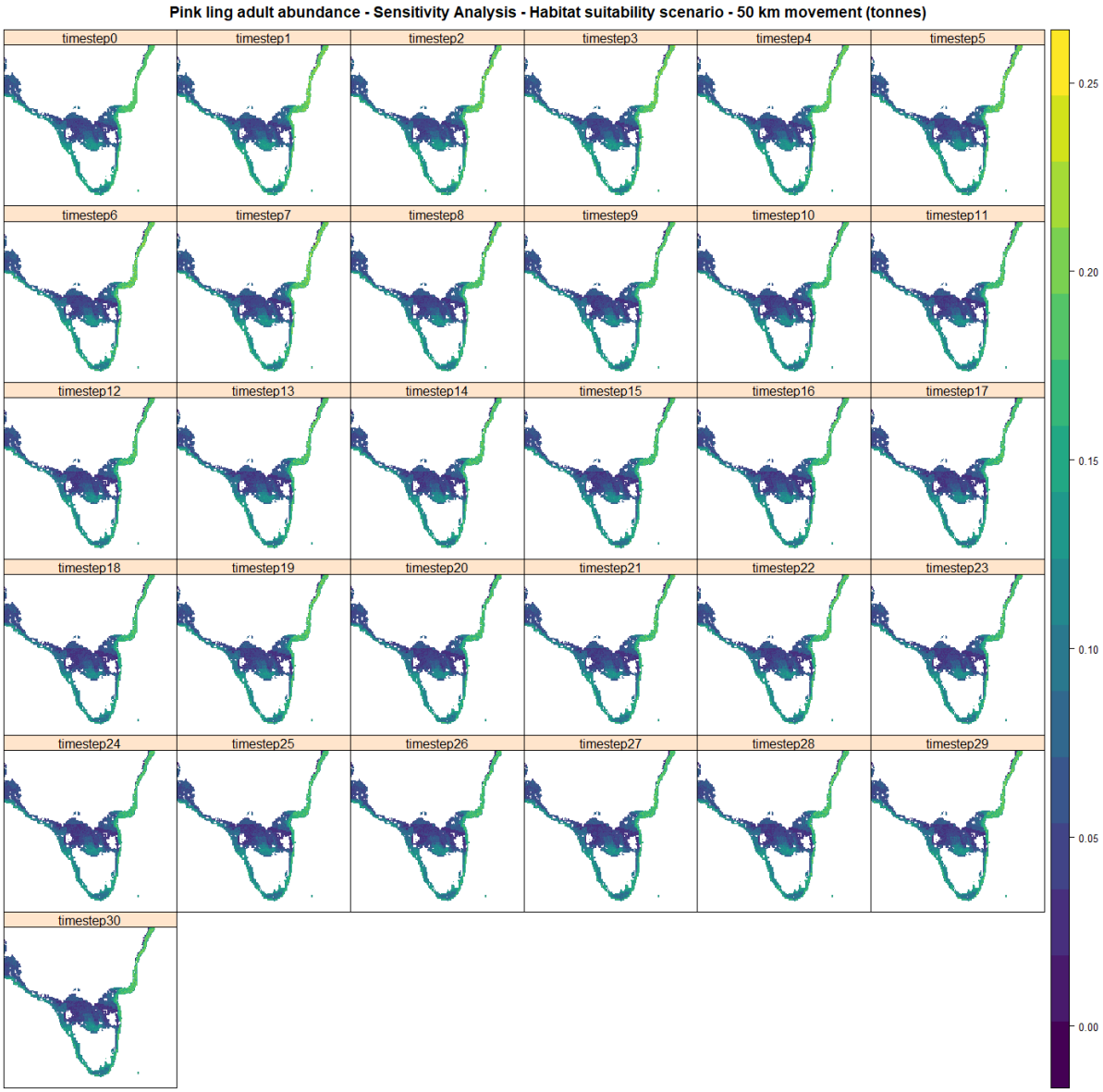

Pink ling adult abundance - Sensitivity Analysis - Habitat suitability scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.21

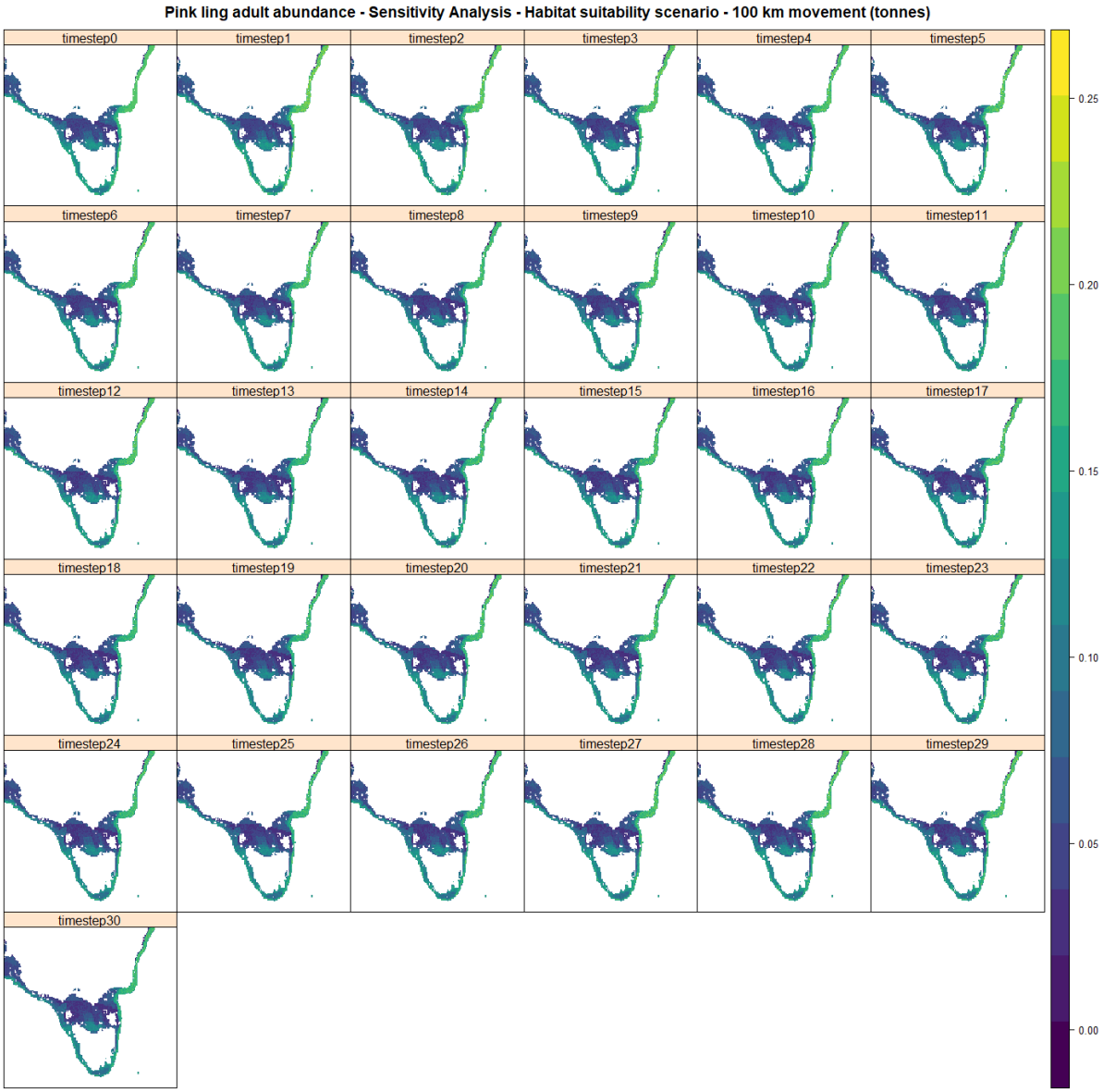

Pink ling adult abundance - Sensitivity Analysis - Habitat suitability scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.22

