

**Prediction, characterisation
and detection
of**

regime

shifts

**in
ecological systems**

by Delphi Ward



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PREDICTION, CHARACTERISATION, AND DETECTION OF REGIME SHIFTS IN ECOLOGICAL SYSTEMS

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ABSTRACT

Regime shifts are persistent changes in ecosystem structure and function that can result in loss of ecosystem services upon which people depend. Thus, there is a clear need for methods capable of assessing ecosystems for vulnerability to, and occurrence of, regime shifts. Methods available for predicting and detecting ecological regime shifts generally require extensive data and understanding of ecosystem processes. However, for many ecosystems data availability is patchy, limiting the application of available methods to assess for regime shifts. This thesis uses qualitative and quantitative methods to improve capability for assessing ecosystems for vulnerability to regime shifts, predicting the nature of future regime shifts, and detecting regime shifts after they have occurred.

I first undertake a review of the prediction, characterisation, and detection of regime shifts and in doing so, develop a framework for assessing ecosystems for regime shifts. This framework outlines ecosystem attributes that are linked to stability (and loss of stability), and describes methods that ecosystem practitioners can use to assess and incorporate understanding of these attributes for improved ecosystem management. The framework also explores a broader set of questions that ecosystem practitioners may want to answer about the nature and timing of regime shifts. A key question in this context relates to the consequences of not acting – i.e. the likely future state of a given system – and how urgently action must be taken – i.e. how imminent a regime shift is, or when it is likely to occur. Suggested approaches for answering each question are provided by the framework. Finally, in this chapter I provide an overview of methods available for ascertaining whether a regime shift has occurred. Southern Ocean ecosystems are used as a case study to illustrate how this framework can help identify current capacity to assess for regime shifts, and to guide future targeted data collection where gaps in capacity exist.

A key finding from the review is that ecosystems prone to regime shifts are often characterised by the presence of destabilising positive feedbacks. However, identifying positive feedbacks is particularly challenging for pelagic or remote ecosystems, because such feedbacks often involve non-trophic interactions which are difficult to observe (and quantify). An interesting case study is the presence of potentially important positive feedbacks in Southern Ocean ecosystems, which involve the release of a chemical cue (dimethyl sulfide) by phyto-

plankton that attracts the predators of the phytoplankton-grazers. A qualitative modelling approach is applied to explore the potential importance of this feedback in driving regime shifts in the Southern Ocean, and to identify key interactions determining the stability of the community. Thus, in this chapter I provide the first demonstration of the use of qualitative models with simulation to assess the importance of positive feedbacks for ecosystem stability, an approach that could usefully be applied to other systems.

This thesis also improves capability for detecting regime shifts once they have occurred, and to distinguish regime shifts from an ecological fluctuation without a regime shift. In some ecosystems it is not always evident that a regime shift has occurred, and data constraints prevent the application of existing methods for detecting regime shifts. This thesis develops a new approach for detecting regime shifts from transect (1-dimensional spatial) data. This method (1D Characteristic Length Scale estimation) involves reconstruction of the system attractor and nearest neighbour prediction to identify the emergent spatial scale of the system, with a shift in this scale indicating regime shift. The method is tested successfully on model systems and then applied to a coral reef data set, which shows evidence of past regime shifts. This methodological advance broadens the range of ecosystems which can be tested for evidence of regime shifts, and removes some ambiguity in characterising the nature of community change.

The final element of the thesis is a discussion of the management of ecological regime shifts in the context of global tipping points in climate and human systems, and some thoughts on how this thesis might help progress the study and management of regime shifts.

Together the tools provided in this thesis help deepen our understanding of regime shifts, direct future research, and assist ecosystem managers adapt to a future in which these complex changes occur more frequently.

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Statement of co-author contributions

The following people contributed to the publication of the work undertaken as part of this thesis: Chapter 4 (Detecting ecological regime shifts from transect data):

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Contents

List of Tables	v
List of Figures	viii
1 Context of the thesis	1
1.1 How do regime shifts happen? Why are they challenging? Understanding from case studies of ecological regime shifts	2
1.2 Southern Ocean ecosystems as the muse for the thesis	5
1.2.1 Southern Ocean ecosystems are important and interesting	5
1.2.2 Ecosystem structure	6
1.2.3 Challenges for assessing Southern Ocean ecosystems and hints of regime shifts	8
1.3 Outline of the thesis	9
2 Is my ecosystem a shifter? A framework for predicting, characterising and detecting ecological regime shifts	13
2.1 Introduction	13
2.2 Ecosystem properties implicated in regime shifts	15
2.2.1 The importance of ecosystem network features for stability	19
2.2.2 Dynamic and spatial features of ecosystems that affect regime shift vulnerability	21
2.2.3 Assessing regime shift risk in practice	24
2.3 Prediction of regime shifts	26
2.3.1 Some specific questions and approaches to predict them	26

2.3.2	Considerations emerging from the findings of Section 2.3.1	36
2.4	Detection of regime shifts	38
2.5	Southern Ocean case study	40
2.5.1	Vulnerability	41
2.5.2	Predicting regime shifts for Southern Ocean ecosystems	42
2.5.3	Detection of past regime shifts in Southern Ocean ecosystems	46
2.5.4	Summary for Southern Ocean ecosystems	47
2.6	Conclusion	48
3	Trophic mediation and ecosystem stability: an assessment using qualitative network models	50
3.1	Abstract	50
3.2	Introduction	50
3.3	Methods	53
3.3.1	Qualitative network modelling	53
3.3.2	Alternative model structures	53
3.3.3	Stability analysis with QPress	57
3.3.4	Edge importance	58
3.3.5	Stability analysis and feedback identification with symbolic loop analysis	59
3.3.6	Southern Ocean models	60
3.4	Results	62
3.4.1	Stability of simulated matrices	62
3.4.2	Edge importance for stability	63
3.4.3	Symbolic analysis of stability and feedbacks	63
3.4.4	Larger Southern Ocean models	66
3.5	Discussion	67
3.5.1	Network stability patterns	67
3.5.2	Comparison with quantitative models	68
3.5.3	Interactions and feedbacks important for stability	69

3.5.4	Incorporating DMS-mediated interactions into Southern Ocean networks	71
4	Detecting ecological regime shifts from transect data	74
4.1	Abstract	75
4.2	Introduction	75
4.3	Methods	79
4.3.1	CLS estimation process	79
4.3.2	Detection of regime shifts	83
4.3.3	Model test systems	84
4.3.4	Real world test case	87
4.3.5	Analyses	88
4.4	Results	88
4.4.1	Model test cases	88
4.4.2	Coral reefs	93
4.5	Discussion	100
4.5.1	Model test systems	100
4.5.2	Coral reefs	102
4.5.3	Application of the 1D-CLS method	104
4.5.4	Conclusion	105
5	Managing ecological regime shifts in the context of global tipping points	107
5.1	Specific recommendations for Southern Ocean ecosystems	108
5.2	Regime shifts and stability	109
5.3	The importance of multifunctional organisms	111
5.3.1	<i>Phaeocystis antarctica</i> : a Southern Ocean example	111
5.3.2	Humans as multifunctional players in ecosystems	112
5.4	System scope	113
5.5	Managing ecological regime shifts in the context of global tipping points . . .	114
5.5.1	Some next steps towards management of ecological regime shifts . . .	116

Glossary	120
A Supplementary material to Chapter 2	124
B Supplementary material to Chapter 3	126
C Supplementary material to Chapter 4	132
D ‘CLS1D’ <i>R</i> package documentation	139
E Application of the 1D-CLS method to a Southern Ocean dataset	152
List of References	155

List of Tables

1.1	Summary of chapter aims, approaches and case study ecosystems used in this thesis.	12
2.1	Ecosystem network features associated with stability. System stability may change when disturbance alters the balance of these features within an ecosystem, thus making the ecosystem vulnerable to regime shifts. Southern Ocean ecosystem examples are given here, but see the main text (Section 2.5) for a more general description of Southern Ocean ecosystems, important species, and discussion of vulnerability to regime shifts. Numbers refer to references given in the footnote of the table.	16
2.2	Dynamic/spatial features of ecosystems that affect vulnerability to and dynamics of regime shifts. Southern Ocean ecosystems are used as an example to illustrate how these features can be explored for a real ecosystem, but see main text (Section 2.5) for more general introduction of Southern Ocean ecosystems and important species. Numbers refer to references given in the footnote of the table.	22
2.3	Methods and approaches available for predicting aspects of ecological regime shifts. Methods numbers (MX) are those referred to in the main text Section 2.3.1. Questions the method could be useful for addressing are given in the final column, and refer to the question numbers in Section 2.3.1 (parentheses around question numbers indicate those that may be addressed with the method, but to which the method is less generally suited).	31

3.1	Symbolic loop analysis results for models not including nutrient feedbacks (results for models including nutrient feedbacks are provided in Appendix B Table B.2). Reported for each model is the connectance (C), class (based on Hurwitz criteria for Lyapunov stability; weighted feedback at highest level wFn, weighted determinant wDn, and ratio of the weighted determinant to a control model C, as per Dambacher et al. 2003), net sign of feedbacks (at highest level), total number of feedbacks with total positive feedbacks in parentheses. The unique positive feedback sequences at each level of feedback are listed, with the total number of times each sequence is repeated in higher positive feedback cycles in the model stated in parentheses.	65
3.2	Results of qualitative analysis of the larger Southern Ocean models. Refer to the main text for detailed description of the models. In brief, SOM1 is a trophic model, SOM2 includes DMS-mediated interactions involving organisms with recognised DMS attraction, and SOM3 includes hypothetical DMS attraction by baleen whales as well as their contribution to the nutrient pool via defecation. Colours as per Fig. 5: orange edges are those that tend to be weak, and blue edges strong in unstable matrices. Abbreviations: Baleen = baleen whales; DMS = dimethyl sulfide; N = nutrients; SBkf = krill-feeding seals & birds; TP = top predators. Class is based on Hurwitz criteria for Lyapunov stability and wF ₁₂ is the weighted feedback at highest level (as per Dambacher et al. 2003).	66
4.1	Summary of all the analyses performed on each system and the species analysed.	85
4.2	Blue Bowl reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).	94
4.3	Coral Gardens reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).	96
4.4	Sampela1 reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).	98
4.5	Hoga Buoy2 reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).	98

5.1	Synthesis of advances and suggested future work. (Ticks and bullet points coloured orange for contributions to the general field of ecological regime shifts, while blue refers specifically to the Southern Ocean)	119
B.1	Comparison of results of selected model simulations in QPress between models with a grazer \rightarrow predator edge, and the same models without. Removing the gr \rightarrow pr edge reduced the stability of the models, but for most models it resulted in only slight differences in the relative importance of the edges for distinguishing between stable and unstable community matrices.	126
B.2	Symbolic loop analysis results for models including nutrient feedbacks. Reported for each model is the connectance (C), class (based on Hurwitz criteria for Lyapunov stability; weighted feedback at highest level wF_n , weighted determinant wD_n , and ratio of the weighted determinant to a control model C, as per Dambacher et al. 2003), net sign (at highest level) of feedbacks, total number of feedbacks and the total number of positive feedbacks in parentheses. The positive feedback sequences at each level of feedback are listed, with the total number of times each sequence appears in different positive feedback cycles in the model stated in parentheses.	128
B.3	Comparison of results of selected model simulations in QPress when excluding constraints and validators (see also Fig. B.3). Note that use of constraints varies in the models due to differences in mediated interactions, and that Model 1n did not contain constraints because DMS did not mediate any interactions in that model.	129

List of Figures

1.1	‘Cusp’ diagram illustrating the theoretical continuity between continuous and discontinuous regime shifts. a) Ecosystems can change linearly with changes in driving conditions; b) they can change abruptly at a certain level of the driving conditions; or c) there can be hysteresis where the forward and reverse transitions occur at different levels of the driving conditions, with overlap in the range of conditions at which the two regimes can persist. This latter relationship is also called a critical transition. Figure redrawn based on Collie et al. (2004), Petraitis (2013), and van de Leemput et al. (2016).	3
1.2	Global importance of Southern Ocean ecosystems. Thanks to McCormack et al. 2019a for sharing this figure.	6
2.1	Framework for assessing the likelihood, nature and detectability of regime shifts in ecosystems, presented to help the reader conceptualise and integrate the different elements of this review. The data available from the ecosystem will determine if and how, and to what degree regime shifts can be predicted or detected - this is represented here by the ‘data filter’. The network feature diagrams link to Table 2.1 and symbolise (in order) distribution of interaction types (over the network), distribution of interaction strengths, lack of functional redundancy, higher-order interactions, sign and arrangement of feedbacks, network complexity, and importance of ecosystem engineers in the network. Spatial and dynamic feature diagrams link to Table 2.2 and symbolise spatial connectivity, heterogeneity and homogeneity, evolutionary history and life-history traits, self-organised spatial patterns, and step-changes in drivers or disturbance regimes.	14

- 3.1 Alternative model configurations examined. Abbreviations are: DMS = dimethyl sulfide; DP = DMS-producing phytoplankton; GR = grazers; PR = predators; OP = other (not DMS-producing) phytoplankton. See the text for explanations of the different model structures. Arrows signify positive effects and circles negative effects. Dashed edges represent those that mediate another edge, while solid edges are direct effects. Listed below each model are the pairwise effects resulting from the mediated edges. Additionally, below Models 8 & 9 are indicated the edges that are constrained (in addition to the constraints on DMS mediated edges and attraction). Grey edges represent nutrient addition from predators to phytoplankton, and are only present in the nutrient versions of the models. 55
- 3.2 Stability analysis in QPress. Diagram illustrating the process for building alternative realisations of network configuration. Stable realisations of the community matrix are those for which the real roots of the characteristic equation are negative. Classification to identify edges which differ in strength in stable versus unstable matrices is carried out with machine learning algorithms, such as random forest as used here. Adapted from Melbourne-Thomas et al. (2012). 58
- 3.3 Simple Southern Ocean trophic network model used as a basis for exploring implications of DMS-mediated interactions and feedbacks. SOM1 includes trophic edges plus release of DMS shown in green; SOM2 additionally includes blue edges and SOM3 additionally includes orange edges. Solid edges indicate direct effects and dashed edges mediation of other edges. Black dotted edges indicate uncertain trophic links (included in 50% of simulations). Arrows signify positive effects and circles negative effects. All nodes have negative self-effects (not shown in diagram). Thanks to Rowan Trebilco for assistance with this figure. 60
- 3.4 Percentage of simulated community matrices (of 10,000) that were stable for each model. Dark blue-green bars correspond to models including predator contribution to a nutrient pool (via faeces), realised as a positive effect from predators to phytoplankton (grey edges in Fig. 3.1); light green bars correspond to models without that edge. Group 1 models are predator-prey models, Group 2 are the same but include an additional phytoplankton node and competition between the two phytoplankton nodes, and Group 3 represent prey-switching (by grazers) in different ways. 62

3.5	The importance of edges in distinguishing between stable and unstable matrices is consistent across model structures. Here each column represents one model structure and each row an edge. Random forests were used to rank the importance of each edge in classifying stable and unstable matrices. The most influential edges are denoted with a coloured square. Edges that tended to be weak (values closer to 0) when the simulated community matrices were unstable are shown in orange. Edges that tended to be strong (values closer to 1 or -1) when the simulated community matrices were unstable are shown in blue. Shading indicates relative importance of the edges for stability within that model (where shading value 1 - strongest colour - indicates the most important edge in that model, and shading value 0.3 indicates an edge whose importance is 30% that of the most important edge in that model, based on the relative decrease in accuracy from the random forest). Boxes with grey crosses indicate interactions not represented in that model. The bottom rows show the proportion of simulations that were stable for each model and the class error rates for that random forest model. Phytoplankton and DMS limitation, and phytoplankton competition were particularly important in determining stability across all models. Abbreviations: DMS, Dimethyl sulfide; DP, DMS-producing phytoplankton; OP, other phytoplankton; GR, grazers; PR, predators.	64
4.1	Schematic representation of attractor reconstruction from time series data. The top panel shows how time series of three interacting “species” relate to the ecosystem attractor, using the Lorenz attractor as a hypothetical example. The bottom panel shows how a topologically equivalent shadow of the real system attractor can be reconstructed from the time series of a single species, by delay embedding its time series on itself. The Lorenz system typifies a time series that has large swings in state within a single attractor.	78

- 4.2 Flow diagram showing the steps in the characteristic length scale (CLS) estimation method. Panels a–c illustrate the process for the one-dimensional sliding window approach. A similar diagram is provided for the one-dimensional short time-series approach in Appendix C.1. For more detailed descriptions of the techniques, see Kantz and Schreiber (2003). (a) Slide the 1D window of observation along the transect and calculate mean number (density) of the target species in each window (0 = absent, 1 = present). (b) Delay embed the spatial data series so that the trajectory over d_E sequential windows becomes a single point on the reconstructed attractor (shown in panel c). (c) Identify k nearest neighbours of each point in the reconstructed attractor space and predict density X in the subsequent window based on the trajectory of neighbouring points. Here, the blue square represents the three-dimensional point of interest in the attractor space, and the star and circle its nearest neighbours. The orange square is the point being predicted, based on the orange star and circle. The lower plot illustrates how each d_E dimensional point in the reconstructed attractor maps to a d_E trajectory of densities in space, and that nearest neighbours in the attractor space have similar trajectories in space but are not neighbouring in space. (d) The characteristic length scale (CLS) is the window length at which prediction error begins to plateau. 80
- 4.3 Test case 1 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes as indicated by the color bar. For each of three species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. The reduction of the growth rate of Species 5 in regime 2 did not result in a change in the CLS in this test case. 89
- 4.4 Further Test case 1 spectra obtained from one-dimensional “transect” data. Sliding window (SW) *Prediction r^2* spectra for (a) regime 1 and (d) regime 2; short time series (STS) *Error X* spectra for (b) regime 1 and (e) regime 2 and short time-series *Prediction r^2* spectra for (c) regime 1 and (f) regime 2. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. Colors as per Fig. 4.3. 90