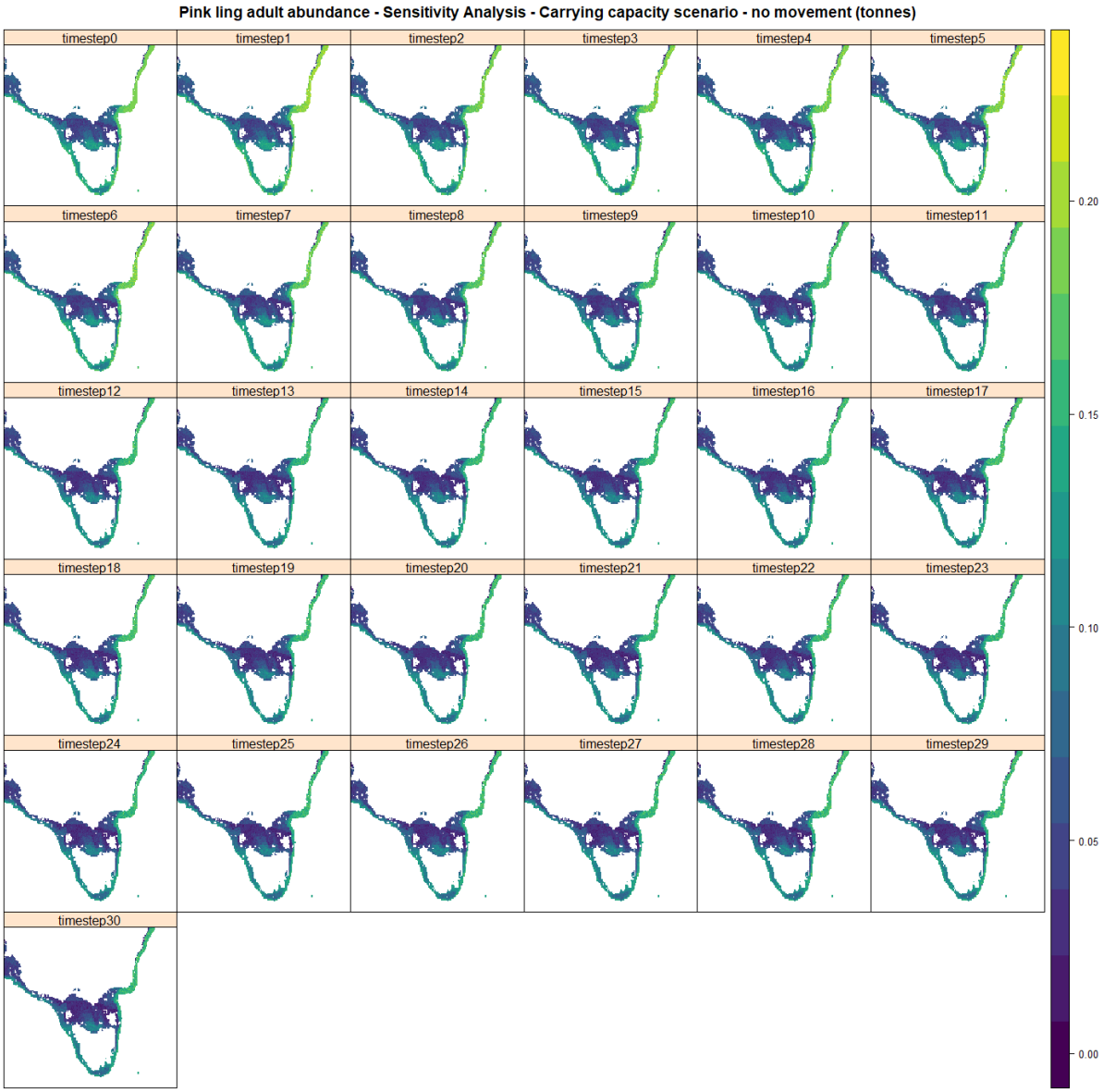

Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - no movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.23