- 4.5 Test case 2 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes, as indicated by the color bar. For each species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. In this test case, the CLS increased from 15 to 20 pixels in the first regime, to 20–25 pixels in the second regime following a change in the interaction between Species 1 and 2. See Appendix C.3 for spectra of Species 3 from regime 2 on a smaller y-axis scale. 91
- 4.6 Test case 3 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes, as indicated by the color bar. For each species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (3 windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. There was no change in the CLS following the cessation of open recruitment in this test case. 92
- 4.7 Test case 4 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes; the invasive species is Sp.21 in black. For each species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. In this test case, there was a decline in CLS from 15 to 20 pixels in regime 1 to 10–15 pixels in regime 2 following the invasion of a new species to the landscape. 94

- 4.8 *Error X* spectra determined from cover of five morphotypes from Blue Bowl reef in 2007, 2010, 2011. Solid lines are a rolling mean (three windows) of the Error X estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each spectra. CLSs indicated by hard corals (left column, foliose coral [CF] in orange, branching coral [CB] in blue) declined markedly from 2007 (top row) to 2010 (middle row). In the right column, spectra from soft coral (SC) is shown in orange, algae (A) in green, and dead coral (DC) (2007), and dead, algae-covered-coral (DCA) (2010 and 2011) are shown in dark blue. 95
- 4.9 *Error X* spectra determined from cover of four morphotypes for each of Coral Gardens (left) and Sampela (right) reef slopes in 2007 (top), 2010 (middle), and 2011 (bottom). Soft coral (SC) spectra are shown in orange, sponges (SP) in green, encrusting coral (CE) in black. Blue lines are branching coral (CB) at Coral Gardens and massive coral (CM) at Sampela. The black boxes indicate the estimated CLS range from each spectra. 97
- 4.10 *Error X* spectra determined from cover of seven morphotypes Hoga Buoy 2 reef slope for 2007 (top row), 2010 (middle), and 2011 (bottom row). Spectra from cover of hard coral morphotypes are presented in the left column: massive (CM, green), branching (CB, blue), and laminar (CL, orange), and other morphotypes (coralline algae [CA, blue], encrusting coral [CE, black], sponges [SP, green], and soft corals [SC, orange]) are presented on the right. The black boxes indicate the CLS range estimated from cover of each morphotype. . . . 99

- 5.1 Illustration of how ecological and social-ecological (and other) systems could be managed to avoid tipping points, using the cusp diagram as a theoretical example (top panel). In the cusp diagram (top panel) the z-axis represents internal system structure or ecological-environmental feedbacks, where greater strength of positive feedbacks can increase the degree of non-linearity in the response of the system to changes in the driving parameters. In the case where hysteresis exists, to retain the system in a ‘safe operating space’ and avoid a change in regime altogether, one approach would be to control the drivers (on the x-axis) to avoid the region of hysteresis (to ensure stochastic events don’t push the system towards the alternative basin of attraction) (lower right panel). Where controlling the drivers is not possible on relevant timescales, then an alternative approach is to change the internal structure and feedbacks (on the z-axis) to steer the system towards a smoother transition pathway and avoid tipping points (lower left panel). In both lower panels, the green area represents the more desirable operating space. 118
- A.1 Flow diagram illustrating the dependence of ecological predictions related to regime shifts on other predictions. The most uncertain predictions (when a regime shift will occur, and what the future state will be) depend on predicting and understanding the ecological mechanisms and drivers. 125
- B.1 Connectance versus the proportion of matrices (from QPress) that are stable for each model. The smaller motif models are indicated with points and the larger Southern Ocean models with triangles. Left = stability results from models as described in main text, with some validators and/or constraints applied; Right = stability results of the same models without any validators or constraints applied in QPress. 127
- B.2 Proportion of the total feedbacks that are positive versus the proportion of matrices (from QPress) that are stable for each model. The smaller motif models are indicated with points and the larger Southern Ocean models with triangles. Left = stability results from models as described in main text, with some validators and/or constraints applied; Right = stability results of the same models without any validators or constraints applied in QPress. 127

B.3	Percentage of simulated community matrices (of 10,000) that were stable for each model, in the absence of any validators or constraints. Dark blue-green bars correspond to models including predator contribution to a nutrient pool (via faeces), realised as a positive effect from predators to phytoplankton (grey edges in Fig. 3.1); light green bars correspond to models without this edge. .	131
C.1	Short time series approach to delay embedding and prediction. a) Transects are collected at four points in time (for $d_E=3$) and the mean species occupancy in each window position (X_P) is tracked through time. b) Each time step represents different dimension in the delay embedding, and the mean occupancy in the final time step is what we want to predict. c) The nearest neighbours in the reconstructed attractor have similar trajectories (of mean species occupancy) through time. Refer to Fig. 4.2 in the main text for the equivalent images for the sliding window method and further description of the method.	133
C.2	Test case 2 Prediction r^2 spectra from sliding window and short time series Error X spectra, and prediction r^2 spectra from short time-series	134
C.3	Test case 2, Sliding window Error X spectra for Species 3 from three different transects in regime 2. These are the same spectra as those presented in Fig 5c of the main text, except that they are presented over a smaller y-range. This makes it clear that the CLS for Species 3 in regime 2 is 20-25 pixels – similar to that of the other species - and highlights the variability between transects for this species.	135
C.4	Test case 3 Prediction r^2 spectra from sliding window and short time series Error X spectra, and prediction r^2 spectra from short time-series	136
C.5	Test case 4 Prediction r^2 spectra from sliding window and short time series Error X spectra, and prediction r^2 spectra from short time-series	136
C.6	Coral Gardens and Sampela Error X spectra as estimated from select morphotypes presented on a smaller y-scale than they appear in Figure 4.9 of the paper.	137
C.7	Hoga Buoy Error X spectra as estimated from select morphotypes presented on a smaller y-scale than they appear in Figure 4.10 of the paper.	138

E.1	Map of the Southern Ocean Continuous Plankton Recorder (SO-CPR) data set. The SO-CPR is a device that captures zooplankton from surface waters when towed behind a ship. Different coloured lines represent the SO-CPR transects completed by different ships, as named in the lower left corner. Figure taken from the Australian Antarctic Data Centre.	153
E.2	Transect of zooplankton occurrence collected by the Southern Ocean Continuous Plankton Recorder (SO-CPR) in January 1998.	154
E.3	Error X spectra estimated from occurrence of the ubiquitous copepod <i>Oithona similis</i> (left panel) and from the total counts of all zooplankton (right panel) from a Continuous Plankton Recorder trawl during a voyage from Hobart to Mawson Station, Antarctica, in January 1998 (see map E.2). The average distance represented by each silk segment is 5.1 nautical miles, so the maximum window size considered here corresponds to 204 nautical miles.	154

CHAPTER 1

Context of the thesis

Persistent shifts in ecosystem structure and function can occur unexpectedly, and sometimes abruptly (Biggs et al. 2012). Coral reefs can become overgrown by macroalgae causing the loss of a wide range of species dependent on coral (Hughes 1994). Highly productive kelp forests can be suddenly decimated by urchin grazing, leaving behind barren rock and causing the loss of important fishery species (Ling et al. 2015). Formerly clear shallow lakes become turbid and rooted vegetation is replaced by floating plants (Scheffer et al. 1993). Arid ecosystems can lose their vegetation to become bare desert (Rietkerk et al. 2004). Tropical rainforest can shift to open savanna woodlands and cloud forest to dry forest (Biggs et al. 2012; Hirota et al. 2011). Such shifts - termed regime shifts - can cause the loss of important ecosystem services on which people depend, for example, loss of fisheries and reduction in food security, loss of income, recreational activities and natural aesthetics, and altered patterns of precipitation and fire (Biggs et al. 2012; Rocha et al. 2015b).

Regime shifts are complex dynamics which can seemingly occur without warning and can be difficult to detect. This is particularly problematic for ecosystem managers – a regime shift means that the most appropriate way to manage an ecosystem might be radically different in the new regime compared to the old regime. However, to respond to such changes promptly, ecosystem managers need some forewarning as to the likelihood of a regime shift occurring in the ecosystem they are managing, the circumstances where a regime shift is more likely, the types and mechanisms of potential changes, and perhaps most importantly, they need to be able to assess whether a regime shift has occurred so that they can adapt their management practices. Managing a new ecological regime according to the dynamics of a previous regime could result in further, potentially deleterious, changes. Since ecological regime shifts present such a multifaceted problem, a multifaceted research approach is required. In this thesis I present new tools for assessing ecosystems for evidence of regime shifts, and draw together existing tools to create a cohesive framework that can be used to improve ecosystem management for regime shifts.

1.1 How do regime shifts happen? Why are they challenging? Understanding from case studies of ecological regime shifts

The drivers and mechanisms of regime shifts are specific to each ecosystem, but there are some general patterns that have emerged from intensive study of a few ecosystems. Shallow lakes, for example, can either exist in a clear water regime containing benthic plants, or a turbid state where loss of those plants results in sediments being stirred up by winds and benthivorous fish, which inhibits the regrowth of vegetation on the benthos (Scheffer et al. 1993). The transition from a clear-water to turbid state is typically driven by nutrient input increasing above a certain threshold, which drives algal blooms on the surface of the lake which then causes overshadowing and loss of rooted benthic plants due to light limitation. The loss of benthic rooted plants leads to increased perturbation of the benthic sediments by wind and by benthivorous fish, causing waters to remain turbid. In these lakes the nutrient threshold at which the ecosystem transitions depends on the water depth, so a sudden loss of water from a lake can drive the transition even where the nutrient level remains constant. To return a turbid shallow lake to a clear water regime requires reducing the nutrients to a concentration below that which triggered the shift to the turbid state, such that there is an overlap in the level of nutrients at which either the turbid or clear water state can exist – a feature of regime shifts known as hysteresis (see Figure 1.1).

Positive feedbacks between the environment and the ecological community are important features of hysteresis in shallow lakes (and other systems), but the dynamics within the community preceding and during a regime shift are also interesting. There is some evidence that the stability of the food web in shallow lakes gradually decreases as nutrient levels increase until the community rapidly reorganizes into a new, stable configuration at the nutrient threshold (Kuiper et al. 2015). Interestingly, this change in stability is driven primarily by changing interaction strengths at lower trophic levels, with zooplankton gradually increasing their per capita consumption rate of diatoms and detritus as nutrients increase. The changes in interaction strengths result in decreasing community stability towards the nutrient threshold, but it is only once that threshold is reached that biomass rapidly changes - zooplankton decline and phytoplankton dominate (Kuiper et al. 2015). The same changes in interaction strengths and stability occur during the reverse transition towards clear water state, which suggests that monitoring community stability (interaction strengths) could provide an early warning of impending transition (Kuiper et al. 2015), but in practice would be challenging to do. In some lakes (depending on the community present), it is also possible to trigger the shift back to a clear state by fishing, which causes a trophic cascade, e.g. removing the benthivorous fish gives the benthic plants a chance to take root, and removing planktivorous

fish allows zooplankton abundance to increase and graze down phytoplankton stocks (Meijer et al. 1989; Scheffer et al. 1993; Wright and Phillips 1992).

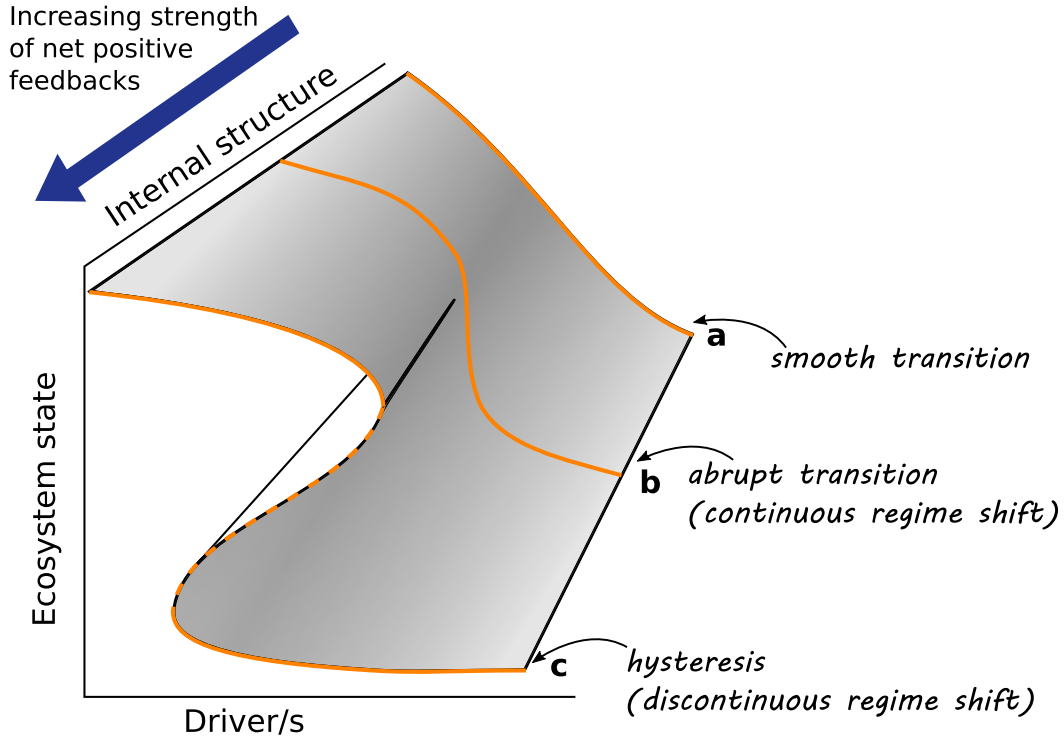


Figure 1.1: ‘Cusp’ diagram illustrating the theoretical continuity between continuous and discontinuous regime shifts. **a)** Ecosystems can change linearly with changes in driving conditions; **b)** they can change abruptly at a certain level of the driving conditions; or **c)** there can be hysteresis where the forward and reverse transitions occur at different levels of the driving conditions, with overlap in the range of conditions at which the two regimes can persist. This latter relationship is also called a critical transition. Figure redrawn based on Collie et al. (2004), Petraitis (2013), and van de Leemput et al. (2016).

Combinations of sustained stressors with occasional perturbations can interact to push an ecosystem towards a threshold or alternative regime in ways that are difficult to predict or even detect (e.g. Dal Bello et al. 2019; Hughes 1994; Ratajczak et al. 2017). The response of an ecosystem to different pressures depends on its intrinsic ecological properties and its history of perturbations, which together determine the resilience of the system (e.g. to withstand or recover from pressure and maintain ecosystem function). Combined impacts of pulse and press perturbations can also drive regime shifts, where the press perturbation slowly erodes resilience, and the pulse perturbation shifts the system closer towards (or over) the boundary of its basin of attraction (Scheffer et al. 2008). For example, the transition from coral-dominated to algal-dominated reefs in Jamaica in the 1980s followed the gradual loss of resilience through overfishing of herbivorous fishes, then a pulse disturbance to corals from Hurricane Allen, and finally a disease outbreak decimated the remaining herbivores – urchins (Hughes 1994).

For coral reefs, evidence indicates that there may be a number of different possible pathways

between alternative regimes and also a number of possible regimes. For example, coral reefs could become dominated by algae through increased sedimentation, loss of herbivores, or through direct loss of corals (e.g. by bleaching, storms or disease), but coral reef communities can also shift structure with differences in the types of coral and fish that dominate (e.g. Bozec and Mumby 2015; Donovan et al. 2018; Fung et al. 2011). Whether each of these pathways involves a critical transition is unclear, and probably varies spatially and temporally with varying strength of feedbacks (van de Leemput et al. 2016). The dependence of tipping points on combinations of multiple different factors, makes it difficult to predict at which point a critical transition will occur, even in systems for which there is clear evidence of alternative regimes. For those systems in which evidence of alternative regimes is lacking, the interdependence of thresholds on multiple drivers makes investigation into whether the ecosystem is susceptible to regime shifts particularly daunting.

Pelagic ecosystems also experience regime shifts, but because they are hidden from view and lack foundation species that provide physical habitat, the changes may be less evident than in the examples described above. Typically, regime shifts in pelagic marine ecosystems have been detected decades after they occurred (Lees et al. 2006). As a consequence, marine scientists have led the development and application of methods aimed at detecting regime shifts from time-series data (e.g. Hare and Mantua 2000; Rodionov and Overland 2005). Application of these approaches has shown that pelagic regime shifts tend either to be driven by climate, or by fishing, or a combination of the two - although in more enclosed seas eutrophication can also be a driver (Daskalov et al. 2007; Lees et al. 2006; Möllmann et al. 2009). There is even evidence that climatic changes in the 1980s drove synchronous marine regime shifts in different ocean basins in the Northern Hemisphere (Beaugrand et al. 2015). In some cases pelagic ecosystems shift back towards a similar regime following further climatic changes, however, in other cases changes in food webs prevent the system from shifting back (Lees et al. 2006). For example, multiple abiotic (human and climate) drivers, together with fishing, drove a regime shift in the central Baltic Sea in the late 1980s (Möllmann et al. 2009). The changes in abiotic conditions (e.g. temperature, salinity, oxygen) drove a shift in the ecosystem, with sprat replacing cod as the dominant fish species (along with changes in other ecological variables). When the abiotic factors returned to their previous levels, the ecosystem did not. In general, such shifts have been better studied in the Northern Hemisphere than in the Southern Hemisphere, where data for large ocean regions such as the Southern Ocean are more sparse.

1.2 Southern Ocean ecosystems as the muse for the thesis

In this thesis I aimed to develop tools and approaches for assessing ecosystems for regime shifts, and particularly to increase capacity for doing so in data-poor ecosystems. Southern Ocean ecosystems (especially pelagic ecosystems) have been the guiding focus for the approaches taken, in that I wanted to develop methods and approaches that could be applied to this region. The Southern Ocean is remote, and relatively little travelled. Opportunities for data collection in person are few, and tend to be temporally and spatially restricted to areas close to Antarctic bases, or on occasional marine science voyages. Remotely sensed satellite data (e.g. chlorophyll-*a*, ice cover) is used as much as possible, but is hampered by high cloud cover over the Southern Ocean, and long periods of darkness over winter. The Southern Ocean experiences high interannual variability at a range of temporal frequencies, with multiannual fluctuations in many environmental and ecological variables (e.g. Hobbs et al. 2016; Jenouvrier et al. 2005; Massom et al. 2013). As a result, longer time series are required to distinguish cyclic patterns, or linear responses to environmental changes, from shifts in structure and dynamics. In considering these challenges, and attempting to develop methods to overcome them, I also aimed to ensure that the methods and approaches developed were general and that they could usefully be applied to other ecosystems. To acquaint the reader with the particularities of Southern Ocean ecosystems, the following sections provide a brief overview of the importance of the Southern Ocean ecosystem and its structure, drivers and trends.

1.2.1 Southern Ocean ecosystems are important and interesting

Southern Ocean ecosystems are important both regionally and globally, and make an interesting case study for the investigation of regime shift dynamics (Fig. 1.2). Globally, the Southern Ocean is responsible for 40% of the total oceanic anthropogenic carbon uptake (Frolicher et al. 2015). A significant proportion of that uptake (and export) is thought to be performed by the Southern Ocean pelagic ecosystem (the biological pump), though exactly how much has not yet been quantified (MacGilchrist et al. 2019). A regime shift in this ecosystem could therefore have important flow-on impacts to global climate. Indeed, it has been estimated that loss of physiological carbon sinks (of which the Southern Ocean is an important one) could result in an extra 0.25 to 2.0°C of warming – substantially more than any other feedback considered (Steffen et al. 2018). In addition to their importance in climate regulation, Southern Ocean ecosystems host important fisheries, very large marine bird and mammal populations, and considerable biodiversity and tourism values (Grant et al. 2013; Rogers et al. 2019). The Antarctic krill (*Euphausia superba*) fishery has the potential to become the largest fishery (by weight) in the world and in the future could be an impor-

tant source of protein for the growing global population (Fig. 1.2). Antarctic krill are an important prey in the ecosystem (Trathan and Hill 2016), and so a shift to a regime which supports a lower biomass of krill would have considerable feedbacks to the ecosystem, as well as for global food security and for carbon export (Cavan et al. 2019).

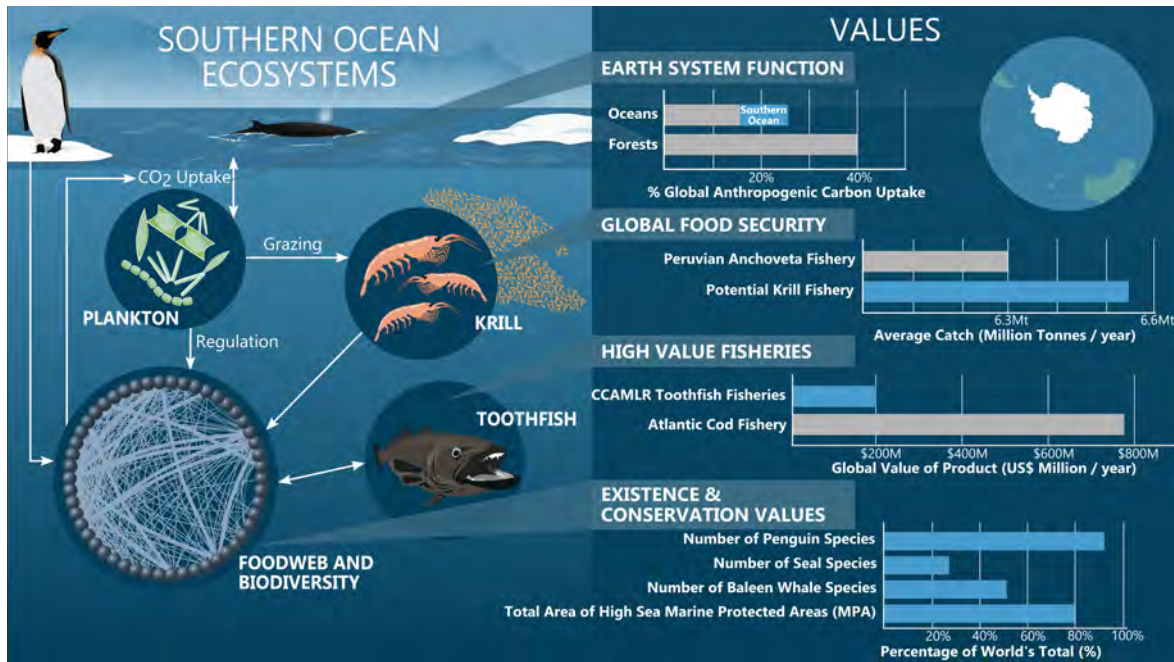


Figure 1.2: Global importance of Southern Ocean ecosystems. Thanks to McCormack et al. 2019a for sharing this figure.

1.2.2 Ecosystem structure

Southern Ocean ecosystems encompass a range of habitats, including pelagic habitats, sea-ice zones and deep-sea, slope, shelf, and near-shore benthic habitats around Antarctica and sub-Antarctic islands (De Broyer et al. 2014). The whole system is highly seasonal, and closer to Antarctica it experiences extremes of light and temperature, with little productivity over the dark winter months, but very high productivity in spring and summer, especially associated with the melting sea-ice edge as it releases nutrients (particularly iron) into the water column (De Broyer et al. 2014).

At the base of the foodweb, blooms of large diatoms dominate seasonally in many areas of the Southern Ocean (Deppeler and Davidson 2017). Their large size enables them to be captured by relatively large organisms, such as krill (whereas smaller phytoplankton are eaten by smaller zooplankton). There is concern that predicted shifts to smaller phytoplankton dominating community composition in some areas of the Southern Ocean could reduce the flow of energy to higher trophic levels, and entrain energy and carbon in the microbial loop - decreasing productivity at higher trophic levels, and reducing carbon export to the deep

(Deppeler and Davidson 2017).

Another important and interesting phytoplankton species in the Southern Ocean is *Phaeocystis antarctica*. This small species has high genetic diversity, a complex lifecycle and has evolved a complex suite of grazer avoidance strategies (Gäbler-Schwarz et al. 2015; Verity et al. 2007; Whipple et al. 2005). For example, *P. antarctica* can form colonies surrounded by extracellular polysaccharides which both helps them compete for nutrients (by concentrating the nutrients within the colony), and also escape from grazing pressure by increasing their size (Verity et al. 2007). This species also produces a strongly smelling chemical compound - dimethyl sulfide (DMS, see Glossary), which is unpalatable to many grazers (Haberman et al. 2003a,b). Dimethyl sulfide has a range of physiological functions (e.g. Nejtgaard et al. 2007; Stefels et al. 2007; Sunda et al. 2002), and also contributes to climate regulation by triggering the formation of clouds when aerosolized (Charlson et al. 1987; Cropp et al. 2007). The chemical ecology of this species, and other DMS-producing phytoplankton, is especially interesting because DMS attracts organisms across the size spectrum (including bacteria, zooplankton, fish, mammals and birds, e.g. DeBose et al. 2008; Nevitt et al. 1995; Seymour et al. 2010).

The high spring and summer-time primary productivity supports very large biomasses of higher trophic levels, including Antarctic krill, migratory whales, seals and seabirds. The main prey of baleen whales, and several other marine mammals and birds is Antarctic krill (*Euphausia superba*), which is a swarming crustacean that grows to a few centimetres in length and lives for a number of years. There is some evidence that Antarctic krill biomass has declined since the 1970s (Atkinson et al. 2004), but estimates of krill biomass and trends are highly variable and uncertain due to highly localised distributions (in dense, mobile swarms), episodic recruitment events (a large recruitment event every few years), and avoidance of nets (e.g. Atkinson et al. 2019; Cox et al. 2019; Hill et al. 2019). Nevertheless, the most recent evidence indicates that krill habitat has contracted southwards due to climate change in the South Atlantic region (Atkinson et al. 2019; IPCC 2019a) and will continue to contract under future climate change. Krill are also likely to be vulnerable to ocean acidification, warming, and climate-related changes in sea ice habitats (which they depend on over winter), as well as to other changes that are likely to act synergistically with these (Flores et al. 2012; IPCC 2019a). Impacts of future declines in Antarctic krill populations are likely to be spatially heterogeneous both due to differences in climate impacts, but also due to regional differences in their importance in the food web (McCormack 2019; Piñones and Fedorov 2016).

Short, highly efficient food chains from diatoms, to krill to whales and other large predators have typically been thought of as characteristic of Southern Ocean ecosystems, but there is growing understanding of the importance alternative energy pathways in the system as well as regional difference in the dominance of the krill-based food chains (McCormack 2019). Longer

energy pathways including copepods and fish are also known to be important, especially in the sub-Antarctic (Murphy et al. 2016). Understanding of the pelagic Southern Ocean food web is still developing. For example, as new methods for assessing predator diet have become available (e.g. DNA metabarcoding, stable isotope analysis, video loggers) there is growing awareness of the importance of jellyfish as prey items, which previously could not be identified via traditional methods of diet analysis (visual inspections of stomach-content) (Hays et al. 2018; McInnes et al. 2017; Thiebot et al. 2016).

1.2.3 Challenges for assessing Southern Ocean ecosystems and hints of regime shifts

A challenge in assessing for regime shifts in the Southern Ocean is a lack of baseline data combined with the fact that the system is still on a trajectory of recovery following the past near-extirpation of whales (as well as of some seals and fishes) (Ainley and Pauly 2014). Whales are thought to be important ecosystem engineers (Roman et al. 2014), and their loss from Southern Ocean pelagic ecosystems may have led to increases in krill-eating seal and bird populations through release from competition for prey (Ballance et al. 2006). In addition, there is evidence that large populations of whales may have supported larger populations of phytoplankton and Antarctic krill in the past (Lavery et al. 2014; Nicol et al. 2010; Ratnarajah et al. 2014). The mechanism for this is nutrient enrichment, both through stirring of the water column as whales descend and ascend, and also through release of their iron-rich faeces into the water column, promoting greater phytoplankton productivity (Ratnarajah et al. 2016; Smetacek and Nicol 2005). This positive feedback has the potential to create alternative stable states in the pelagic system – one with large populations of whales, krill and phytoplankton, and another with smaller whale, krill and phytoplankton populations.

High whale numbers would also have led to greater whale fall (sinking of dead whales to the ocean floor) in the past. Whale carcasses provide important benthic habitat and food source in Antarctic waters (Smith 2006), and so the decrease in whale numbers would have resulted in decreased habitat and connectivity for many benthic organisms (and also decreased carbon export) (Pershing et al. 2010). Whale harvesting is likely to have triggered species losses in Southern Ocean benthic ecosystems (Roman et al. 2014), but there are insufficient data prior to the commencement of commercial whaling to demonstrate whether whaling triggered a benthic regime shift. Some whale populations in the Southern Ocean are recovering, but it is not known whether the system is on a trajectory towards a past ecosystem state, or towards a novel ecosystem state. Present and future changes in climate are likely to alter the ecosystem further, as well as the carrying capacity of different species. Recovery of whale populations and whale fall is predicted to increase carbon export and thus help mitigate climate change (Pershing et al. 2010); however, continued population recovery is threatened

by climate change (Tulloch et al. 2019). Coupled climate-biological models predict future declines in baleen whale populations to be driven by decreasing availability of their main prey, krill and copepods, which itself is driven by declining primary productivity and sea ice (Tulloch et al. 2019).

More recently, shifts in bird and mammal predator populations, shifts in phytoplankton community size structure and potential changes in krill and salp abundance have all been cited as evidence of regime shifts (Atkinson et al. 2004; Montes-Hugo et al. 2009; Reid and Croxall 2001; Weimerskirch et al. 2003). For example, widespread declines in squid and krill predators based on sub-Antarctic islands in the southern Indian Ocean and south-western Pacific during the 1980s, and coincident increases in myctophid predators is suggestive of a regime shift (Weimerskirch et al. 2003). These changes were associated with positive air temperature anomalies, however, the scope of the shift (number of trophic levels affected) is unclear due to a lack of data (combined with the fact that one of the species - subantarctic fur seals, *Arctocephalus tropicalis* - was also recovering from past harvesting (Weimerskirch et al. 2003). Similar declines in krill predators occurred in the Atlantic sector of the Southern Ocean during the 1990's, which was associated with a decline in the average size of krill in their diet (Reid and Croxall 2001).

Predicting, detecting and characterising regime shifts in Southern Ocean ecosystems therefore requires development of innovative solutions to overcome challenges of detecting ecosystem change in a dynamic ocean environment, with patchy data availability.

1.3 Outline of the thesis

The overarching goal of this thesis is to explore and draw together a range of tools and approaches for assessing ecosystems for regime shifts. In particular, the aim is to enhance capability for assessing ecosystems such as in the Southern Ocean, which face challenges due to data limitations. The following section describes the different approaches taken in each of the chapters of this thesis for addressing this problem, and Table 1.1 summarises the specific aims and methods.

The literature around ecological regime shifts is large and growing rapidly. Chapter 2 is my attempt to bring together the disparate research on regime shifts into a single, synthetic framework for assessing ecosystems for regime shifts. This work draws on theoretical advances and real ecological regime shift examples to develop a framework that describes how to identify ecosystem features that could increase vulnerability to regime shifts, approaches for predicting and characterising different aspects of regime shifts, and approaches for detecting regime shifts once they have occurred. To illustrate how this framework can be used, I then apply it to Southern Ocean ecosystems as a case study.

From Chapter 2, the presence of net positive feedbacks stands out as a key quality implicated in propensity for regime shifts. A further finding is that non-trophic interactions are often key components of feedbacks. However in pelagic systems generally, including in the Southern Ocean, understanding of non-trophic interactions is poor. In the Southern Ocean a number of positive feedback mechanisms have been proposed, but determining the importance of these feedbacks is challenging in such a remote and hostile environment. One mechanism for positive feedback that has been proposed in Southern Ocean ecosystems involves attraction of predators to dimethyl sulfide (DMS) released by phytoplankton. It is thought that by attracting predators of their grazers with DMS, phytoplankton are able to either reduce their own mortality or to increase their productivity by creating a hotspot of defecating predators (which increases nutrient availability) (Savoca and Nevitt 2014). Nevertheless, the arrangement of these non-trophic links remains uncertain, as do their strengths and potential importance for the stability of the system. Because the strength and structure of these feedbacks are unclear, traditional quantitative approaches to stability analysis are impractical. Chapter 3 uses a qualitative modelling approach to explore the stability of alternative arrangements of these links in a component of the ecosystem. In this chapter I discuss the utility and limitations of this qualitative approach for determining community stability and likelihood to transition to an alternative regime. This piece of work is also the first to examine and compare network stability in simulation and symbolic approaches to loop analysis.

Perhaps a more immediate problem is that there are currently no available techniques for evaluating whether a regime shift has already occurred in Southern Ocean ecosystems. Scarcity and lack of concurrency in Southern Ocean ecological datasets mean that methods used elsewhere to detect regime shifts are not appropriate to use. Chapter 4 addresses this problem directly by successfully developing, testing and presenting an example application of a new method for detecting regime shifts from limited data. This chapter presents ‘1D CLS estimation’, and identification of changes in the optimal scale at which to observe an ecosystem (the Characteristic Length Scale; see Glossary), as a means of detecting regime shifts. This work makes it possible to detect regime shifts that have occurred between two sampling events, using 1-dimensional spatial (transect) data. In this chapter, an Indonesian tropical coral reef system is presented as a first test application of the method to real data, because suitable data were available (Haapkylä et al. 2016), and because there was previous indication that a regime shift may have occurred in at least one of the reefs in this system (Haapkylä et al. 2015), which was confirmed in this study. The development of this method greatly enhances the possibility for detecting regime shifts in Southern Ocean ecosystems, for example using benthic video transect data, and can be used to guide future monitoring program data collection. This chapter has been published in *Ecological Monographs* (Ward et al. 2018), and

the method has been made freely available as an *R* package on the code-sharing site GitHub (Ward and Wotherspoon 2018; Appendix D).

Ecological regime shifts are particularly concerning because the welfare of human populations depends so heavily on the services ecosystems provide, and also because regime shifts often have deleterious effects on biodiversity and ecosystem functioning. However, the same type of non-linear behaviour also occurs in other systems, e.g. physiological, financial, social, climatic, and others. Chapter 5 discusses the findings and contributions of this thesis in the context of tipping points that could occur in global climate and human systems, the feedbacks between the different system scopes, and how the tools provided in this thesis can be used to improve management of ecological regime shifts.

In summary, ecological regime shifts are, and will continue to be, a challenge to study and manage. This thesis offers a number of practical tools to deepen understanding of ecological regime shifts (e.g. Chapters 2 and 3) and importantly highlights future research directions to further extend this understanding. The method for detecting regime shifts offered in Chapter 4 reduces the lag between a regime shift occurring, and managers being able to detect and adapt to it. Together, these advances enhance the capacity of ecosystem managers to proactively adapt their management strategies as (or before) regime shifts occur, and more generally, to adapt to a future in which these complex changes are increasingly common.