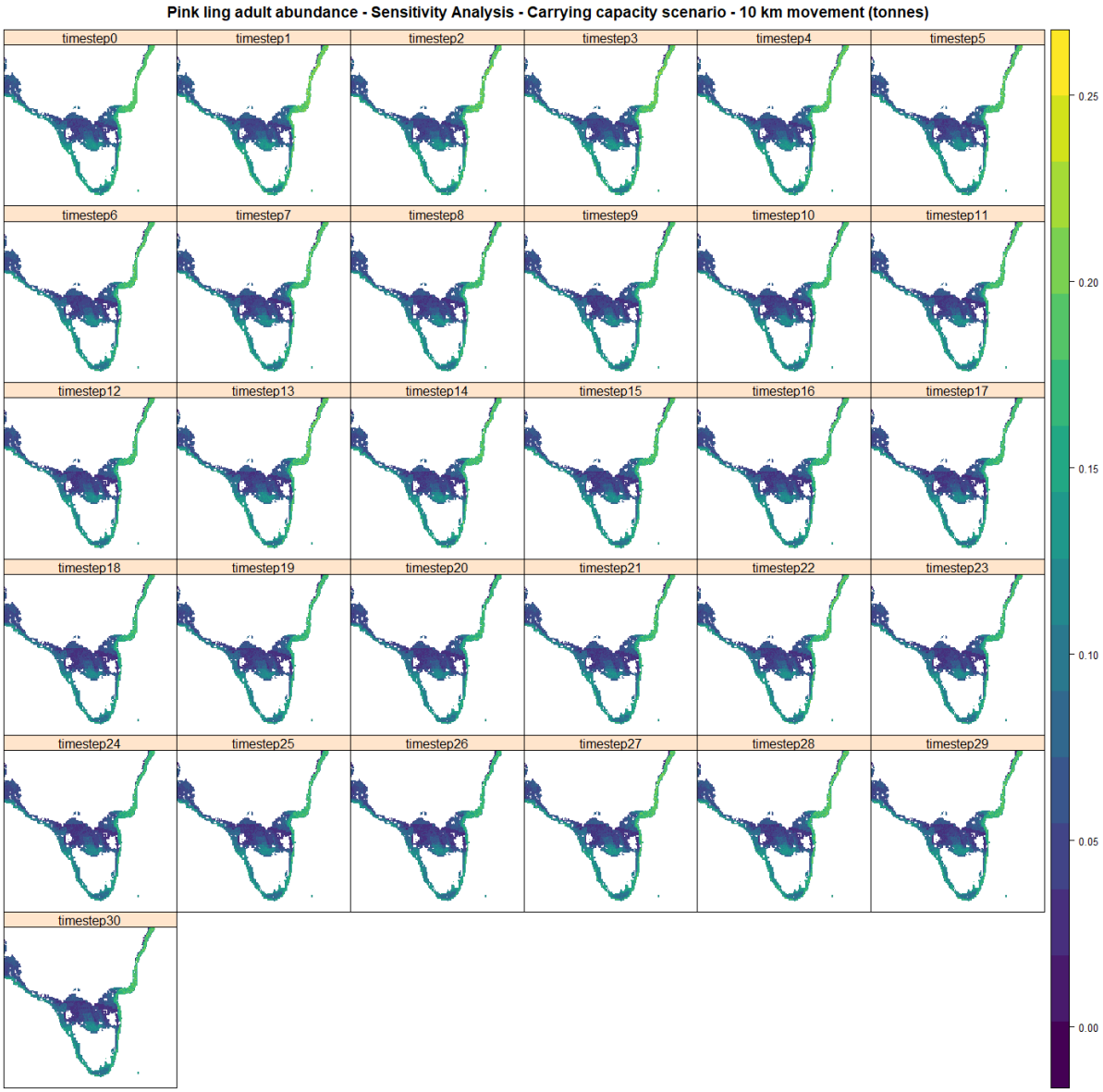

Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.24

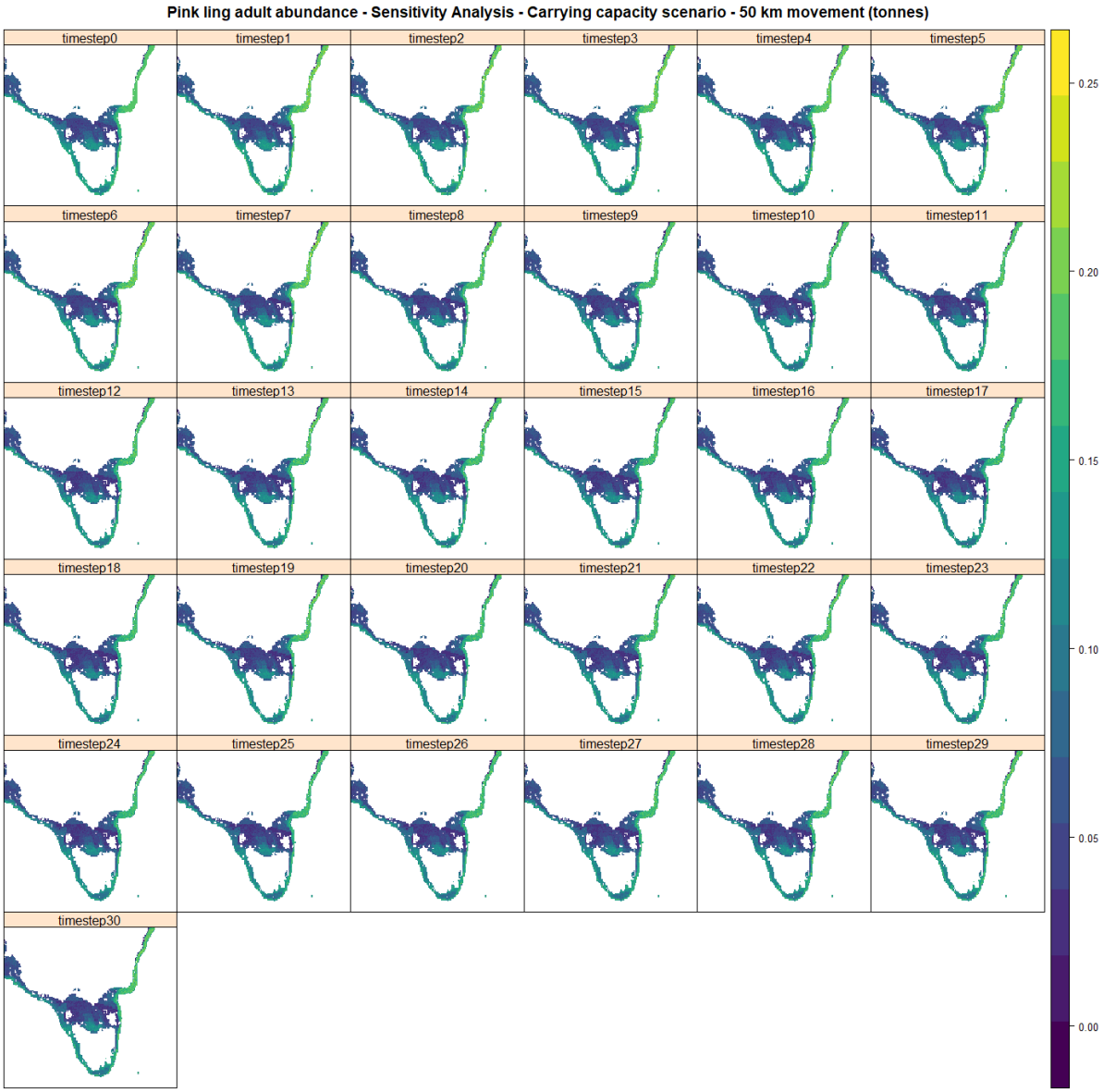

Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.25

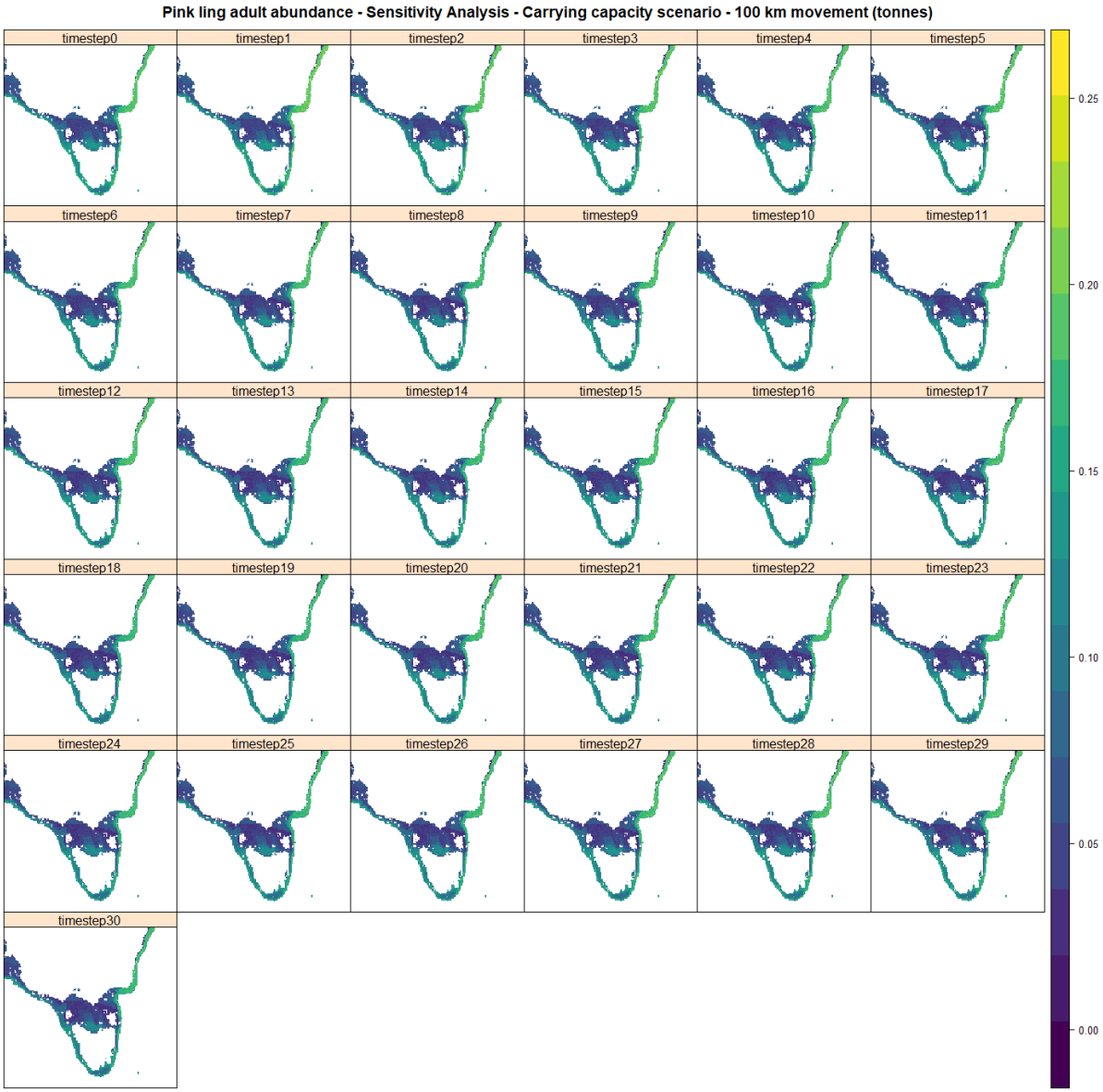

Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.26

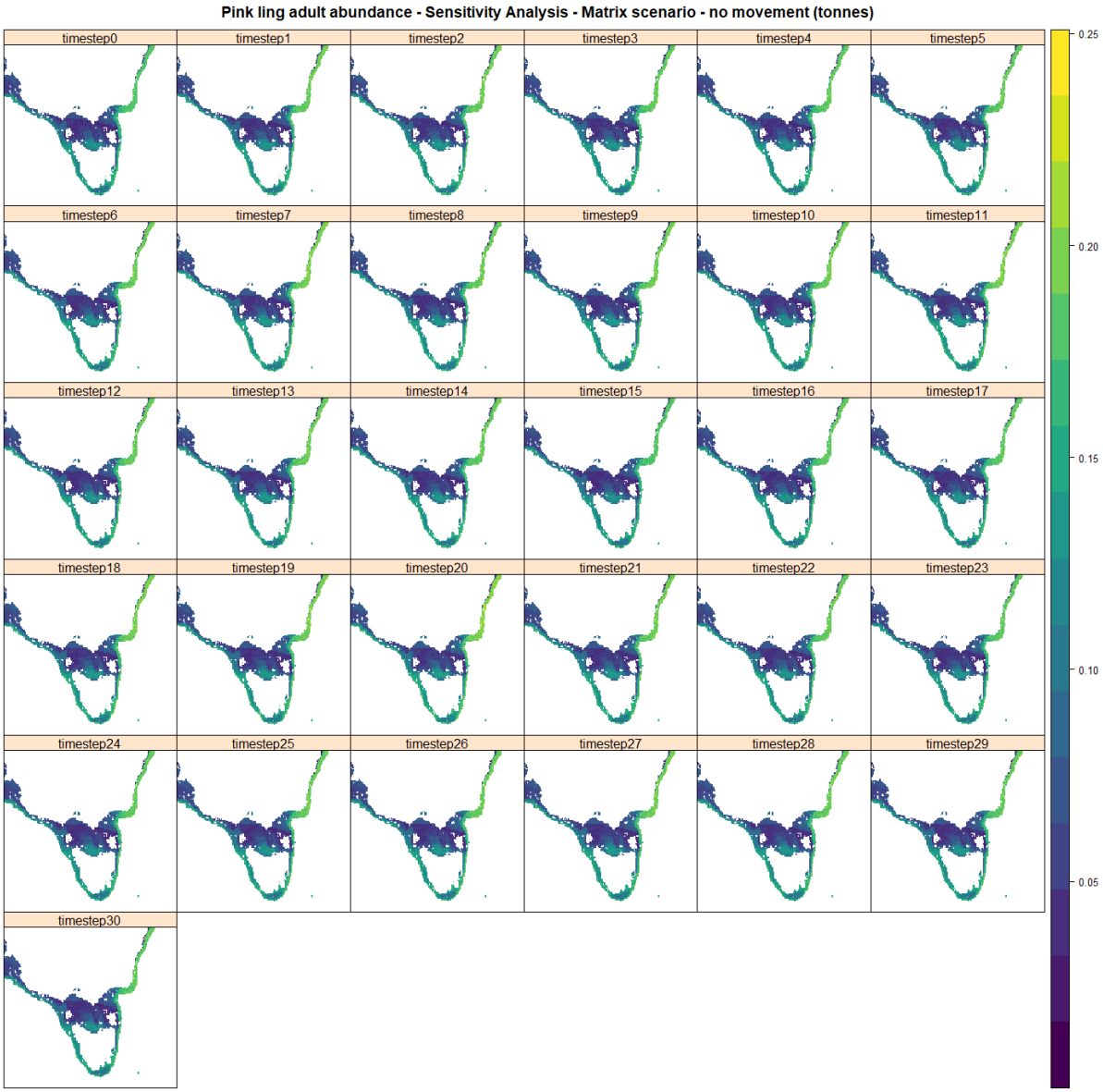

Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - no movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05