Table 1.1: Summary of chapter aims, approaches and case study ecosystems used in this thesis.

Chapter	Aims	Approach	Ecosystems
2	<ul style="list-style-type: none"> -Develop a framework for assessing ecosystems for likelihood, nature and detection of regime shifts. -Summarise ecosystem properties affecting vulnerability to regime shifts, and how these can be used to inform management. -Detail approaches that can be used to predict different aspects of regime shifts, and highlight available methods for doing so. -Provide overview of methods for detecting regime shifts once they have occurred. -Use Southern Ocean ecosystems as a case study to illustrate how the framework can be applied to summarise understanding of the system and guide future research. 	<ul style="list-style-type: none"> -Network theory -Case studies -Prediction and detection methods -Synthesis -Framework development 	<ul style="list-style-type: none"> -Southern Ocean ecosystems. -A variety of others including coral reefs, shallow lakes, pelagic ecosystems.
3	<ul style="list-style-type: none"> -Explore the potential for feedbacks to destabilise a Southern Ocean ecological community. -Explore how uncertainties in feedback structure affect conclusions of stability. -Identify key interactions that could destabilise the community. 	<ul style="list-style-type: none"> -Qualitative network models (simulation and symbolic loop analysis) -Machine learning (random forest) 	<ul style="list-style-type: none"> -A Southern Ocean pelagic community
4	<ul style="list-style-type: none"> -Adapt the method of 2D Characteristic Length Scale estimation so that it can be estimated from 1D spatial data. -Test the method on model data. -Apply the method to real ecological transect data. 	<ul style="list-style-type: none"> -Attractor reconstruction -Non-linear prediction -Characteristic length scale estimation 	<ul style="list-style-type: none"> -Probabilistic cellular automata -Indonesian coral reef
5	<ul style="list-style-type: none"> -Synthesise the contribution of this thesis, and describe how it can be used to improve management of ecological regime shifts in the context of global changes. 	<ul style="list-style-type: none"> -Synthesis 	<ul style="list-style-type: none"> -Southern Ocean communities -Climate -Social-ecological systems

CHAPTER 2

Is my ecosystem a shifter? A framework for predicting, characterising and detecting ecological regime shifts

2.1 Introduction

Regime shifts are persistent changes in ecosystem structure, function and dynamics, and often involve the loss of ecosystem services upon which people depend (Biggs et al. 2012). Climate change and direct human pressures are generating cumulative impacts at levels not previously experienced by ecosystems, and so the likelihood of regime shift responses is increasing globally (Rocha et al. 2015b). It is therefore increasingly important to understand when and how ecological regime shifts occur, and how to manage them. The literature on regime shifts is extensive and the topic has so many facets that it is challenging for individual researchers or ecosystem practitioners to synthesise learning on the topic. This makes it very difficult to make policy-relevant assessments of the vulnerability of a particular ecosystem to regime shifts. This review synthesises existing literature - including theoretical, observational and experimental studies - to present a framework for assessing ecosystems to evaluate the likelihood, nature and occurrence of regime shifts.

This framework comprises a three-pronged approach to assessing ecosystems: 1) assessment of ecological features that may make ecosystems vulnerable to regime shifts; 2) predicting whether regime shifts are imminent, and the nature of regime shifts; and 3) detecting regime shifts once they have occurred (Fig. 2.1). This framework could be used in applied research and by ecosystem practitioners such as environmental agencies, conservation planners, local and regional management authorities, policy advisors, and agencies engaged with restoration activities. The format of the chapter is designed such that a reader who works on more applied aspects of ecosystem management could most usefully refer to and step through the most pertinent elements of the Tables, and Sections 2.3.1 and 2.4 (depending on their system

of interest, and using the case study in Section 2.5 as a guide), while the main text of the chapter provides a higher level synthesis of the key emergent issues from the tables and boxes, and is more targeted to academic readers. To illustrate how this framework can be used, the final section of this review presents an example application to Southern Ocean ecosystems. This region provides a useful case study in that it typifies many of the key challenges that researchers and practitioners might face in understanding and managing regime shifts (i.e. paucity of data and difficult to observe, undergoing rapid environmental change and subject to both historical and current human pressures) and also because it has received limited attention to date in the regime shift literature.

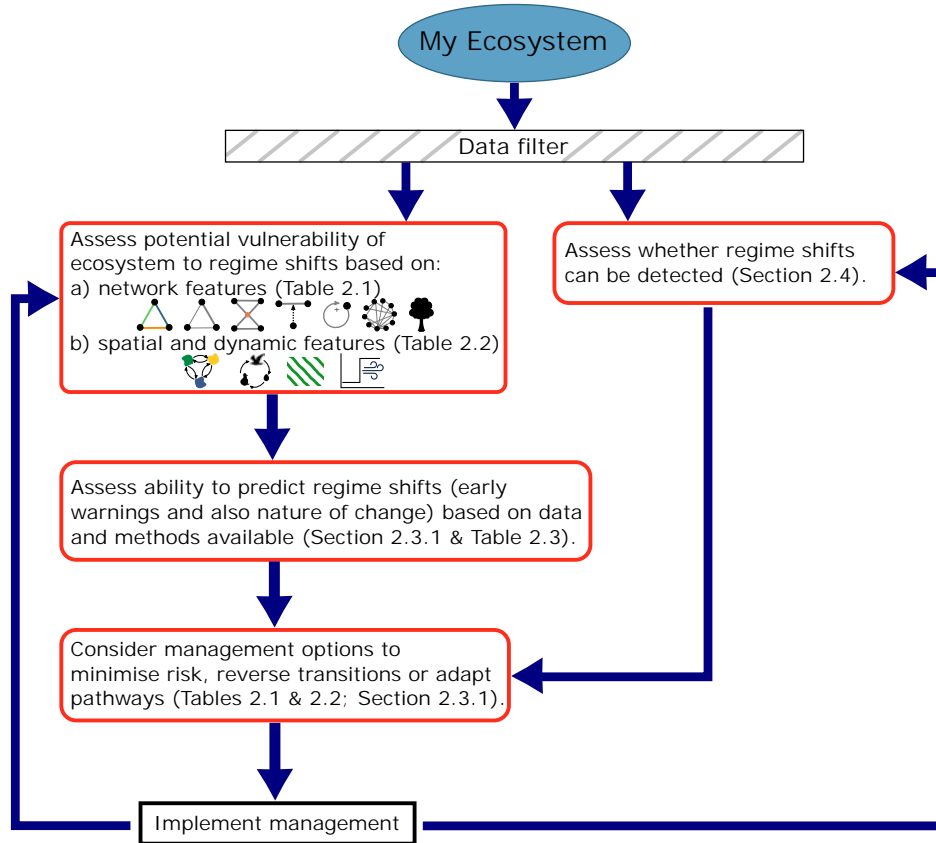


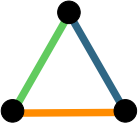
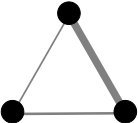
Figure 2.1: Framework for assessing the likelihood, nature and detectability of regime shifts in ecosystems, presented to help the reader conceptualise and integrate the different elements of this review. The data available from the ecosystem will determine if and how, and to what degree regime shifts can be predicted or detected - this is represented here by the ‘data filter’. The network feature diagrams link to Table 2.1 and symbolise (in order) distribution of interaction types (over the network), distribution of interaction strengths, lack of functional redundancy, higher-order interactions, sign and arrangement of feedbacks, network complexity, and importance of ecosystem engineers in the network. Spatial and dynamic feature diagrams link to Table 2.2 and symbolise spatial connectivity, heterogeneity and homogeneity, evolutionary history and life-history traits, self-organised spatial patterns, and step-changes in drivers or disturbance regimes.

2.2 Ecosystem properties implicated in regime shifts

Ecosystem practitioners need to know whether regime shifts are likely their ecosystem. Accordingly, an understanding of the different features that affect ecosystem vulnerability to regime shifts is needed for ecosystem practitioners to diagnose their own system (or systems). Regime shifts occur when the current regime becomes unstable, causing the system to transition towards a different regime. A growing body of literature shows that ecosystem stability is affected by the way ecological interactions are structured in a network, and the nature of these interactions (Kéfi et al. 2019; Landi et al. 2018). Table 2.1 summarises ecosystem network features known to be important for stability and suggests how these features can be assessed and used to inform management practices. While assessment of all the network features described is perhaps impractical for all ecosystems, the hope is that this table can also be a prompt for considering how perturbations might act on an ecosystem to alter its network and stability characteristics, and thus affects its vulnerability to regime shifts.

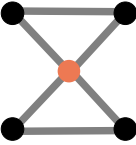
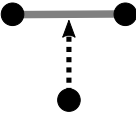
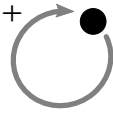
Equally important for ecosystem stability is the spatial and temporal context in which interactions play out (Garcia-Callejas et al. 2019). Table 2.2 details spatial and temporal ecosystem features that affect vulnerability to, and dynamics of regime shifts. In the following sections I provide a general review of the importance of different ecosystem features in the context of regime shift risk, while the tables provide detailed guidance on how researchers and practitioners might assess each network feature (Table 2.1) and spatial and temporal features (Table 2.2). To help the reader connect the text with the tables, the ecosystem features from these two tables are written in bold font in the first instance they are mentioned within each of the paragraphs in this section.

Table 2.1: Ecosystem network features associated with stability. System stability may change when disturbance alters the balance of these features within an ecosystem, thus making the ecosystem vulnerable to regime shifts. Southern Ocean ecosystem examples are given here, but see the main text (Section 2.5) for a more general description of Southern Ocean ecosystems, important species, and discussion of vulnerability to regime shifts. Numbers refer to references given in the footnote of the table.

Network features	Why is this a risk factor?	How can it be assessed?	How can it inform management?	Southern Ocean (see also section 2.5 of text)
Distribution of interaction types <i>(trophic, negative non-trophic, positive non-trophic)</i> 	<i>Distribution of interaction types over ecosystem network is non-random (1), and likely balanced for high stability (2), productivity and community persistence (1, 3, 4).</i> <ul style="list-style-type: none"> •Biased loss of one interaction type, or changes in strength of one interaction type, can destabilize the network (3). •Some species perform multiple interaction types and their loss triggers cascading losses (1). •Facilitation especially increases likelihood of hysteresis (5, 6). •Higher-order interactions and feedbacks often involve non-trophic interactions (see rows below). 	<ul style="list-style-type: none"> •Requires (long-term) observation and experimentation. (1, 7). •Generally, non-trophic interactions poorly understood, so difficult to assess changes in distribution of interaction types. •Impact of non-trophic interactions investigated through modelling (e.g. 1, 8-15). •Possible short-cuts: explore interactions driving spatially self-organised patterns (16) (see Table 2.2), and ecosystem engineers, to identify species that perform key non-trophic roles. 	<ul style="list-style-type: none"> •Rigorous assessment of distribution of interaction types unfeasible in most ecosystems; ecosystem engineers and other non-trophic functional roles should be targeted for monitoring and management. •Models (1, 15) can help identify key functional ‘hubs’ in the ecosystem which can be targeted for protection and management. •For degraded systems, understanding non-trophic interactions can support ecosystem recovery (17). 	<ul style="list-style-type: none"> •Very little known about non-trophic interactions. •Competitive (negative non-trophic) interactions implicated in trophic networks, but more difficult to incorporate other non-trophic interactions. Some positive non-trophic interactions documented (that could potentially increase vulnerability to regime shifts): •The role of DMS in attracting seabirds (18, Chp. 3). •Some flying seabirds benefit from following cetaceans (and fishing vessels) to locate prey (19, 20). •Predators at multispecies feeding aggregations benefit from each other as diverse foraging strategies scatter prey (21-23). •Facilitation by habitat-formers in benthos.
Distribution of interaction strengths 	<i>Natural food webs tend to have a skewed interaction strength distribution, with many weak and few strong interactions (24).</i> <ul style="list-style-type: none"> •Changes to distribution of interaction strengths likely to destabilise the ecosystem. •Effect of changes in the distribution of interaction strengths depends on interaction types (25, 26). E.g. decreased strength of mutualistic compared to antagonistic interactions could decrease community persistence (27). •Can change dynamically (e.g. seasonally) and hence system stability also changes (28). 	<ul style="list-style-type: none"> •Observation & experimentation followed by modelling/network analysis (e.g. 28). •Need to identify appropriate temporal scale, given interaction strength changes dynamically (28). •Need to select appropriate measure of interaction strength (e.g. energy flow, Jacobian matrix elements, 29). •Dynamic assessment of interaction strengths and stability possible from high-resolution time-series (28, 30). •Possible short-cut: Use allometric scaling to predict interaction strengths (31). 	<ul style="list-style-type: none"> •Preferentially deal with stressors that are more likely to destabilise the system (e.g. those that change the distribution of interaction strengths). •Reassess exploitation targets and quotas: targeting species with strong interactions may increase likelihood of trophic cascades (32). •Possible approach: Assess seasons with lower stability (e.g. more strong links) and prioritise management of perturbations that reduce resilience at those times. 	<ul style="list-style-type: none"> •Highly seasonal system so interaction strengths likely to vary temporally. •Krill fishing pressure at certain times of year might alter distribution of interaction strengths and decrease system stability. •Climate change-induced stressors likely to alter species fitness and behaviours, altering distribution of interaction strengths. •Observed and predicted phenological changes (33) likely to affect interaction strengths.

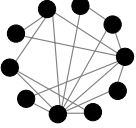

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	Why is this a risk factor?	How can it be assessed?	How can it inform management?	Southern Ocean (see also section 2.5 of text)
Lack of functional redundancy 	<ul style="list-style-type: none"> •Lack of functional redundancy makes the system vulnerable to loss of species that perform unique functions. •‘Wasp-waist’ ecosystems with lack of redundancy at mid-trophic levels implicated in pelagic regime shifts (34, 35). •Redundancy in key functional roles particularly important (e.g. herbivores on coral reefs (36)). 	<ul style="list-style-type: none"> •Characterisation of functional roles performed by different species through observation and experimentation. •Experimentation to identify ‘sleeper’ functional roles (e.g. 37). •Dietary studies to identify trophic roles and redundancies (e.g. DNA-based, stable isotopes). 	<ul style="list-style-type: none"> •If clear lack of redundancy in a key functional role, direct management strategies towards protecting the species performing that role. •Direct management towards increasing resilience by re-establishing redundancy. 	<ul style="list-style-type: none"> •Krill-based system is considered a wasp-waist system (38-40) (although increasing evidence of alternative energy pathways, e.g. 41). Southern Ocean ecosystems particularly vulnerable to changes in krill abundance, dynamics and behaviours. (see also text, and row below re life history strategies and prey-switching).
Higher-order interactions 	<p><i>Higher-order interactions can stabilise community dynamics and support high diversity (42). These often involve non-trophic interactions, e.g. facilitation, fear-induced behaviour modification.</i></p> <ul style="list-style-type: none"> •Loss of species involved in higher-order interactions likely to decrease system stability. 	<ul style="list-style-type: none"> •Experimental manipulation (43, 44). •Behavioural observations (e.g. 23). •Modelling to explore importance of higher-order interactions present for ecosystem stability (9, 11, 42, 45). 	<ul style="list-style-type: none"> •Loss of species that mediate interactions between other species likely to have greater than expected impact; target these species for conservation management. 	<ul style="list-style-type: none"> •Higher-order interactions difficult to observe in pelagic ecosystems. •Presence of multiple predator species in foraging aggregations (e.g. cetaceans, flying seabirds, penguins, seals) thought to enhance prey capture by each species (21-23).
Net sign and arrangement of feedbacks 	<p><i>Negative feedbacks are stabilizing, while positive feedbacks are destabilizing (e.g. 46). The strength of net positive feedbacks determines the degree of hysteresis in a system (5).</i></p> <ul style="list-style-type: none"> •Changes in sign and strength of feedbacks can trigger regime shifts. •Positive feedbacks particularly important if ecosystem engineers or keystone species involved (most well-known case studies of hysteresis involve foundation species: e.g. coral, macroalgae, trees). 	<ul style="list-style-type: none"> •Experiments and observation to identify feedback strengths and possible thresholds (e.g. 47). •Modelling (e.g. loop analysis, 48) to investigate net feedback sign, or (e.g. simulation-based qualitative networks, Chp. 3) to investigate effects of altering feedback strengths. •Modelling (e.g. quantitative, 49) to explore possible thresholds, hysteresis and effects of interacting feedbacks. 	<ul style="list-style-type: none"> •Understanding feedbacks which shape the ecosystem can help direct management strategies (50). •After a transition, understanding of feedbacks can be used to direct recovery of the system (17, 50). •Management actions can create new feedbacks and alter the net feedback sign. 	<ul style="list-style-type: none"> •Positive feedbacks largely unknown, a few hypothesised. •DMS-production by phytoplankton attracts predators of grazers, facilitating greater phytoplankton blooms (51, 52, see Chapter 3). •Krill-whale-nutrient feedbacks proposed (53, 54). •Feedbacks exist in some microbial communities (e.g. 55, 56). •Arrangement and net sign of system feedbacks yet to be explored.

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	Why is this a risk factor?	How can it be assessed?	How can it inform management?	Southern Ocean (see also section 2.5 of text)
Complexity <i>(species richness, connectance)</i> 	<p><i>Random complex systems less likely to be stable than simple systems (57), but natural complex systems are not random and have a balance of interaction types, strengths and network structure that often promote stability (58, see also 59 and rows above). Broad, and allometric scaling of degree distribution (e.g. large predators have many prey and few predators) stabilises food webs (60, 61)</i></p> <ul style="list-style-type: none"> •Changes in complexity alter system stability, e.g. increases in complexity of competition networks may reduce stability (27). 	<ul style="list-style-type: none"> •Reconstruct ecosystem as a network including all interactions. •Complexity measured as function of connectance and species richness (57, 62). •Measure degree distribution as number of prey and number of predators for each species/functional group (61, 62). •Where ecosystem structure is unclear, proxies could be used to infer presence of interactions e.g. (63). 	<ul style="list-style-type: none"> •Monitor changes in complexity (e.g. arrival/loss of species, changes in connectance) that may destabilise the system. •Shifts often towards simpler regimes, so restoration of complex regime likely to be challenged by reduced species pool. 	<ul style="list-style-type: none"> •Traditionally considered as a fairly simple system with short food chains, but growing evidence of greater complexity, and the extremity of environment drives species to have broad trophic niches, increasing the connectance and thus complexity. •Climate-driven poleward range shifts likely to alter system complexity.
Presence of ecosystem engineers 	<ul style="list-style-type: none"> •Ecosystems with dependence on foundation species, or other ecosystem engineers, appear to be particularly prone to critical transitions including hysteresis (e.g. coral reefs, kelp forests, tropical rainforests, drylands, shallow lakes). 	<ul style="list-style-type: none"> •Identify ecosystem engineers as species which create, significantly modify, maintain or destroy habitat. •Observation and experimentation. 	<ul style="list-style-type: none"> •Target monitoring and management around ecosystem engineers (and other key functional species, see row above re functional redundancy). •Consider actively removing or reintroducing ecosystem engineers to support habitat persistence. •Develop understanding of feedbacks involving engineer species and any potential stressors and thresholds. 	<ul style="list-style-type: none"> •Both ecosystem engineers and hysteresis harder to identify in pelagic systems. •Large whales considered ecosystem engineers (64). •Sea-ice is habitat forming. It is a 3D substratum for biota at different scales, has a strong seasonal dynamic and is under threat from climate change. •Benthic systems characterised by habitat-forming macroinvertebrates may be prone to regime shifts (65).

References: ¹Kéfi et al. 2016a. ²Kondoh and Mougi 2015. ³Mougi and Kondoh 2012. ⁴Morris et al. 2007. ⁵Kéfi et al. 2016b. ⁶Xu et al. 2015a. ⁷Scheffer et al. 1993. ⁸Vasas and Jordán 2006. ⁹Dambacher and Ramos-Jiliberto 2007. ¹⁰Fontaine et al. 2011. ¹¹Kéfi et al. 2012. ¹²Kéfi et al. 2015. ¹³Pilosof et al. 2017. ¹⁴Lurgi et al. 2016. ¹⁵Hutchinson et al. 2018. ¹⁶Xu et al. 2015b. ¹⁷Suding et al. 2004. ¹⁸Nevitt et al. 1995. ¹⁹Sakamoto et al. 2009. ²⁰Hodges and Woehler 1994. ²¹Lett et al. 2014. ²²Veit and Harrison 2017. ²³Harrison et al. 1991. ²⁴McCann et al. 1998. ²⁵Melián et al. 2009. ²⁶Allesina and Tang 2012. ²⁷Sauve et al. 2014. ²⁸Ushio et al. 2018. ²⁹Wootton and Emmerson 2005. ³⁰Deyle et al. 2016. ³¹Berlow et al. 2009. ³²Bascompte et al. 2005. ³³Chambers et al. 2013. ³⁴Bakun 2006. ³⁵Cury et al. 2000. ³⁶Hughes 1994. ³⁷Bellwood et al. 2006. ³⁸Flores et al. 2012. ³⁹Atkinson et al. 2014. ⁴⁰Murphy et al. 2016. ⁴¹McCormack et al. 2019b. ⁴²Grilli et al. 2017. ⁴³Heithaus et al. 2008. ⁴⁴Billick and Case 1994. ⁴⁵Golubski et al. 2016. ⁴⁶Dambacher et al. 2003. ⁴⁷Ling et al. 2009. ⁴⁸Marzloff et al. 2011. ⁴⁹van de Leemput et al. 2016. ⁵⁰Nystrom et al. 2012. ⁵¹Savoca and Nevitt 2014. ⁵²Lewis et al. 2012. ⁵³Smetacek and Nicol 2005. ⁵⁴Nicol et al. 2010. ⁵⁵Bertrand et al. 2015. ⁵⁶Subramaniam et al. 2016. ⁵⁷May 1972. ⁵⁸Borrelli et al. 2015. ⁵⁹Landi et al. 2018. ⁶⁰Otto et al. 2007. ⁶¹Allesina et al. 2015. ⁶²Dunne et al. 2002. ⁶³Morales-Castilla et al. 2015. ⁶⁴Roman et al. 2014. ⁶⁵Clark et al. 2013.

2.2.1 The importance of ecosystem network features for stability

Many ecosystems are highly complex, yet debate continues as to whether **complexity** confers stability or instability (Landi et al. 2018). Complex, random interaction networks tend to be unstable (May 1972, 1973), but natural, persistent ecosystems are not random; they are the product of evolutionary and selective processes occurring simultaneously at multiple levels and scales of the ecosystem (Borrelli et al. 2015). These processes result in ecological networks with a mix of features that are balanced for maximal stability, given the environment and range of conditions in which they exist (Borrelli et al. 2015); however, if environmental conditions change, then these same systems may become unstable. Some network structures are more stable than others, but this is balanced by the **distribution of interaction types and strengths** over the network (Sauve et al. 2014), and the optimal mix of features will depend on the nature of variability and perturbations in the system. For example, nested network structures (see Glossary) are more stable for mutualistic communities (e.g. flower-pollinator networks), but more modular networks (with clusters of interactions compartmentalised, e.g. into different habitats) are more stable in networks of mixed interaction types (Lever et al. 2014; Stouffer and Bascompte 2011; Thebault and Fontaine 2010). Environmental change or disturbance that alters network structure or interaction types could alter the balance of these features, and thus reduce stability and affect susceptibility to regime shifts (e.g. Kuiper et al. 2015). Moreover, cyclical changes in interaction strengths (as might occur in highly seasonal systems) may make ecosystems more vulnerable to disturbance at certain times of the year (Ushio et al. 2018).

As ecosystems become more **complex** (greater diversity and connectance), there is opportunity for more **feedbacks** - both positive and negative - to be present. The presence of positive feedbacks is implicated for hysteresis (Table 2.1) because above a certain strength they can destabilise an ecosystem, causing it to switch to an alternative stable state (e.g. of the same network structure), where each alternative state is reinforced by a different set of dominant feedbacks (Marzloff et al. 2011). If low level feedbacks are weak in comparison to high level feedbacks, the system may experience divergent oscillations until it crashes (and may then be replaced by a different community, e.g. with a different network structure) (Dambacher et al. 2003). Perturbations that alter the **distribution of interaction strengths** in the ecosystem are likely to change the relative strengths of negative versus positive feedbacks, and so are likely to have greater impact on system stability than if perturbations had a uniform impact on interaction strength. Similarly, perturbations that have a biased impact on certain **types of interactions** (e.g. facilitation) or on species involved in multiple interaction types (e.g. ‘multiplex hubs’ *sensu* Kéfi et al. 2016a) are likely to alter the pattern of positive and negative feedbacks in the system, and thus ecosystem stability and vulnerability to regime shifts. Importantly, even positive feedbacks that are too weak to individually cause tipping

points, can collectively create tipping points when aligned with other weak positive feedbacks (van de Leemput et al. 2016). This has important implications for decisions about the scope of the system to assess (Box 1). For example, ecosystem practitioners might observe positive feedbacks in their system of interest (e.g. an ecological community), but conclude that they are too weak to cause tipping points. But these weak feedbacks could align synergistically with positive feedbacks beyond the scope of consideration (e.g. including abiotic variables or neighbouring communities) to create unidentified tipping points.

Protection of biodiversity is a key conservation goal and regime shifts tend to result in loss of biodiversity (Biggs et al. 2018). High species diversity implies greater ecosystem **complexity**, greater likelihood of high **functional redundancy**, more stable **distribution of interaction strengths** (i.e. many weak, few strong), greater variance in responses to disturbance, and potentially greater adaptive capacity of the ecosystem, meaning the system might evolve gradually rather than shift suddenly (Folke et al. 2004; Loreau and Mazancourt 2013). Loss of biodiversity can reduce the range of possible ecosystem configurations, and capacity to buffer perturbations (Peterson et al. 1998). For example, on the Great Barrier Reef experimental manipulation of an area of reef resulted in overgrowth of coral by macroalgae (an alternative state), amongst which even herbivorous fish avoided feeding because of the risk that predators could hide in the algae (Bellwood et al. 2006). Surprisingly, batfish, a planktivorous fish, acted outside its known functional role to graze all the macroalgae from the experimental plots (Bellwood et al. 2006). Without batfish to remove the macroalgae, the section of reef is likely to have remained in its alternative, macro-algae dominated state, yet prior to these experiments the importance of this species performing this function could not have been predicted. Loss of species can thus have larger than expected impacts on functional diversity, and the ability of the system to avoid or recover from regime shifts.

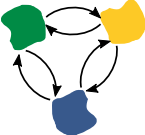
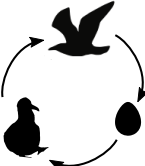
Most well-characterised examples of systems with alternative stable states involve the loss of (or stress to) **habitat-forming species** or other **ecosystem engineers** (e.g. coral, kelp, urchins on reefs, trees in woodlands/forests, submerged vegetation in shallow lakes). The research focus on these systems may be because regime shifts are more evident in those systems, but it also highlights the importance of key functional species in determining ecosystem state. Habitat-forming species and other ecosystem engineers tend to be involved in multiple **types of interactions** (e.g. facilitation, inhibition/competition, trophic), as well as **higher-order interactions** which can stabilise systems and promote species coexistence (Grilli et al. 2017; Levine et al. 2017). Loss of species performing multiple types of interactions - ‘multiplex hubs’ - have been shown to have disproportionate impacts on ecosystems, and are more likely to result in cascading losses of species, than loss of species involved in fewer types of interaction (Kéfi et al. 2016a). Accordingly, disturbance or stress on species that perform key functions or multiple functions in an ecosystem are likely to increase risk

of regime shifts (see Table 2.1).

2.2.2 Dynamic and spatial features of ecosystems that affect regime shift vulnerability


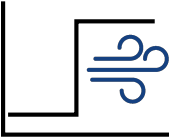
There is a diversity of risk factors posed by different dynamic and spatial ecosystem features in relation to regime shifts (Table 2.2). **Spatial patterns** of the ecosystem, **connectivity**, and how these interact with spatial patterns of disturbance, affect the nature and apparent rapidity of regime shifts (Gravel et al. 2016; Schneider and Kéfi 2016; van de Leemput et al. 2015; van Nes and Scheffer 2005) (Table 2.2). For example, **spatially heterogeneous** landscapes tend to shift gradually (patch-by-patch) which theoretically provides greater warning of the regime shift (unless there is a smooth gradient, high connectivity, and depending on spatial patterns of drivers) (van Nes and Scheffer 2005); however in practice it remains challenging to recognise when change in one patch of an ecosystem indicates vulnerability to a broader regime shift (Hughes et al. 2013). Self-organised spatial patterning can arise through positive feedbacks and change in the emergent spatial patterns can sometimes be used as an indicator of approaching regime shifts (e.g. Rietkerk and van de Koppel 2008; Rietkerk et al. 2004). Use of spatially explicit models to understand and predict regime shifts is necessary but can be challenging as the presence of thresholds depends strongly on the way the models are implemented (e.g. representation and simplification of spatial patterns, processes and feedbacks), the way that space itself is represented in the model, as well as the spatial scale of observation (Bathiany et al. 2016; Marzloff et al. 2016b).

Table 2.2: Dynamic/spatial features of ecosystems that affect vulnerability to and dynamics of regime shifts. Southern Ocean ecosystems are used as an example to illustrate how these features can be explored for a real ecosystem, but see main text (Section 2.5) for more general introduction of Southern Ocean ecosystems and important species. Numbers refer to references given in the footnote of the table.

Dynamic & spatial features	Why is this a risk factor?	How can it be assessed?	How can it inform management?	Southern Ocean? (see also section 2.5 of text)
Spatial connectivity, heterogeneity and homogeneity 	<p><i>Metacommunity complexity (number of and connectedness among food webs in heterogeneous system) enhances system stability (1), and changes to this can alter resilience</i></p> <ul style="list-style-type: none"> • Mobile consumers stabilise large, spatially heterogeneous systems (but destabilise spatially constrained ecosystems) (2), so changes in their populations could destabilise an ecosystem. • Spatial connectivity promotes both recovery from and spread of perturbations. • Heterogeneous landscapes tend to transition gradually (patch by patch), unless connectivity is strong, whereas homogenous systems tend to transition suddenly (3, 4). • Loss of resilience in homogenous systems can be difficult to reverse (4). 	<ul style="list-style-type: none"> • Satellite observations, tracking studies (to monitor metacommunity structure at large scales). • Monitoring and modelling of dispersal and recruitment (e.g. establish coral settlement plates; particle tracking models). 	<ul style="list-style-type: none"> • Important to assess resilience of homogeneous systems, or highly connected heterogeneous systems, as transition between alternative states can be sudden. • Assess implications of changes in connectivity and spatial patterns (e.g. fragmentation, increases in dispersal) for system stability and use to inform management strategies to maximise resilience and stability. • Action to avert transitions may be most effectively targeted towards the spatial front of a regime shift (5). 	<ul style="list-style-type: none"> • Highly mobile top-predators exert enormous predation pressure seasonally. Declines in predator numbers (6-8) of concern. • System spatially heterogeneous, but highly connected via circumpolar currents and mobile predators. • Modelling studies (e.g. 9-11) highlight connectivity by investigating patterns of dispersal through Southern Ocean. • Molecular observations suggest that despite connectivity, gene flow between regions can be low (12).
Evolutionary history and life history traits 	<p><i>Evolutionary history and resultant set of life history traits (and phenotypic diversity) in an ecosystem can influence how the system might buffer or respond to change.</i></p> <ul style="list-style-type: none"> • Ecosystems adapted to low stochasticity or variability in conditions more susceptible to strong perturbations compared to systems that are highly seasonal (13). • Life history and behavioural adaptations (e.g. dispersal strategies, reproductive 'bet-hedging', diapause or stasis, prey-switching, 14-16) can potentially buffer system against change in short-term, and mask loss of resilience in the face of longer-term changes to drivers. 	<ul style="list-style-type: none"> • The impact of life history traits and evolutionary history on the resilience of ecosystems (particularly in terms of likelihood of ecological transitions) requires investigation. • Monitor biological rates (e.g. breeding success, diet, dispersal) in conjunction with environmental parameters. • Observations of bet-hedging (17); of prey-switching; of dispersal (12). • Modelling (e.g. of dispersal strategies, population level consequences of bet-hedging, prey-switching to suboptimal diets, etc.). 	<ul style="list-style-type: none"> • Where possible factor evolutionary history into management frameworks. • Use monitoring data of biological rates to understand drivers of changes in life-history traits and implications for system resilience, e.g. diets of longer-lived predators may be more sensitive indicators of change than population size (e.g. 18, 19). 	<ul style="list-style-type: none"> • Bet-hedging is common amongst long-lived seabirds in the Southern Ocean (17, 20). It is unclear how much reduced reproductive output of these predators will impact (or already has impacted) the ecosystem. • Many organisms adapted to high seasonality and to extremes in some drivers. This may buffer against some environmental changes (but the loss of sea-ice could be catastrophic - see Table 2.1). • Prey-switching over different time scales may affect resilience (e.g. 21, 22).

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	Why is this a risk factor?	How can it be assessed?	How can it inform management?	Southern Ocean? (see also section 2.5 of text)
Self-organised spatial pattern 	<p><i>Self-organised spatial patterns are an emergent feature of internal dynamics (interactions) taking place in a spatial context.</i></p> <ul style="list-style-type: none"> • Bistability of alternative stable states has been associated with spatial patterns that emerge from a combination of short-range positive feedbacks and long-range negative feedbacks (23, 24, 25). This is often associated with resource limitation and facilitation by the ecosystem engineer. 	<ul style="list-style-type: none"> • Assess large-scale patterns aeri-ally, e.g. by satellite, plane, drone. • Need to determine mechanisms to identify whether spatial patterning is self-organised; requires experi-mental observations and modelling (23). 	<ul style="list-style-type: none"> • Could be used as indicator for presence of positive feedbacks (23). • Possible indicator of hysteresis: prioritise exploration of drivers, feedbacks and thresholds (24). 	<ul style="list-style-type: none"> • No obvious application to pelagic sys-tems • Could be investigated in benthic or sea-ice algal ecosystems.
Step-changes in drivers or disturbance regime 	<ul style="list-style-type: none"> • Step-changes in environmental conditions can drive reorganisations in ecosystem structure even in systems not otherwise prone to regime shifts. This appears to be especially true for open pelagic systems (26). • Increased frequency of disturbance limits per-sistence of some organisms and can reduce sys-tem resilience (27). If these organisms play unique functional roles the whole system may change (see Table 2.1 - ecosystem engineers). 	<ul style="list-style-type: none"> • Paleo-reconstructions of local cli-mate to assess frequency of changes in climatic state. • CMIP5/6 models (possibly down-scaled) to assess possible future change. 	<ul style="list-style-type: none"> • Be prepared to adapt manage-ment strategies to new climatic conditions, altered disturbance regimes and consequent changes in ecosystems. 	<ul style="list-style-type: none"> • Some large step-changes already ob-served around the West Antarctic Peninsula (e.g. loss of fast-ice and increase in iceshelf collapse, iceberg scour, glacier retreat and increase in sedimentation) which have driven large changes in benthic ecosystems (28, 29).