Figure A5.27

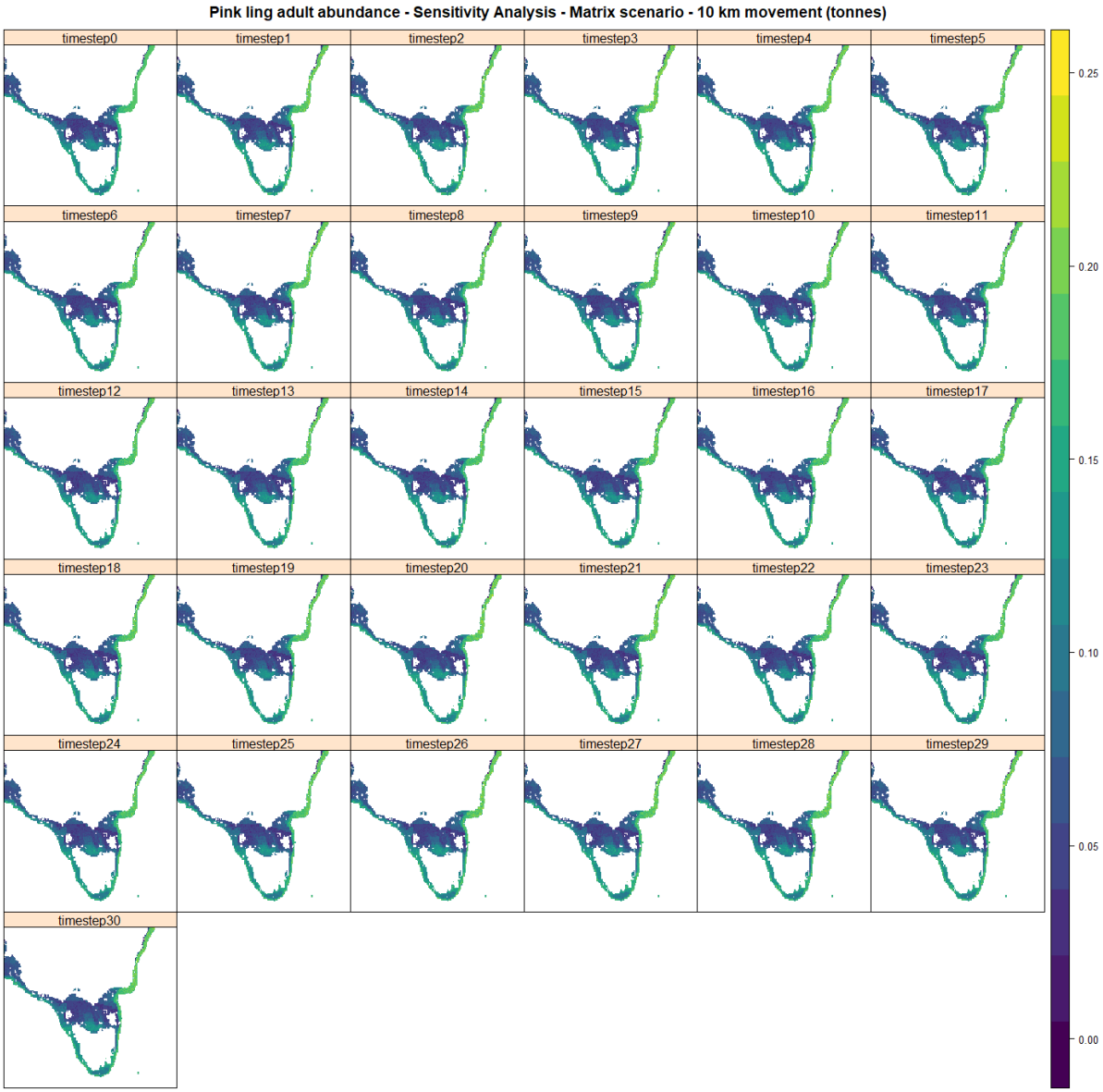
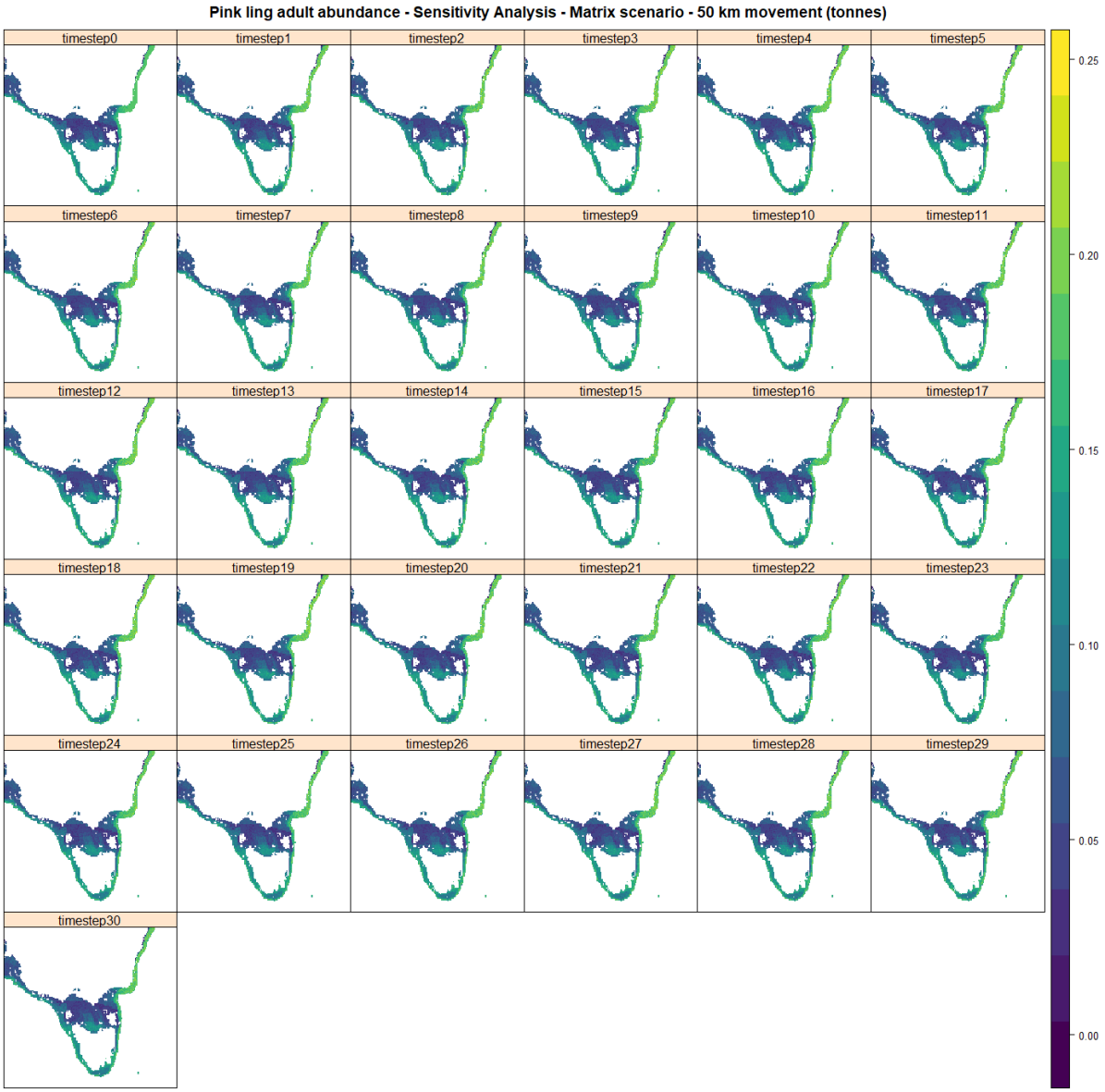

Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.28


Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
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timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.29

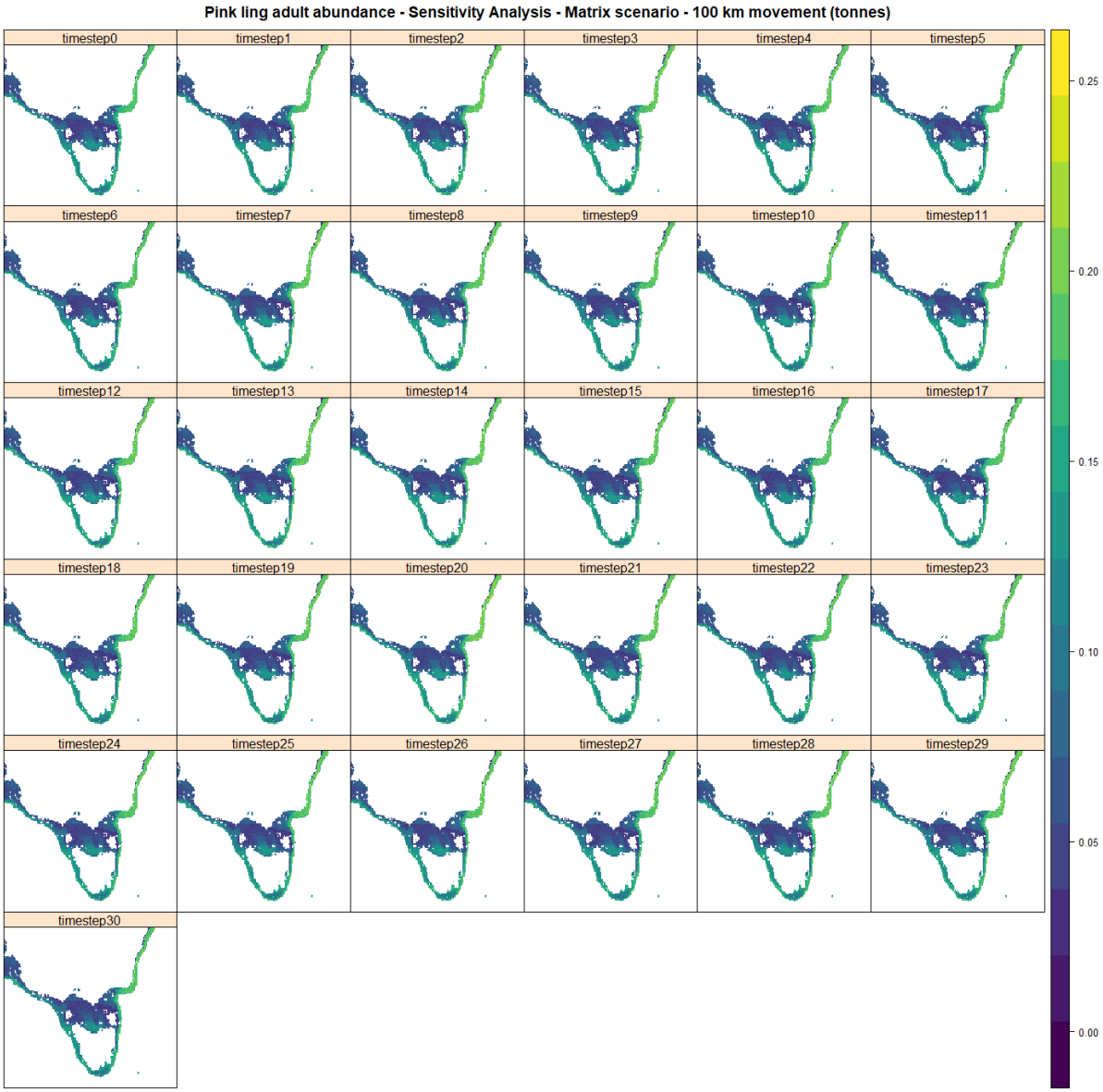
Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.30

Habitat suitability, Carrying capacity and Matrix scenarios for sensitivity analysis (-10%) - maps of pink ling abundance for all timesteps for eastern and western stock (Habitat suitability Fig. A5.31; A5.32; A5.33; A5.34 – Carrying capacity Fig. A5.35; A5.36; A5.37; A5.38 – Matrix Fig. A5.39; A5.40; A5.41; A5.42).

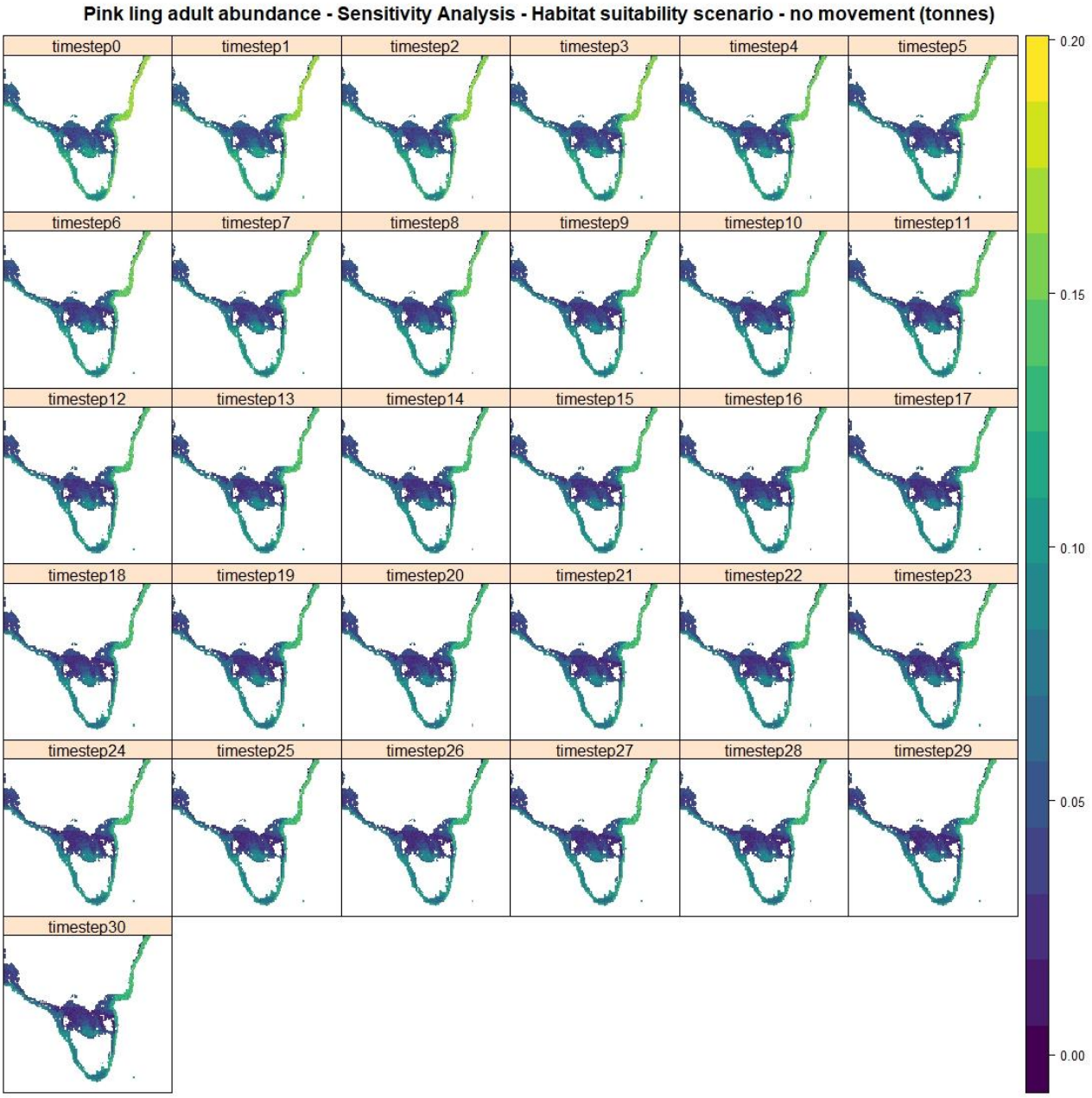

Figure A5.31

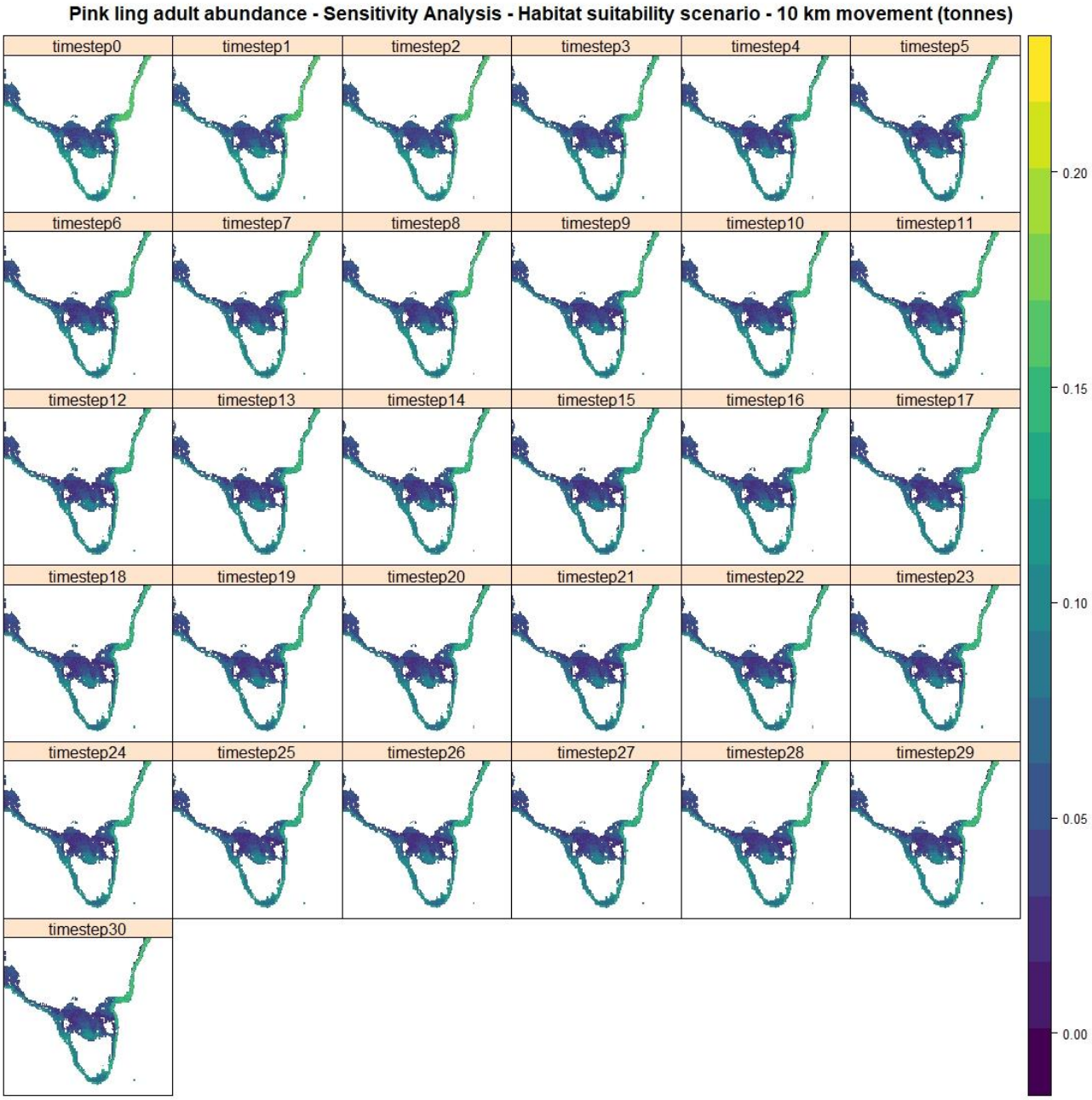
Pink ling adult abundance - Sensitivity Analysis - Habitat suitability scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.32