References:¹Mougi and Kondoh 2016. ²McCann et al. 2005. ³van Nes and Scheffer 2005. ⁴van de Leemput et al. 2015. ⁵Zelnik and Meron 2018. ⁶Weimerskirch et al. 2003. ⁷Reid and Croxall 2001. ⁸Hindell et al. 2017. ⁹Fraser et al. 2017. ¹⁰Mori et al. 2017. ¹¹Young et al. 2018. ¹²Moon et al. 2017. ¹³Holling 1973. ¹⁴Pelletier 2000. ¹⁵Kondoh 2003. ¹⁶Kondoh 2006. ¹⁷Nevoux et al. 2010. ¹⁸Hempson et al. 2018. ¹⁹Huckstadt et al. 2017. ²⁰Jenouvrier et al. 2005. ²¹Croxall et al. 1999. ²²Bedford et al. 2015. ²³Rietkerk and van de Koppel 2008. ²⁴Rietkerk et al. 2004. ²⁵van de Koppel et al. 2005. ²⁶Lees et al. 2006. ²⁷Dal Bello et al. 2019. ²⁸Barnes and Souster 2011. ²⁹Sahade et al. 2015.

The temporal variability of an ecosystem, and the **life history traits** of the organisms within it, shape not only the dynamics of a regime shift, but how easily we can detect that it is occurring. The **evolutionary history** of the organisms within an ecosystem - how they have evolved in response to each other and their environment - determines the range of their possible adaptations to future environmental and ecological changes (Dakos et al. 2019). In strongly seasonal or stochastic ecosystems, organisms evolve a suite of life history traits to persist through environmental fluctuations, and the persistence of the ecosystem as a whole depends on the continuation of the variability to which it has adapted (e.g. Chesson 2000; Nevoux et al. 2010). For example, the persistent co-existence of species depends on the frequency of disturbance, and change to the **disturbance regime** can thus alter community composition by reducing the capacity of some species to persist (e.g. Chesson 2000; Dal Bello et al. 2019). Ecosystems with low variability tend to transition suddenly in response to environmental change, whereas in highly stochastic systems, many of the organisms are able to buffer their populations against unfavourable conditions, for example by reducing their reproductive output, switching to substandard prey or by producing propagules that remain dormant until conditions become favourable (Holling 1973). These kinds of adaptations throughout an ecosystem can buffer the system against short-term change and can mask the loss of resilience (depending on the variables being monitored), but in the face of longer-term changes to drivers or the disturbance regime, the ecosystem is likely to change as species are gradually lost. **Step-changes** in environmental conditions or disturbance regime are likely to drive step-changes in the ecosystem, even where the relationship is linear (e.g. Dakos et al. 2015; Lees et al. 2006).

2.2.3 Assessing regime shift risk in practice

Assessment of the ecosystem features described in Tables 2.1 and 2.2 will typically require a lot of data; it requires in-depth understanding of processes developed through experiments, behavioural observations, long-time series of multiple variables, and so on. For some ecosystems these data will exist, but for systems that are less accessible, or otherwise challenging to study, shortcuts may need to be developed to assess these properties. As an example, identifying emergent spatial patterns may be used to focus research towards understanding the presence of positive feedbacks (Rietkerk and van de Koppel 2008). In general, identification of risk factors will depend on the spatial, temporal and system scope being considered (Box 1). While I have described a range of ecosystem properties that play a role in stability and regime shifts, other important features may yet be discovered. In reality vulnerability to regime shifts involves many interacting factors, and depends on how the intensity and duration of perturbations interact with the inherent ecological properties and biological rates of the system at different scales (e.g. Harris et al. 2018; Kéfi et al. 2019; Ratajczak et al. 2017,

Bergstrom et al. in review). This is the first time (that I am aware of) that these ecosystem properties have been brought together and discussed in the context of regime shifts. It is hoped that this will prompt new research directions and understanding of regime shifts.

Box 1: The problem of scale for the prediction and detection of ecological regime shifts

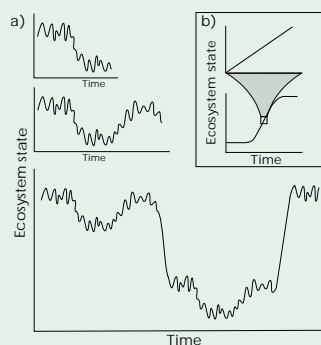
A key consideration for the discussion of regime shifts is that of scale. Scale is an issue for the whole field of ecology (Levin 1992), but in the study of regime shifts it is particularly pertinent: what is considered a regime shift at one scale may not be at another. Here I discuss 4 interrelated aspects of scale: temporal scale, spatial scale, organism scale, the scope of the system (e.g. community, ecosystem, social-ecological system, biosphere), as well as the scale of change (size of shift in terms of system function and structure – i.e. does the change matter?). Integral to this discussion is consideration of the scale of observation, which may not always coincide with the scale of the system of interest, the scale at which change is occurring, or indeed the scale at which a signal is observable. In all cases, expert opinion and conceptual models of the system structure and function are useful for identifying the most relevant scales.

Spatial scale The optimal spatial scale for observing regime shifts will depend on the system scope of interest. For example, a regime shift can be detected through change in the (spatial) characteristic length scale (CLS) of a system (Chapter 4, Ward et al. 2018). A change in the CLS when the underlying data are at millimetre resolution is likely to reflect a physiological, individual or community-scale shift (depending on organism size), but data at kilometre resolution is likely to reflect landscape or oceanographic scale shifts. Regime shifts may appear abrupt in restricted spatial locations, but at a larger spatial scale change may be more gradual, which means that observations conducted at one spatial scale will describe a different pattern of change to those at another (e.g. Bathiany et al. 2016). Observation scale also affects interpretations of network stability; e.g. interaction strengths vary spatially (and temporally) so the scale over which interaction strength is averaged will affect how stable it appears (see Table 2.1).

Temporal scale What appears to be a sustained transition at one temporal scale, might be a normal fluctuation at a longer temporal scale (Fig. a). Similarly, what may appear to be a gradual, linear change in ecosystem state at one temporal scale may be a transition to an alternative stable state over a longer temporal scale (Fig. b).

The temporal resolution of observations will also determine the system scale that is being observed, and the scale of the changes being observed. Generally, shorter, higher resolution observations will signal changes within a smaller system scope (e.g. physiological, population, community), while coarser, longer time-series will contain signals of change for broader system scopes (e.g. community, ecosystem, biosphere), or for drivers that change more slowly, or variables that respond more slowly. Systems with long positive feedback loops (that involve many ecosystem components) will have lags in their responses (tend to spend longer in transient states), and so may require long observational time series to observe the final response.

Organism size Different sized organisms respond to environmental change at different scales, and thus require different scales of observation and of experimental manipulation



to inform prediction and detection of regime shifts. To predict thresholds, experiments are easier to conduct on small, short-lived plants and animals (e.g. plankton) than on long-lived megafauna that can migrate great distances (e.g. whales). At the same time, organisms with faster generation times can adapt and evolve more quickly to changing conditions than animals with longer generation times. This limits capacity to identify distant thresholds for short-lived organisms (because they may adapt to drivers before a threshold is reached) and for long-lived organisms - because the duration and spatial scale of the experiment would need to be so large (as well as potentially involving ethical considerations). Organism size also affects which variables will be appropriate to monitor for signals of (impending) change. Large migratory animals integrate environmental variability across large areas, whereas smaller, sessile organisms will reflect local trends, which has consequences for their usefulness as indicator variables (e.g. for Early Warning Signals) for systems of different scope. Additionally, populations of species at the edges of discontinuities in body size distributions also exhibit greater variability, affecting their use as indicator variables of regime shifts (Nash et al. 2014).

System scope Ecosystems exist within a hierarchy of systems – from the physiological system of organisms to the biosphere or Earth system – and regime shifts can occur within each of these system levels. Regime shifts in one system can also trigger regime shifts in broader or nested systems, either through domino effects or through feedbacks (Rocha et al. 2018). Determining which is the ‘correct’ system scope to consider could be challenging – e.g. an ecosystem may be the system of interest, but if social-ecological feedbacks trigger a regime shift, then predicting, detecting or acting to avert it will require consideration of a larger system scope.

2.3 Prediction of regime shifts

Much of the recent work developing capacity to predict regime shifts has focused on early warning signals of impending transitions (e.g. Scheffer et al. 2015 and references in the first three rows of Table 2.3.1), but here I take a broader view of regime shift prediction. While knowing if a regime shift is imminent is important, ecosystem practitioners also need to know how it will happen (e.g. drivers and ecological mechanisms involved), whether they need to act (or can act) to avoid it (i.e. if the likely future regime is greatly different or undesirable), and how urgently action must be taken (i.e. when it will happen). In the following section, I pose a series of questions about regime shifts for which answers are required to characterise future regime shifts. For each question I describe the approaches that could be taken to obtain answers, and where specific methods exist for addressing the question, I describe those in greater detail in Table 2.3.1 (method numbers given in the text (e.g. MX), are cross-references to rows in Table 2.3.1).

2.3.1 Some specific questions and approaches to predict them

Question 1: Is a regime shift **imminent**? A large number of early warning signals (EWS) have been developed to predict whether ecosystems will suddenly shift to a different regime.

Most EWS metrics are based on two different phenomena found in some systems as they approach a bifurcation point: critical slowing down (CSD) of dynamics (e.g. increase in recovery time, rise in variance, increase in autocorrelation); or, stochastic ‘flickering’ of the community between alternative ecosystem regimes. A few other EWS are based on autonomous dynamics and patterns of the ecosystem (Scheffer et al. 2015), measures of disorder in multivariate time-series (Eason et al. 2013) and food web stability (Kuiper et al. 2015).

Approach: Generic early warning signals (M1-3) can be used to determine whether a regime shift is imminent, though there are a number of limitations and caveats (Table 2.3.1, M1-3). It is best to apply multiple EWS metrics, and preferably multivariate metrics (Drake and Griffen 2010; Spanbauer et al. 2014). Additionally, monitoring disturbance regime in the system for evidence of change might be used as an early warning (Dal Bello et al. 2019). With understanding of thresholds and mechanisms, more system-specific indicators could be developed (e.g. number of urchins in kelp forests, Marzloff et al. 2016b) for greater precision and reliability.

Q2. Which **driver/s** will cause the shift and what are the **threshold/s**? Most ecosystems respond to multiple drivers, but their dynamics may not involve thresholds or tipping points. Change in one driver may trigger a shift in some ecosystems, whereas in others the tipping point is likely to depend on levels of multiple drivers, and their interactions (multi-driver thresholds), (e.g. Fung et al. 2011; Möllmann and Diekmann 2012). Thus, to accurately predict which drivers are likely to trigger a regime shift requires an understanding of both predicted future trends in drivers, their relationships with key ecological variables, and how drivers might interact to create ‘multivariate’ thresholds. Also, tipping points may change before they are reached as ecosystems and species within them adapt and evolve to changing conditions (Dakos et al. 2019). It is important to note that abrupt shifts can occur in ecosystems even in the absence of external drivers, i.e. arising purely from internal ecological dynamics (e.g. Beninca et al. 2015; Hastings et al. 2018).

Approach: Observational data can be used to explore relationships between ecological variables and drivers by applying statistical models to observations e.g. GAMS (M4), potential analysis of probability distributions (M7), or others to identify possible thresholds. These approaches will only identify thresholds within the range of the observations. It is difficult to tease apart influence of different drivers purely from observations, and many drivers are predicted to reach levels beyond what has been previously observed. Thus, experimentation (especially multi-stressor, multi-species experiments) is required to extend understanding of ecological response to drivers and thresholds (Schroder et al. 2005). Dynamic ecosystem modelling can help understand synergies between drivers (e.g. Fung et al. 2011), and differences in drivers of forward and reverse transitions and management of those (e.g. Marzloff et al. 2016b) (M9), but these models need to be informed by deep understanding of the

system developed through experimentation.

Q3. Is there **hysteresis**? The presence of hysteresis increases the importance of avoiding a regime shift, as it makes reversing the shift much harder. However, the presence of hysteresis may not matter if the drivers cannot be controlled or reversed (e.g. climate change related drivers). There is also a spatial consideration: at a small spatial scale there may be alternative stable states, but at a larger spatial scale the shift may be continuous (e.g. Bathiany et al. 2016, Box 1).

Approach: Experimentation (Schroder et al. 2005) and dynamic ecosystem modelling (M8 & M9), where the skill of the models to detect hysteresis depends on how (well) the dynamics of the ecosystem are parameterized, and the spatial scale of the model. The presence of strong positive feedbacks could potentially indicate presence of hysteresis, but experimentation and modelling are required to confirm this. ‘Potential analysis’ (M7) of observational data can be used to identify alternative stable states (hysteresis) of the past, but future changes may not be consistent with this past behaviour of the system. Statistical exploration of relationships between species and drivers (M4) can be used to identify differences between forward and reverse thresholds. Spatial or temporal patterns and dynamics of the system could also be explored for evidence of flickering, which could indicate presence of an alternative regime (M2).

Q4. What are the key **ecological mechanisms**? Non-linear ecological responses to environmental change can take multiple forms, e.g. thermal physiological thresholds (e.g. Boyd et al. 2018; Hughes et al. 2017b), prey overcompensation (e.g. Gardmark et al. 2015), trophic cascades (e.g. Pershing et al. 2015), competition (e.g. Prowse et al. 2014), role reversal in predator-prey relationships following population depletion (e.g. Barkai and McQuaid 1988; Fauchald 2010). Positive feedbacks particularly create nonlinear responses. The ecological mechanisms that lead to a regime shift may be highly reliant on the nature of environmental change, and differ from those that prevent a reverse shift. Organisms with fast generation times relative to change in drivers may evolve or adapt to changing conditions in unforeseen ways, altering predicted biological responses.

Approach: Experimentation combined with modelling (M8 & M9) is the best approach to understand ecological mechanisms that might be involved in a regime shift. In ecosystems where experimentation is not possible, statistical exploration of observational data can provide insight into mechanisms (M5 & M6).

Q5. Can the system be guided towards a ‘**safe operating space**’? A safe operating space would be far enough away from thresholds or regions of bistability that stochastic events would be unlikely to push the system across a threshold. This would require understanding of multivariate thresholds (both forward and reverse tipping points), understanding of feedbacks and ecological mechanisms as well as the ability to control the drivers or ecological response

to changes in drivers. It may be possible to maintain or guide small, manageable systems towards a ‘safe operating space’, but more challenging/unlikely in large, open systems. It may also be the case that desirable ecosystem services depend on feedbacks that create hysteresis. *Approach:* Modelling to inform management: see M6 for an example with a single-species focus, but for ecosystem-based management, using ensembles of models (e.g. including M8-11) will be more informative. It may be difficult to predict outcomes of management actions that interact with complex, or poorly understood, feedbacks. It is therefore important to capture key processes and interactions between them in conceptual models (M12) developed through expert opinion (e.g. Margoluis et al. 2009).

Q6. When will the system shift? Knowing when an ecosystem might shift is important for planning and prioritising management actions. It requires knowledge of the likely pathway (driver + ecological mechanisms causing a shift), the thresholds, and if hysteresis is present, the likelihood of stochastic perturbations causing a shift before the threshold is reached. It is also important to understand lags between change in drivers and ecosystem responses, e.g. if some variables respond slowly to changes, or if long feedback loops (i.e. involving many intervening components) delay the impact of changes (Hastings et al. 2018; Walker et al. 2012). Key challenges include difficulty predicting large step changes in other systems (e.g. climate) which may trigger a shift sooner, and evolution or adaptation of ecosystem and components before the predicted threshold is reached.

Approach: Coupled dynamic ecosystem models incorporating projected changes in driver trends and stochasticity (M11).

Q7. What is the future state of the ecosystem? Is the future state likely to be one that is undesirable (i.e. do we need to act to avoid it)? Key considerations include likely bias in predictions depending on which species are monitored, and that future ‘state’ is not the same as future ‘regime’ (see Glossary for definitions). While a future state (e.g. initial species composition) might be predicted based on methods below, this is indication only of one future state, not the future regime (e.g. nature of species interactions, feedbacks and dynamics), or even the final community composition as the predicted state may be transitional. Species biomass trends on the approach to a regime shift are not reliable indicators of species dominance after the shift (e.g. Dakos 2018). The pathway (drivers and ecological mechanisms) will determine the available species pool that can make up a future ecosystem regime.

Approach: Some early warning signals may give an indication of future state, for example multivariate autocorrelation patterns (M1) and flickering (M2) tend to be towards the alternative regime. Past changes or regime shifts in similar systems may indicate one potential future regime, but similar systems can have inherently different dynamics (e.g. Ling et al. 2015), and ecosystems can change such that a pathway to a previous regime is no longer possible. Experiments can be used to predict future state, but observed outcomes depend on

drivers tested and available species pool. Using ecosystem models with predicted or conjectured responses to changes in drivers, and predicted available species pool can be useful for describing potential future states (e.g. M11 & M12), but can be highly uncertain.

Table 2.3: Methods and approaches available for predicting aspects of ecological regime shifts. Methods numbers (MX) are those referred to in the main text Section 2.3.1. Questions the method could be useful for addressing are given in the final column, and refer to the question numbers in Section 2.3.1 (parentheses around question numbers indicate those that may be addressed with the method, but to which the method is less generally suited).