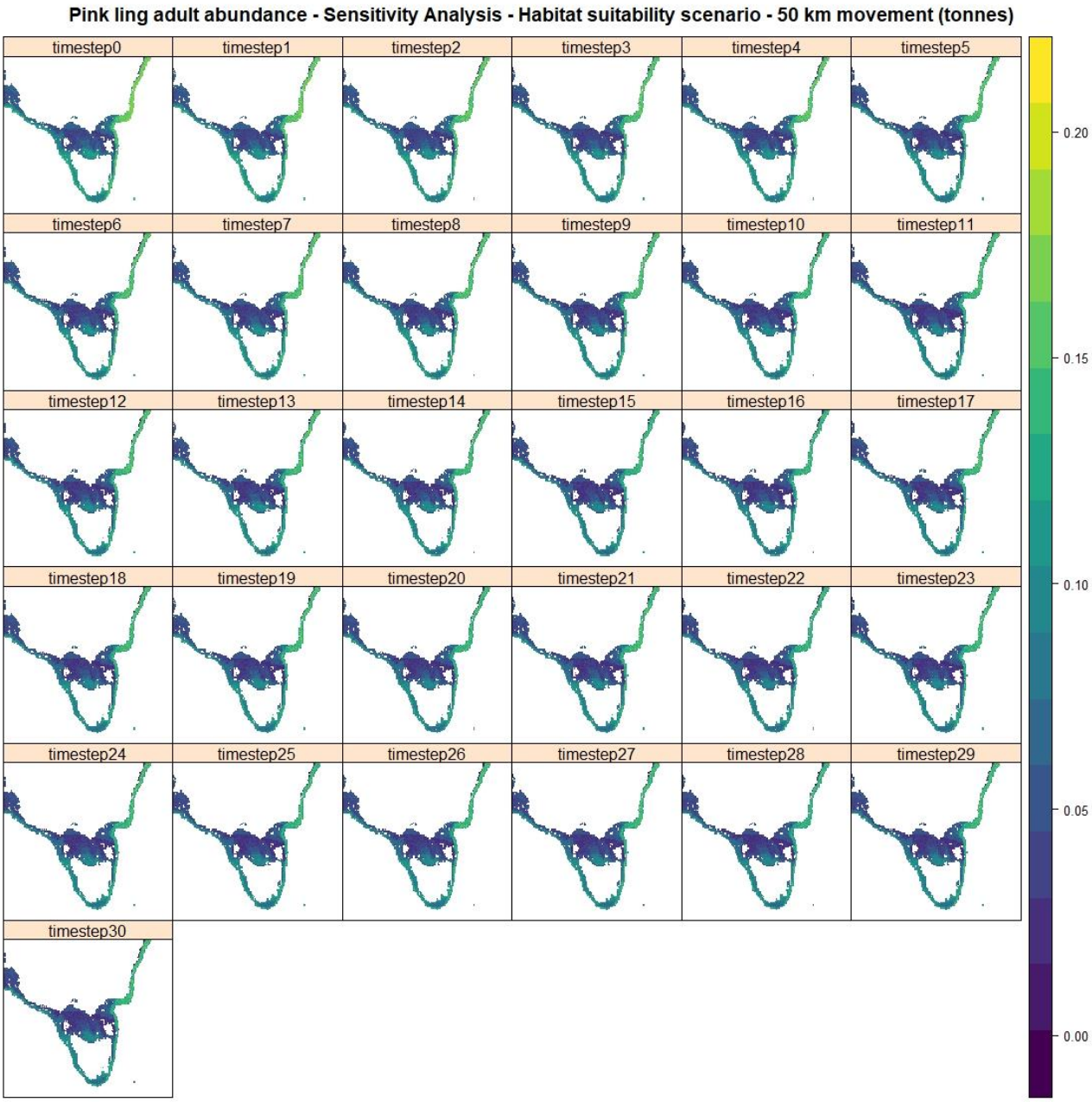
Pink ling adult abundance - Sensitivity Analysis - Habitat suitability scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.33

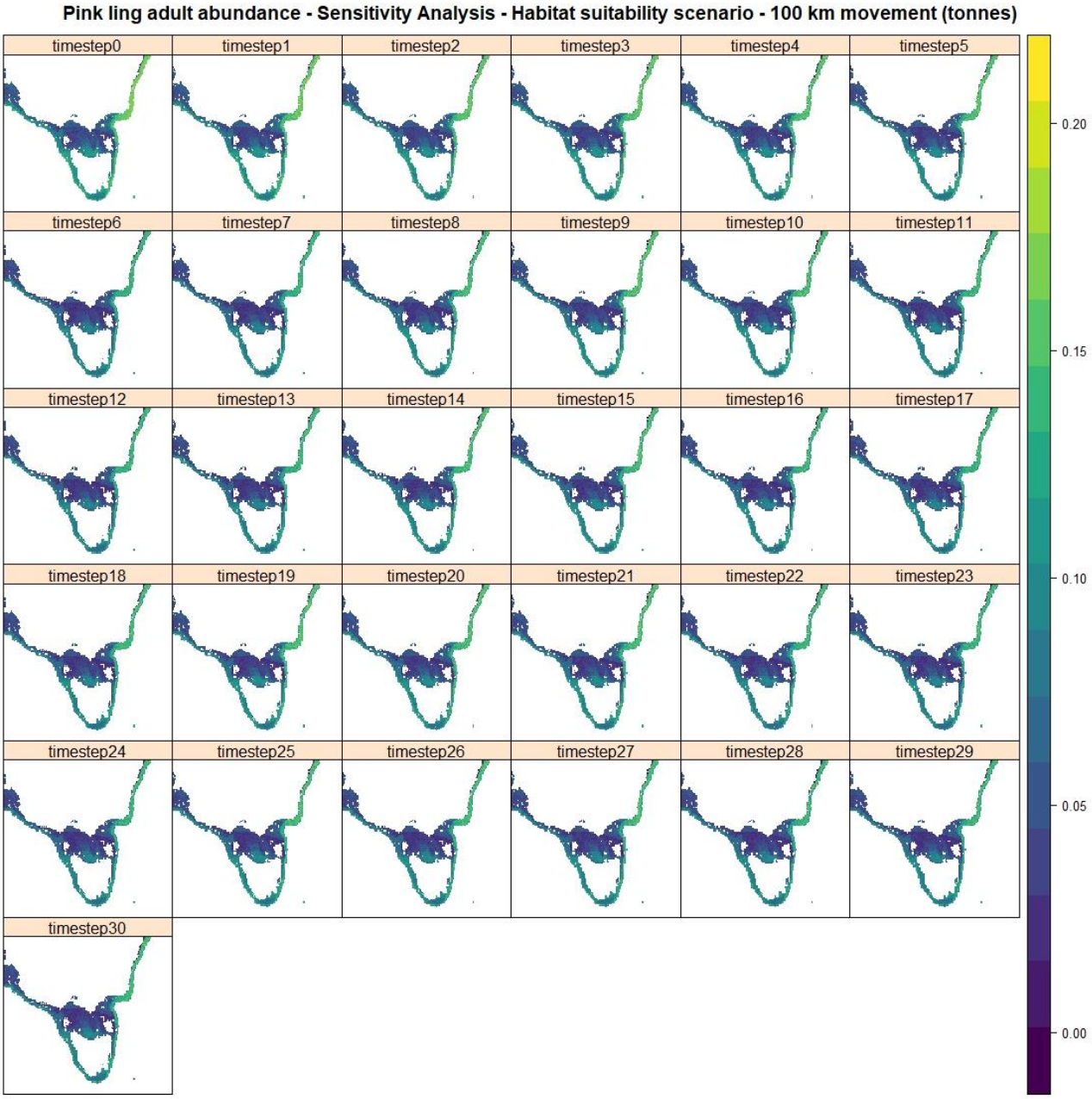
Pink ling adult abundance - Sensitivity Analysis - Habitat suitability scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.34


Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - no movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.35

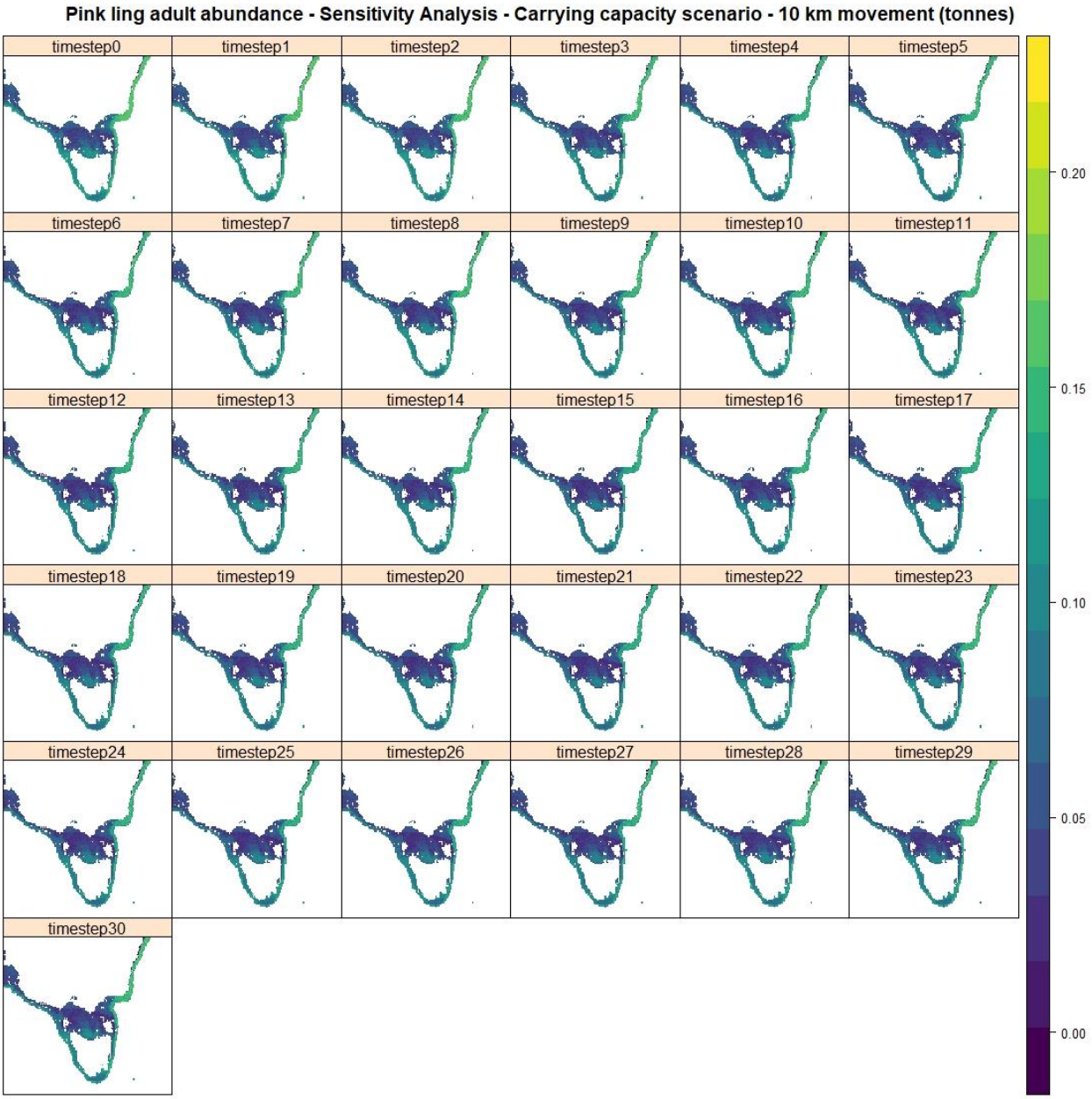
Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.36

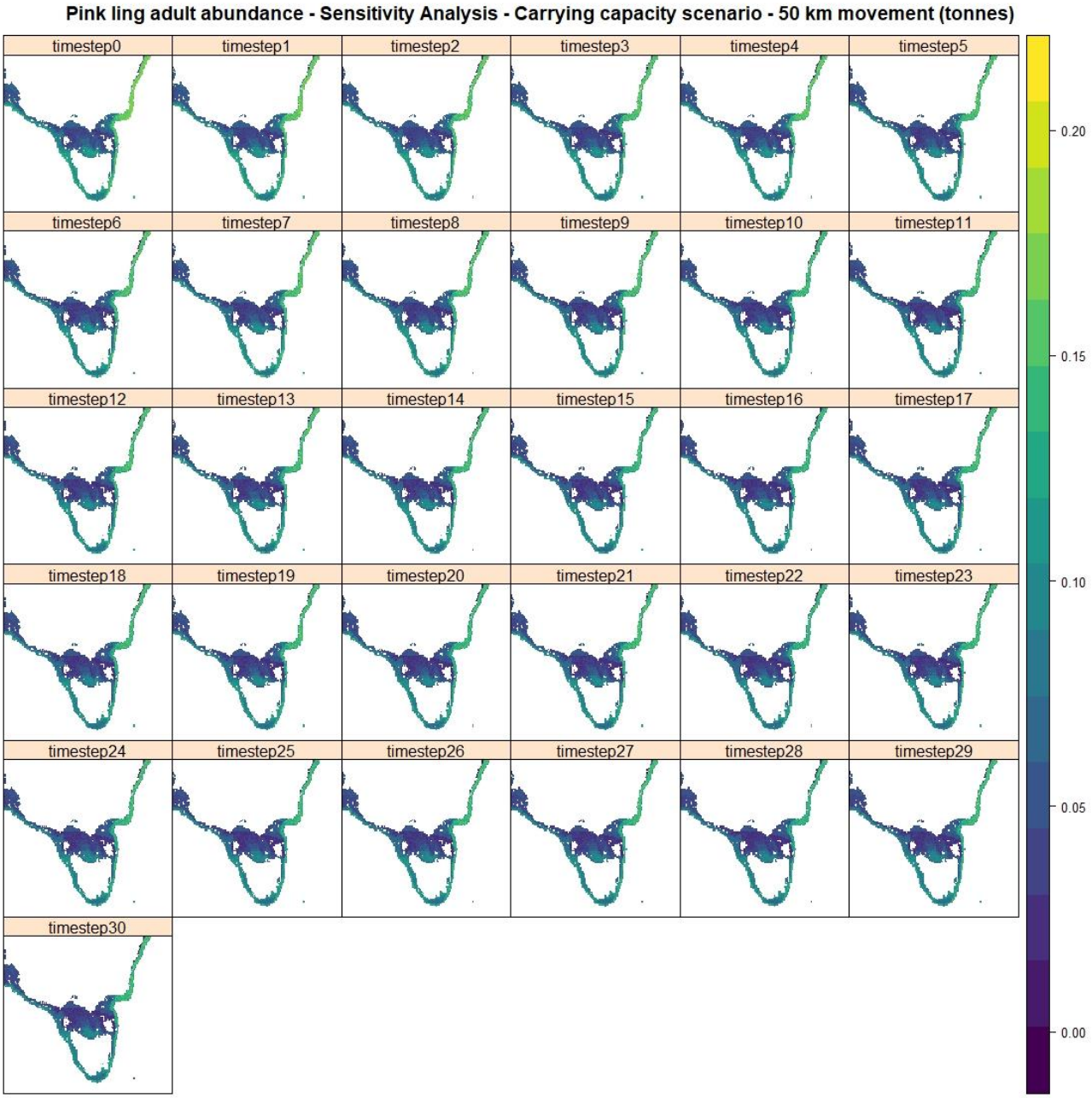
Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.37

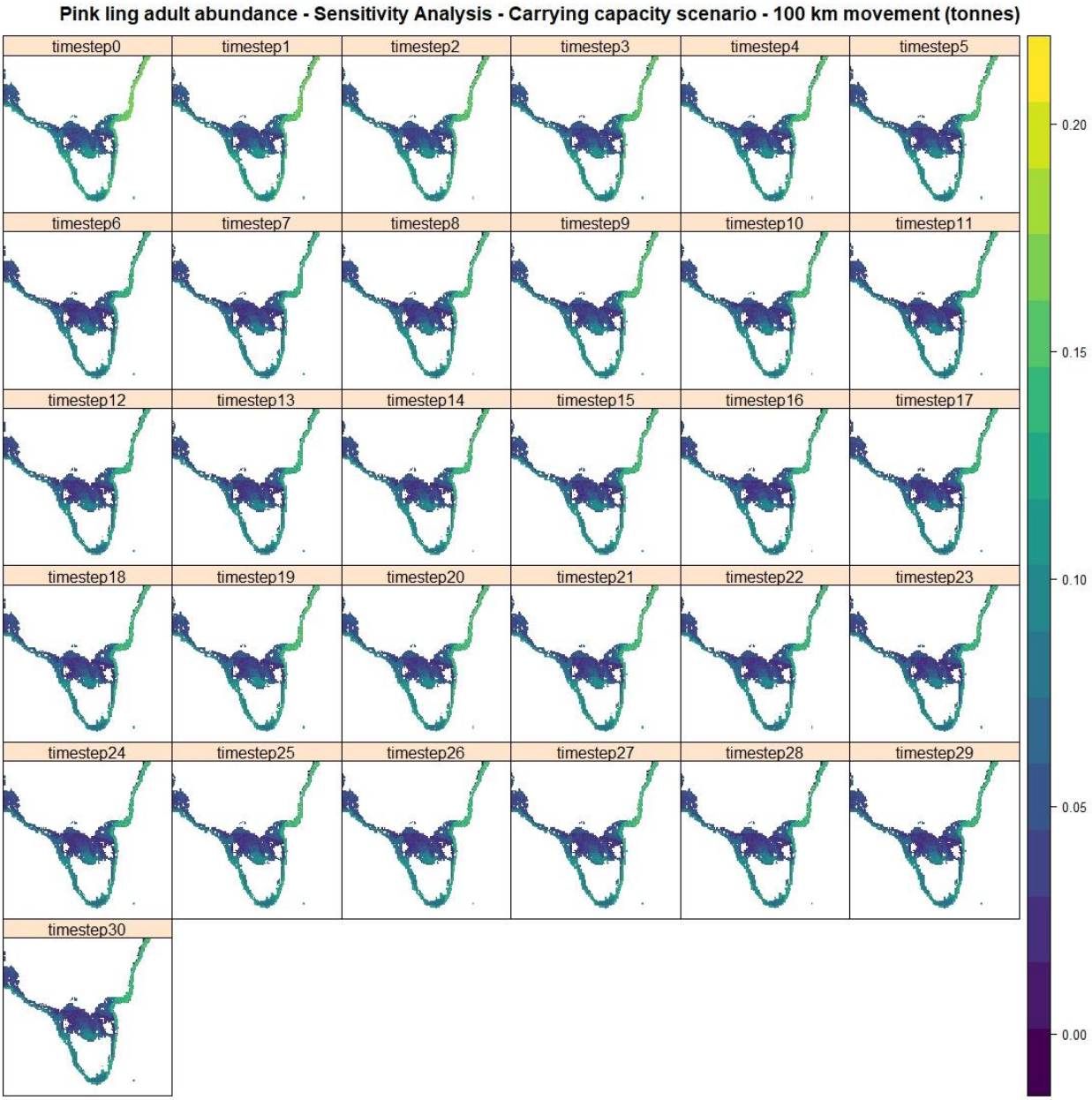
Pink ling adult abundance - Sensitivity Analysis - Carrying capacity scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.20
0.15
0.10
0.05
0.00