Method No.	Method and example references	Requirements	Limitations	Advantages	Q's
<i>Generic early warning signals (EWS)</i>					
M1	Critical Slowing Down (CSD) EWS <ul style="list-style-type: none"> •Group of measures based on system dynamics slowing down as approach tipping point (e.g. increase in recovery time, rise in variance, increase in autocorrelation). •Many, many papers. Some example overviews: Dakos et al. 2015, 2013, 2012; Génin et al. 2018; Jager and Fullsack 2019; Kéfi et al. 2014; Majumder et al. 2019; Nijp et al. 2019; Scheffer et al. 2009; Scheffer et al. 2015. 	<ul style="list-style-type: none"> •Data: High resolution, regularly sampled ecological data (either temporal or spatial) •Ideally, need understanding of system to select appropriate state variables to monitor (e.g. Dakos 2018; Dakos and Bascompte 2014; Gsell et al. 2016). •Species with body sizes at the edge of discontinuities in body size distributions may be less useful than those at the centre (Nash et al. 2014). 	<ul style="list-style-type: none"> •Limited applicability to real, noisy systems. •Limited by changes in stochasticity or speed of system. •Not all species time-series will give signal. •Detection of EWS may be too late to act to avoid shift (e.g. in fast moving system). •Signal not expected for all types of regime shifts (e.g. step-change in the driver won't cause a CSD signal in ecological data). •If multiple stressors and thresholds being approached, the signal will be masked/confounded. •Challenging/unlikely to work for open pelagic systems due to system scale; ecological signal masked by movement of species. •Detection depends on data series length and resolution and false alarms possible. •For spatial methods, signal depends on spatially self-organised patterns, but these affected by spatial patterns of human disturbance, geomorphological features and gradients. •See e.g. Boettiger and Hastings (2012) and Dakos et al. (2015) for discussion of limitations. 	<ul style="list-style-type: none"> •If appropriate time series available, detection possible even without extensive understanding of the system. •Recommended for use as indicators of relative resilience of the system (over time or compared to similar systems)(Scheffer et al. 2015). •Presence of CSD EWS might give indication of type of pathway/mechanism (Dakos et al. 2015). •Able to apply spatial metrics in areas lacking high resolution temporal data. •Patterns of correlation between species CSD metrics approaching transition may provide indication of future state (Dakos and Bascompte 2014; Scheffer et al. 2015; van de Leemput et al. 2014). 	Q1 (Q7)
M2	Flickering EWS <ul style="list-style-type: none"> •Group of measures for systems that 'flick' between alternative states (basins of attraction) as approach tipping point. •Dakos et al. 2013; Kéfi et al. 2014; Scheffer et al. 2015 	<ul style="list-style-type: none"> •As for CSD EWS •Understanding of whether system is likely to 'flick'. 	<ul style="list-style-type: none"> •Large data requirement •System (or selected variables) may not flicker. •Detection of EWS may still be too late to act to avoid shift <p>For Q7:</p> <ul style="list-style-type: none"> •Likely bias in predictions based on which species are monitored. •Indication of future 'state' rather than future 'regime'. 	<ul style="list-style-type: none"> •Detection possible even without extensive understanding of the system. •May be detectable in systems where CSD EWS are not detectable due to high stochasticity. •Presence of Flickering EWS could potentially address multiple questions •For Q7: Not reliant on past observations of regime shifts, or on finding similar systems with alternative states. 	Q1 Q3 Q7

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Table 2.3 – Continued from previous page

Method No.	Method and example references	Requirements	Limitations	Advantages	Q's
M3	Information theoretic metrics to detect changes between ordered and disordered behaviour <ul style="list-style-type: none"> •Fisher information (Eason et al. 2019, 2016; Fath et al. 2003; Karunanithi et al. 2008; Spanbauer et al. 2014). •Global transfer entropy (GTE) (Bossomaier et al. 2018). 	<ul style="list-style-type: none"> •Methods developed for Fisher Information require multivariate time series or spatial information. •Global Transfer Entropy can be calculated from high-resolution univariate data (e.g. Bossomaier et al. 2018), but for ecosystems multivariate data is recommended. 	<ul style="list-style-type: none"> •Large data requirement •Have only been applied <i>post hoc</i> to time series of containing regime shifts. •Global Transfer Entropy not yet tested on ecological data. •May work best for systems with long transient states leading to regime shifts. 	<ul style="list-style-type: none"> •May provide earlier warning signal than other EWS. •Multivariate approach may provide clearer signal in complex ecosystems. •Also used to detect regime shifts after they occur, and to assess ecosystem resilience and its limits (Konig et al. 2019). 	Q1
Statistical models					
M4	Statistical exploration of relationships between drivers and species <ul style="list-style-type: none"> •Application of GAMs to observational data to identify non-linearity (Hunsicker et al. 2016). •Application of regression analysis to experimental data, where dual relationships between driver and species can indicate hysteresis (Scheffer and Carpenter 2003). 	<ul style="list-style-type: none"> •Concurrent observations of drivers and ecological response data, over range of driver levels (could be temporal or spatial replicates). •Or, results from appropriate experimental studies, ideally testing multiple driver combinations on multiple variables. 	<ul style="list-style-type: none"> •Difficult to tease apart effects of different drivers, unless this is based on experiments rather than observations. •Difficult to predict relationship beyond what has been observed. •Different drivers and thresholds may interact in ways not captured in the observations. •Relationships based on observations are not necessarily causal, and so not definitive evidence of a threshold. Also, because observational data required from either side of a threshold, the threshold can only be determined after it has been crossed. •Changes in system might alter shape of relationship between drivers and species before identified thresholds reached. 	<ul style="list-style-type: none"> •Option for systems where experimentation not feasible. •Useful for identifying trends before further investigation via experimentation. 	Q2 Q3
M5	Statistical exploration of relationships between species <ul style="list-style-type: none"> •Multivariate Autoregressive models (Ives et al. 2003) •Manipulation of observational timeseries (Pershing et al. 2015) •Non-linear approaches (Ushio et al. 2018) 	<ul style="list-style-type: none"> •Time series of multiple species observations •Preferably also time-series data of drivers. 	<ul style="list-style-type: none"> •Large data requirement: requires time-series (preferably long & high-resolution) of multiple species. •Scope limited by type of data available and range of conditions over which observations made. 	<ul style="list-style-type: none"> •Useful in ecosystems for which experimental manipulation not feasible. 	Q2 Q4

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Table 2.3 – Continued from previous page

Method No.	Method and example references	Requirements	Limitations	Advantages	Q's
M6	Statistical exploration of population dynamics <ul style="list-style-type: none"> •<i>Post-hoc</i> exploration of time series to diagnose mechanisms, e.g. Gardmark et al. (2015) •Bayesian approaches to avoid unknown tipping points (Boettiger et al. 2015). 	<ul style="list-style-type: none"> •Time series of species biological rates, population size structure and prey availability. 	<ul style="list-style-type: none"> •Single-species focus. <i>Post-hoc</i> exploration of time series to determine mechanisms: •Has a large data requirement and is indicative of mechanisms but not conclusive. •Only useful for <i>a posteriori</i> exploration of mechanisms: requires data from different regimes. 	<ul style="list-style-type: none"> •Useful for populations of key functional groups, e.g. ecosystem engineers. •Useful in ecosystems for which experimental manipulation not feasible. •Bayesian approach of Boettiger et al. (2015) useful to support management decisions where limited data available as it takes into account uncertainty in regions of parameter space unsupported by observations. 	Q3 Q4 (Q5)
M7	Analysis of probability distribution of ecosystem states <ul style="list-style-type: none"> •“Potential analysis” is a method for identifying alternative states from multimodal data (Hirota et al. 2011; Livina et al. 2010; Scheffer et al. 2012a) 	<ul style="list-style-type: none"> •Spatial replicates of alternative ecosystem state in spatially multimodal system or long time series data on ecosystem state (e.g. from single location). •Understanding and data on drivers. 	<ul style="list-style-type: none"> •Large data requirement •Different drivers and thresholds may interact in ways not captured in the observations. •Challenging to predict the relationship beyond what has been observed. •Changes in system might alter shape of relationship before reaching identified thresholds. •Identifies existence of past regimes or alternative regimes in similar systems, but not necessarily an indication of future dynamics. 	<ul style="list-style-type: none"> •Option for systems where experimentation not feasible. •Can be used to identify thresholds, and hysteresis (and potentially future state). 	Q2 Q3 (Q7)
Dynamic ecosystem models					
M8	Qualitative loop analysis of feedbacks <ul style="list-style-type: none"> •Dambacher et al. 2003; Justus 2006; Marzloff et al. 2011; Puccia and Levins 1985 •Qualitative simulation analysis, e.g. with QPress (Chapter 3) 	<ul style="list-style-type: none"> •Understanding of relationships between ecosystem components (existence and sign of interactions, but not strength). 	<ul style="list-style-type: none"> •Equilibrium approach - not applicable to systems without an equilibrium. •Only describes behaviour in local neighbourhood of equilibrium. •Imprecise: cannot quantify thresholds. •Spatial and temporal characteristics of interactions not captured. •Focuses on press perturbations, but cannot assess impact of pulse perturbations. 	<ul style="list-style-type: none"> •Can use to assess ecological thresholds (ie. ecological conditions under which system is stable) •Don't need to know interaction strengths. •Indication of possible hysteresis if strong net positive feedbacks, and negative correlations between sets of ecosystem components. 	(Q3) Q4

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Table 2.3 – Continued from previous page

Method No.	Method and example references	Requirements	Limitations	Advantages	Q's
M9	Quantitative modelling to elucidate drivers and thresholds ●Faassen et al. (2015), Fung et al. (2011), Griffith and Fulton (2014), Marzloff et al. (2016b), Scheffer (1989), and van de Leemput et al. (2016).	●Drivers, response of ecosystem to changes in drivers ●Predicted driver trajectories ●Relationships between drivers and ecological response, thresholds ●Understanding of system feedbacks	●Limited by information available for parameterisation, e.g. responses of ecosystem to interacting drivers, understanding of ecological mechanisms and their response to drivers.	●Can assess for hysteresis ●Can assess likely efficacy of different management actions in avoiding or promoting shifts.	Q2 Q3 Q4
M10	Quantitative modelling to predict future states ●Model scenarios based on either observed relationships or on conjectured responses (e.g. Ainsworth and Mumby 2015; Marzloff et al. 2016b)	●Balanced ecosystem simulation model (e.g. Ecopath with Ecosim) ●Experimentally observed or predicted responses to changing stressors	●Future changes often beyond what has been observed in the past, making it difficult to project ecological responses into models (e.g. previously unobserved functional responses). ●Unobserved relationships with drivers difficult to predict and therefore implement in models.	●Can test multiple scenarios (e.g. impact of pathway on future state). ●Could explore role of management actions in determining future state.	Q7
Integrated modelling approaches					
M11	Coupled models ●Species distribution models coupled with dynamic models to predict shifts in the future (e.g. Conlisk et al. 2013; Franklin 2010) ●End-to-end models incorporating multiple submodels for subsystems e.g. CMIP5/6 (Griffith and Fulton 2014; Melbourne-Thomas et al. 2017).	●Validated species distribution models coupled with dynamic climate (e.g. CMIP5/6) and/or ecosystem models (e.g. Atlantis, Ecopath with Ecosim). ●Projected trends and variability in drivers. ●Predicted lags between thresholds and shift (e.g. if slow variables involved, e.g. Ling et al 2015).	●All the limitations of separate models (e.g. information-in constrains information-out). ●Species may evolve/adapt to changing environment in a way not captured in the models, and which may alter predicted thresholds. ●Difficult to predict large step-changes in other systems (e.g. climate) which may trigger an ecological shift.	●Can explore multiple scenarios, and over longer time period than possible with field experiments. ●May be able to identify most likely pathway (driver + ecological mechanism) where multiple pathways possible.	Q6 Q7

Continued on next page

Table 2.3 – Continued from previous page

Method No.	Method and example references	Requirements	Limitations	Advantages	Q's
<i>Conceptual models</i>					
M12	<p>Conceptual models and expert judgement</p> <ul style="list-style-type: none"> •Collaborative development of conceptual models of ecosystem, its drivers and processes, as well as targeted ecosystem regime/state and strategies to mitigate drivers (e.g. Gladstone-Gallagher et al. 2019; Lindenmayer and Likens 2010; Margoluis et al. 2009). 	<ul style="list-style-type: none"> •Experts from diverse backgrounds and disciplines to workshop and crystallise understanding of the processes playing out in a system (Margoluis et al. 2009). Structured processes for training, eliciting and assessing expert opinions are important for reducing bias and improving accuracy and calibration of judgements (e.g. Burgman et al. 2011; Hemming et al. 2018; Sutherland and Burgman 2015). 	<ul style="list-style-type: none"> •Will capture biased view of ecosystem and its processes, depending on scope of interest, breadth of backgrounds, understanding and experience of the experts, but this can be overcome with appropriate elicitation processes and through revisiting the model over time. 	<ul style="list-style-type: none"> •Useful for identifying key processes and variables in systems for which data are insufficient to quantify. •Facilitates identification of interacting processes and drivers, as well as opportunities for intervention. •Because current understanding of the system is so clearly mapped out in conceptual models, they can be explicitly updated as new evidence/understanding of the system emerges. 	Q2 Q4 Q5 Q7

2.3.2 Considerations emerging from the findings of Section 2.3.1

In ecology, two broad categories of prediction exist: anticipatory predictions (prediction of the future) and explanatory or corroborative predictions (theoretical models that can be corroborated by data) (Maris et al. 2019; Mouquet et al. 2015). Predicting the answers to the questions we pose in some cases will involve anticipatory prediction, in other cases corroborative prediction, and in some cases both. For example, predicting when an ecosystem will shift is purely anticipatory - the answer cannot be corroborated until a regime shift occurs, or the predicted time passes. Predicting drivers and thresholds can be corroborative - e.g. it is possible to experimentally test thresholds that currently exist for the system; but it can also be anticipatory - will thresholds identified still exist by the time that level of the driver is reached (or will the system adapt/evolve altering the thresholds, or will more influential drivers arise making different thresholds more important). In most cases, anticipatory predictions are highly uncertain (likely to be wrong), making it necessary to use multiple approaches for both making the predictions, and for assessing risks in acting on those predictions (Mouquet et al. 2015).

Predicting the answers to many of the questions posed above depends on understanding the ecological mechanisms likely to be involved in the shift from one regime to another (Fig. A.1, Appendix A). Typically, the ecological mechanisms (e.g. key interactions) might be involved in some sort of positive feedback (see Table 2.1, and discussion above), but the interactions driving the shift will depend on how both negative and positive feedbacks are distributed over the ecosystem, and how the drivers affect the strength of individual interactions and feedbacks (Scheffer and Carpenter 2003). For example, in shallow lakes a shift from a clear to a turbid water regime could be driven by an increase in nutrients beyond what can be absorbed by the submerged vegetation or loss of (a critical mass of) submerged vegetation leading to resuspension of sediments (Scheffer et al. 1993). Submerged vegetation contributes to a number of positive feedbacks supporting the clear state, including stabilising the sediments, providing refuge for zooplankton from planktivorous fish and producing chemical compounds that suppress competing algae (Scheffer et al. 1993). The type of ecological understanding required to predict the ecological mechanisms and feedbacks triggering regime shift behaviour highlights the importance of long-term programs of observation and experimentation (e.g. shallow lakes, kelp-urchin shifts) (Marzloff et al. 2013; Marzloff et al. 2016b). Importantly, the ecological mechanisms and feedbacks need to be well understood to know how to avert (or reverse) a regime shift (e.g. Marzloff et al. 2016b).

Ecosystems frequently face numerous drivers and disturbances, which can interact with each other and ecological processes to modify thresholds (Biggs et al. 2018; Dal Bello et al. 2019; Ratajczak et al. 2018; Ratajczak et al. 2017). This makes predicting thresholds particularly

challenging, as often no single threshold exists, but a range of thresholds depending on levels of multiple drivers, as well as cumulative impacts from recent history of perturbations (Dal Bello et al. 2019; Ratajczak et al. 2017). If long positive feedback loops (i.e. those involving many intermediate interactions; see Glossary) are present, the ecosystem is likely to spend longer in transient states on a trajectory towards (possible) equilibrium and this can affect the ability of researchers and practitioners to recognise that a regime shift is occurring. Single-driver thresholds can be identified through experiments (depending on scale and speed of the system), but it is challenging to design experiments that effectively illuminate how multiple drivers and ecological processes interact to modify thresholds. This is even true for species with relatively short life-spans (e.g. phytoplankton, Boyd et al. 2018), and whether thresholds in these lower trophic levels will trigger larger system-scale regime shifts depends on the structure and nature of feedbacks over the ecosystem. There is added uncertainty around how ecosystems (and their component species) may adapt or evolve to changing conditions, which may alter thresholds before they are reached (Dakos et al. 2019) - especially in the face of increasing climate driven range shifts that create novel ecosystem assemblages (Hobbs et al. 2018; Pecl et al. 2017). Running experiments that capture potential evolutionary responses to drivers is difficult to do at an appropriate scale, and ecosystem models incorporating adaptation and evolutionary processes will be required to fill this gap. In the meantime, since persistence of precise thresholds into the future is difficult to predict, it may be best to focus on the likely pathway - i.e. mechanisms and driver - of the shift, rather than on specific threshold values. In many cases, expert opinion (and conceptual models) will be critical for identifying most likely pathways of transitions where data are lacking, for designing appropriate experiments and monitoring programs to obtain those data and for weighing up and selecting management strategies (see M12, Table 2.3.1, Margoluis et al. 2009).