Figure A5.38

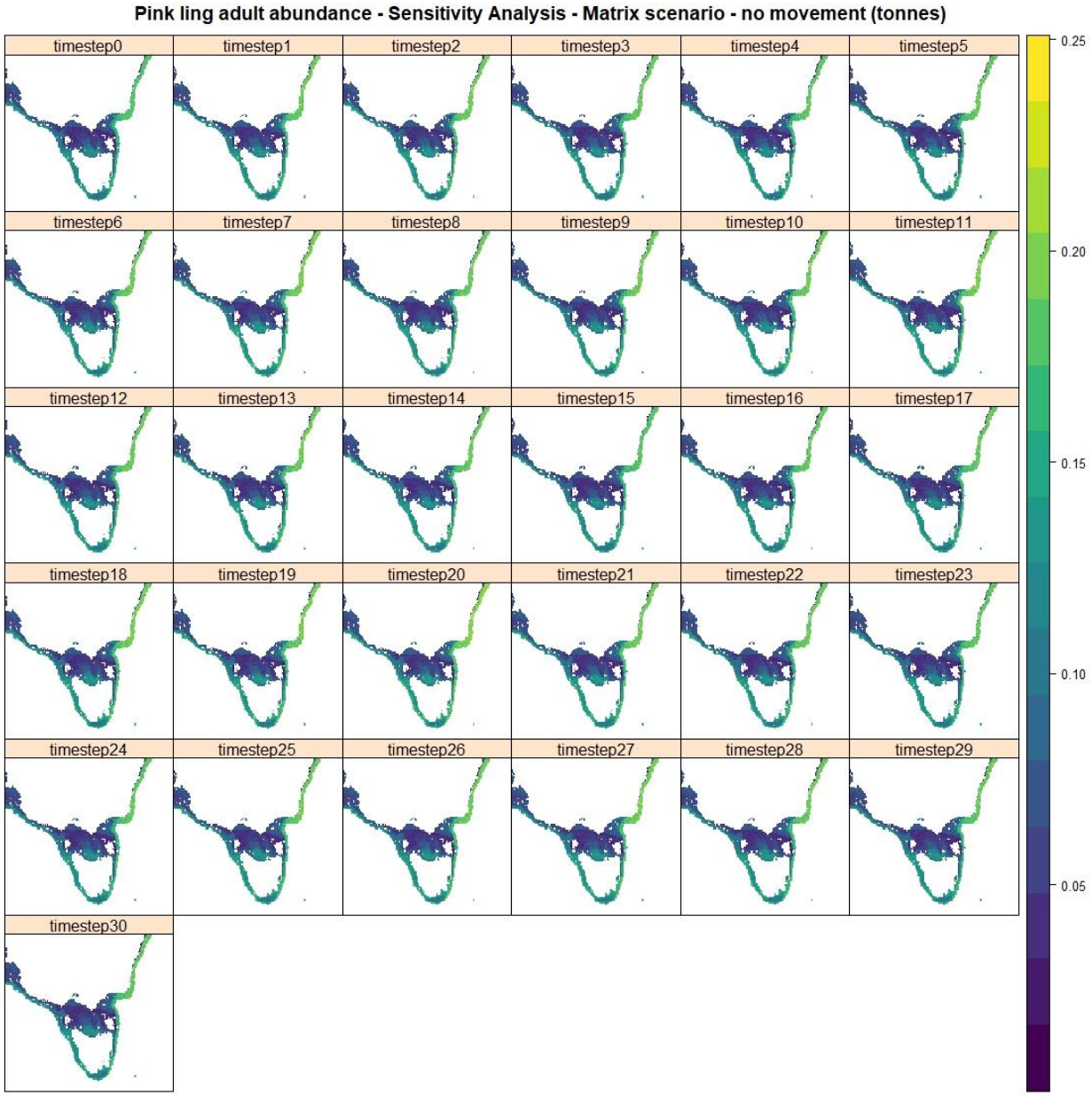
Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - no movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05

Figure A5.39


Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - 10 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
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timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.40

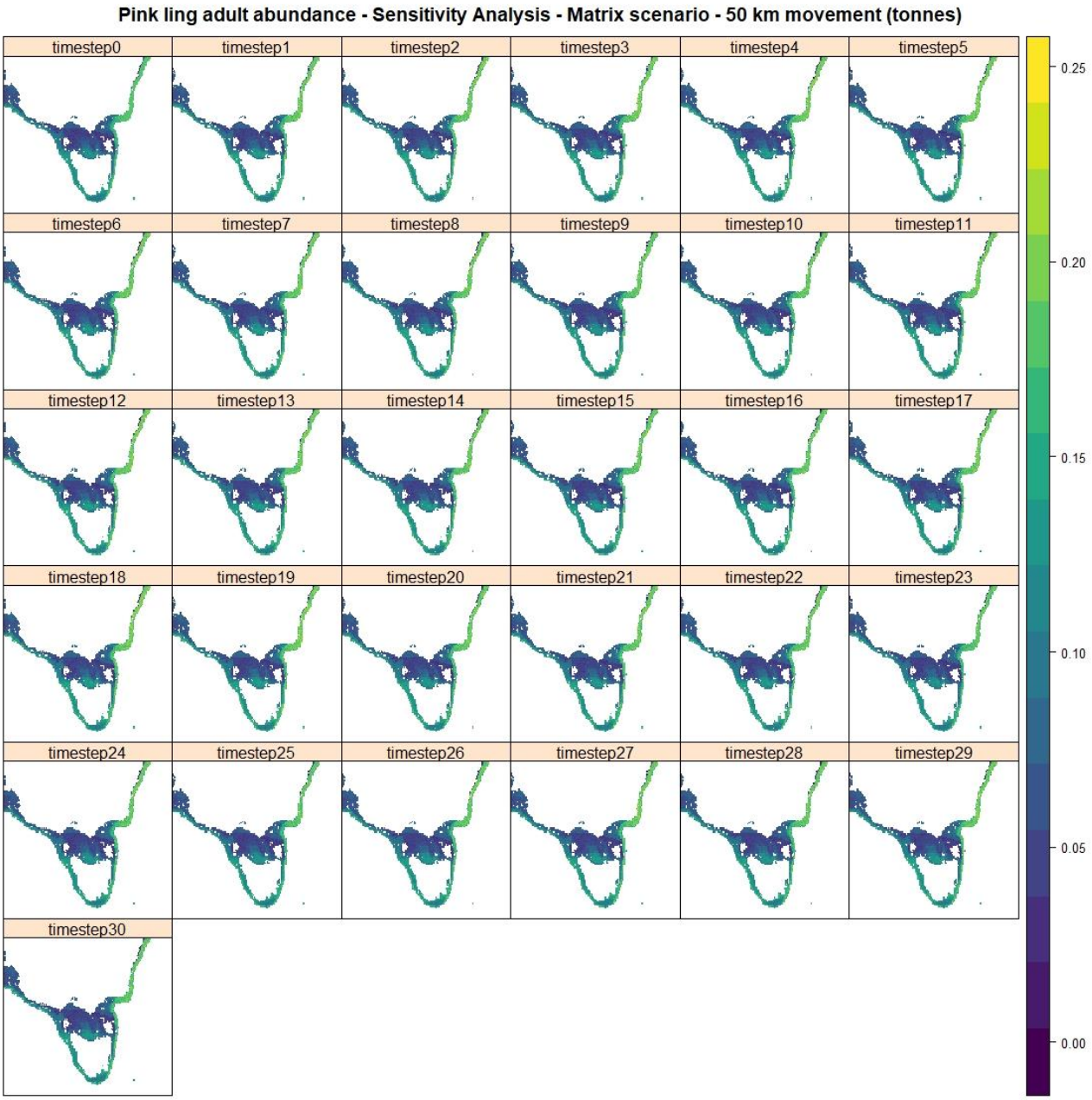
Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - 50 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.41


Pink ling adult abundance - Sensitivity Analysis - Matrix scenario - 100 km movement (tonnes)
timestep0
timestep1
timestep2
timestep3
timestep4
timestep5
timestep6
timestep7
timestep8
timestep9
timestep10
timestep11
timestep12
timestep13
timestep14
timestep15
timestep16
timestep17
timestep18
timestep19
timestep20
timestep21
timestep22
timestep23
timestep24
timestep25
timestep26
timestep27
timestep28
timestep29
timestep30
0.25
0.20
0.15
0.10
0.05
0.00

Figure A5.42