In the face of an impending regime shift, ecosystem practitioners could choose to a) do nothing - i.e. continue managing the system as usual; b) try to avoid the regime shift (e.g. reverse the drivers away from threshold levels); or c) try to avert a sudden shift (e.g. by intervening in the ecological mechanisms/feedbacks of the system itself) to try to guide it along a smoother pathway of change (e.g. Figure 5.1, Chapter 5). The action pathway chosen will depend on the relative desirability of the current versus predicted regime, the practicality of managing the drivers, and how easily the ecological mechanisms can be controlled. Although many drivers cannot be controlled in time to limit their impact on ecosystems (e.g. climate change drivers), because thresholds are often likely to be multivariate (threshold level of each driver depends on the level of other drivers), it may be possible to focus on controllable-drivers to guide the system along a smoother pathway and avoid an abrupt shift. For example, transitions from rainforest to savannah are related to levels of precipitation (which is an emergent

property of the vegetated state and climate) (Hirota et al. 2011), however precipitation itself cannot be controlled. In this case, acting on other drivers such as deforestation will be more effective in supporting the rainforest regime. Control of ecological mechanisms is more complicated. For example, while strong positive feedback may create hysteresis, intervening to alter the feedbacks or reduce their strength could fundamentally change the ecosystem - i.e. cause a regime shift. Whether it is necessary to avoid a regime shift (from an anthropocentric perspective) depends on the importance of the emergent ecosystem services of the current regime, and how undesirable the predicted future state is likely to be.

2.4 Detection of regime shifts

Detecting that a regime shift has occurred is fundamental for managing an ecosystem appropriately. If the ecosystem is managed according to the dynamics and patterns of a previous regime, it could result in further regime shifts, or deterioration of ecosystem state (Hughes et al. 2013; Möllmann et al. 2009). Detecting that a regime shift has occurred may be relatively simple in some ecosystems, for example, where alternative stable states are well described or where the physical structure of the system substantially changes. In other ecosystems regime shifts are less evident, demonstrated by decadal lags in identifying their occurrence in several pelagic ecosystems (Hare and Mantua 2000; Möllmann et al. 2009; Reid et al. 2001). Following a regime shift, we might expect the ecosystem state (e.g. abundances of ecosystem components) to have changed, but this alone is not evidence of a regime shift as state can change dramatically within a regime (Biggs et al. 2012; Johnson 2009). Regime shifts involve reorganisation of ecosystem structure and function, with a change in self-reinforcing feedbacks (Biggs et al. 2012). Consequently, changes that might be evident following a regime shift include emergent properties such as spatial and temporal patterns, and dynamics dominated by (fundamentally) different processes.

In systems where regime shifts are difficult to identify (e.g. pelagic systems), detection has primarily been achieved by testing time-series data for evidence of a sustained shift in ecosystem state, and identifying the time of the shift. The different statistical approaches for detecting regime shifts from time-series data, their benefits and limitations have been well summarised and reviewed elsewhere (Andersen et al. 2009; Rodionov 2005). The major classes of approach involve identifying shifts in the mean state, the variance, the frequency structure and shifts in the system (Rodionov 2005). Major challenges for their application to ecological data include having short (and low-resolution) time-series, dealing with underlying trends in the data, identifying small magnitude shifts, distinguishing shifts from longer wavelength fluctuations or dealing with cases with multiple change-points (Andersen et al. 2009). Many of the available tests have limited statistical power to deal with these challenges, or

to quantify the uncertainty in the estimation of change-points in the data set. For example, one of the most popular methods for detecting regime shifts is STARS: a sequential t-test or f-test to identify shifts in the mean and variance respectively, of an ecological time-series (Rodionov 2004; Rodionov 2005). This method can handle multiple change-points and does not require many time-steps after the change-point (Rodionov 2005), but does tend to work better for larger magnitude shifts and if pre-whitening is applied to remove red noise. It requires some trial and error to determine the optimal parameter settings and though it can identify that a regime shift has occurred, the estimation of timing of the change-point tends not to be precise (Stirnimann et al. 2019).

Evidence of ecosystem regime shifts detected from time-series is most convincing where there is data indicating that multiple ecological variables have shifted (e.g. Hare and Mantua 2000; Möllmann et al. 2009) (but where alternative regimes are well characterised, evidence from a single indicator variable may be sufficient, e.g. chlorophyll-*a* in shallow lakes, algal cover on coral reefs). Also, in order to characterise the nature of the shift, understanding of trends in multiple organisms and trophic levels is required but can be difficult to obtain. There is also need to decide from which spatial domain it is appropriate to consider data together, highlighting the importance of expert opinion in identifying appropriate variables and making analytical decisions. Multiple variables can either be tested separately, or they can be combined into an ecosystem-wide metric, e.g. with principle component analysis (Möllmann and Diekmann 2012). Another option to increase certainty that a regime shift has occurred is to apply multiple detection methods to the same time-series (Biggs et al. 2012). Although this will increase the risk of falsely detecting a regime shift, if multiple methods all detect the same regime shift then the evidence is more convincing (Andersen et al. 2009). However, all these approaches depend on the assumption that a change in community structure must represent a regime shift, which while often true, is not necessarily the case.

Emerging methods for detecting regime shifts based on emergent spatial patterns - Characteristic Length Scale (CLS) estimation - provide an alternative approach, especially in ecosystems with little time-series data (Habeeb et al. 2007, 2005; Johnson 2009; Johnson et al. 2017; Ward et al. 2018). This approach is attractive because it requires data from few timepoints; however it still has a high data requirement, needing high-resolution spatial data (either 2D or 1D) of species (or other ecological variable) occurrence, and also depends on the presence of emergent spatial patterns (Habeeb et al. 2005; Keeling et al. 1997; Pascual and Levin 1999; Ward et al. 2018, Chapter 4). Greater availability of 2-dimensional spatial data from drones or satellites makes detection of regime shifts using CLS-estimation of 2D data increasingly feasible (Habeeb et al. 2005). On the other hand, transect (1D spatial) data exist for many more ecosystems, which could be used to detect regime shifts using the

1D-CLS estimation approach; however 1D-CLS may be less sensitive than the 2D approach (Ward et al. 2018, Chapter 4). Importantly, because CLS estimation involves reconstruction of the ecosystem attractor, change in CLS provides more definitive evidence of a shift from one ecosystem attractor to another than does a change in ecosystem state (Johnson 2009; Johnson et al. 2017). A particular feature of this approach is that it distinguishes cases where there is change in structure but no regime shift from those where change in structure is reflective of a regime shift (Johnson 2009; Johnson et al. 2017). How changes in emergent CLS relate to changes in spatial early warning signals remains an outstanding question.

2.5 Southern Ocean case study

In the following section I step through the framework with Southern Ocean ecosystems as a case study to illustrate how it can be used to evaluate capability to predict, characterise and detect regime shifts. First I provide a brief overview of the system, followed by an investigation of its potential vulnerability to regime shifts, based on the characteristics described in Tables 2.1 and 2.2. I then explore available evidence and data that could be used to predict the nature of regime shifts, based on the approaches detailed in section 2.3.1. Finally, I discuss available data that could be used to detect regime shifts once they have occurred.

Southern Ocean ecosystems include a range of coastal, pelagic, benthic and sea-ice habitats (Constable et al. 2014). The pelagic habitat is divided by circumpolar currents, with strong poleward gradients of most parameters, which has resulted in isolation of species and high endemism and biodiversity (Chown et al. 2015). The region is highly seasonal, with high latitude areas experiencing extremes of light, temperature and productivity (Deppeler and Davidson 2017). It seasonally hosts numerous important migratory predators such as whales and seabirds, many of which prey on Antarctic krill, a keystone species (e.g. Bestley et al. 2019; Cleeland et al. 2014). Other (non-krill) trophic pathways (e.g. through copepods and fish, and through gelatinous zooplankton) are also important, especially in some sectors (McCormack et al. 2019b). Though remote, Southern Ocean ecosystems provide important ecosystem services including high volume krill and high value toothfish fisheries, and high seasonal productivity supports high export of anthropogenic carbon (Boyd et al. 2019; Grant et al. 2013; MacGilchrist et al. 2019).

Key challenges for assessing regime shifts in the Southern Ocean include a lack of baseline data and the fact that it is not stationary; the ecosystem is recovering from past over-harvesting, while also being affected by directed changes in climate. By stepping through the process using Southern Ocean ecosystems, I hope to demonstrate how the framework can be used both to directly assess the ecosystem, and how it can be used to direct/prompt future research and data collection by identifying gaps in understanding and capability. Application

of the framework to Southern Ocean ecosystems is detailed in Tables 2.1 & 2.2, and in the Box 2 below, and in the following text I discuss the key issues (with terms in bold font indicating those discussed in Tables 2.1 and 2.2).

2.5.1 Vulnerability

(based on ecosystem properties; Tables 2.1 and 2.2) The potential vulnerability of Southern Ocean ecosystems to regime shifts based on network properties is difficult to assess due to the lack of understanding of the distribution and importance of **non-trophic interactions** over the food web (Table 2.1, see also Chapter 3). Some non-trophic interactions are recognised, for example that some flying seabirds benefit from following whales (and fishing vessels), which locate and concentrate prey items such as krill close to the surface (**a higher-order interaction**) (Hodges and Woehler 1994; Veit and Harrison 2017). However, the importance of these interactions for the functioning of the ecosystem is not known. For example, the proportion of krill consumed by seabirds that results from following whales has not been studied. Additionally, **positive feedbacks** from predator faeces fertilising phytoplankton blooms, and attraction to chemical compounds released by phytoplankton, potentially promote high phytoplankton and krill biomass (Nicol et al. 2010; Savoca and Nevitt 2014), but may increase vulnerability to regime shifts and affect capacity to predict community response to perturbation (Chapter 3).

Krill occupy an important, **wasp-waist link** between phytoplankton and higher trophic levels in the food chain in some sectors of the Southern Ocean (Atkinson et al. 2014), thus the system is vulnerable to changes in krill population and behaviour. For example, many Southern Ocean predators are dependent on the swarming behaviour of krill which concentrates smaller prey items into more energetically beneficial meals. However, it is unclear how krill behaviour, and behavioural responses to chemical cues (e.g. avoidance or attraction), will change in response to changing conditions (e.g. temperature, CO₂) or how this will affect their swarming behaviour and ‘catchability’ by predators. Many predators can switch prey in response to reduced access to their preferred prey, but how and when they are able to, and the energetic and ecosystem consequences of **prey-switching** behaviour are poorly understood, making it difficult to predict long term trends (e.g. Bedford et al. 2015; Croxall et al. 1999; Trathan et al. 2007; Xavier et al. 2018).

While the pelagic habitat has no foundation species to form habitat structure, in the Southern Ocean sea-ice forms an important physical habitat for life at many scales. Sea-ice plays the role of a habitat-forming species and its seasonal growth contributes to a self-supporting **positive feedback** (enhancing sea-ice formation by increasing albedo and decreasing absorption of radiation), but the reverse feedback inhibits sea-ice growth when temperatures

are above freezing (Goosse et al. 2018). Sea-ice provides important habitat and the algae growing beneath it are an important food source for Antarctic krill and other organisms (Kohlbach et al. 2017). Changes in sea-ice extent, thickness and dynamics are likely to drive change in dependent communities (e.g. Trathan et al. 2019). Already in the Western Antarctic Peninsula region (WAP), climate-related changes in the sea-ice environment, together with other environmental changes, have driven ecosystem change at multiple trophic levels (e.g. Bestelmeyer et al. 2011; Montes-Hugo et al. 2009; Trivelpiece et al. 2011). Changes in sea-ice and floating ice-sheet cover will also affect benthic systems through altered light, mixing, sedimentation and ice-berg scour **disturbance regimes**, and is likely to change the type of benthic **habitat-forming species** that dominate (e.g. Clark et al. 2013; Dayton et al. 2019). Additionally, warming waters are likely to drive large-scale species redistribution in the Southern Ocean, with the potential to alter the ecosystem structure and the **distribution of interaction types and strengths** (e.g. Aronson et al. 2015). Together these features make Antarctic benthic systems particularly vulnerable to regime shifts, most likely at local scales (though there may be regional patterns of change) (Griffiths et al. 2017).

2.5.2 Predicting regime shifts for Southern Ocean ecosystems

Box 2 summarises how the prediction questions posed in Section 2.3.1 have been or could be addressed for Southern Ocean ecosystems. The potential for existing data to be tested for evidence of generic Early Warning Signals (EWS) is limited by the patchy, irregularly sampled ecological data available in the Southern Ocean (Brasier et al. 2019), and because it is an open ocean system there is unlikely to be a clear signal of approaching transitions (Dakos et al. 2015). Nevertheless, current development of ecological Essential Ocean Variables (eEOVs) for the Southern Ocean provides an opportunity to target data collection towards variables that could give a signal of impending regime shifts (Constable et al. 2016), though careful consideration of the system scope being observed will be needed (Box 1). Collecting data on multiple trophic levels concurrently (i.e. from the same temporal and spatial domain), targeting spatially constrained regions (e.g. benthos, enclosed bays), observing a mix of specialists and generalists (Dakos 2018; Dakos and Bascompte 2014), and considering body-size distributions (Nash et al. 2014) would maximise capacity for predicting regime shifts. Technological advances (e.g. buoys moored on the shelf, in the sea-ice zone, environmental DNA) are likely to increase capacity for remote, regular sampling of many variables from many trophic levels as well as concurrent environmental conditions (Newman et al. 2019). Ecological variables are likely to give the clearest signals for more spatially constrained communities (e.g. enclosed bays), but given that open ocean systems are thought to be more likely to exhibit shifts in response to climatic regime shifts rather than biological thresholds (Conversi et al. 2015; Lees et al. 2006), it is also recommended to apply EWS to

climatic variables from this region as well, particularly to sea-ice parameters.

Box 2: This box highlights available evidence, data and approaches that could be used to address each of the questions posed in Section 2.3.1 for Southern Ocean ecosystems. A summary of the potential to currently address each question is given in italics, and specific examples and data are provided in the dotpoints. Numbers, MX, are cross-references to methods described in Table 2.3.1. See Sections 2.3.1 and 2.3.2 for more detailed discussion of the general approaches to address these questions, and the main text in this Section for a more detailed discussion of the Southern Ocean case.

Q1: Is a regime shift **imminent**?

This is not currently assessable for the pelagic ecosystem (methods not appropriate), or for most spatially constrained Antarctic marine ecosystems (lack of data). May be possible to assess for approaching climate transitions which could drive shifts in ecosystems.

- For the open pelagic ecosystem Critical Slowing Down EWS unlikely to be appropriate (M1).
- There are few appropriate time series or spatial data at most ecosystem levels, especially multivariate time series. Some predator time-series and a couple of long term ecosystem observation programs exist which could be tested, but these data may not be of sufficient length or resolution (e.g. Hindell et al. 2017; Smith et al. 1995; Weimerskirch et al. 2003).
- Trait-based information such as breeding success time-series of long-lived predators may be more appropriate than population time series for exploration of EWS (Baruah et al. 2018).
- Ecological Essential Ocean Variables (eEOVs) being developed which could be used for this in the future (Constable et al. 2016), for some geographically constrained areas.
- Whale body size used as warning signal of impending stock collapse (*post hoc*) (Clements et al. 2017).

Q2. Which **driver/s** will cause the shift and what are the **threshold/s**?

Addressing these questions is possible (but challenging) for lower trophic levels, and is an active area of research. Predicting thresholds for higher trophic levels, and whole-of-ecosystem transitions would depend on extrapolation and expert opinion (educated guesses). There is need to better understand how thresholds depend on multiple drivers.

- Possible drivers: fishing, species invasions, plus numerous, interacting climate related changes (e.g. Deppeler and Davidson 2017; Montes-Hugo et al. 2009). The Marine Ecosystem Assessment for the Southern Ocean (MEASO) project currently underway is a key avenue for gathering expert opinion and data on the relative importance of these drivers.
- Timing of changes in drivers uncertain - order and succession of changes will determine community responses (Deppeler and Davidson 2017).
- Possible threshold-levels of drivers are likely not contained within the limited ecological time-series.
- Likely CO₂ driven tipping point in phytoplankton community composition (e.g. between 634 and 953 μatm of $f\text{CO}_2$, Hancock et al. 2018), but phytoplankton may evolve, altering this threshold before it is reached.
- Predicted light driven tipping points in benthic community with changing timing of

sea-ice cover (Clark et al. 2013).

- Tipping points predicted for oceanic productivity are multivariate: depending on both changes in light (from changed mixed layer depth), and on iron availability (Llort 2015).

Q3. Is there **hysteresis**?

Drivers and thresholds for which experimental studies of hysteresis could be carried out (climate drivers on lower trophic levels) are changing directionally, making even regime shifts without hysteresis irreversible. There is a lack of threshold data to inform ecosystem modelling studies into community-level hysteresis.

- Experimentation possible in near-shore benthic habitats but not in the open ocean (other than in mesocosms with lower trophic levels).
- Time-frame of changes in driving (climate change related) variables too long for scale-appropriate experiments.
- Hysteresis implied for possible high versus low productivity regimes related to whale abundance and iron recycling (e.g. Nicol et al. 2010; Ratnarajah et al. 2014, 2016).
- There may be paleo records (e.g. phytoplankton in sediment cores) that could be explored with ‘potential analysis’ of probability distributions (M7), but how relevant this will be depends on levels of drivers in the past, compared to what is predicted for the future.
- Multiple ecosystem models (M9, M11) being set-up will make it possible to explore thresholds and assess for hysteresis (Brasier et al. 2019).
- Available ecological time series data may not be of sufficiently high resolution to identify flickering (M2).

Q4. What are the key **ecological mechanisms**?

Challenging to fully develop understanding of possible ecological mechanisms for regime shifts, especially at the fine scale (paucity of multivariate time series data). There is scope to better address this question.

- Most available time-series not matched by data from other ecosystem components (e.g. many predator time-series but few concurrent prey field data, e.g. as part of the CCAMLR Ecosystem Monitoring Program, CEMP). This makes it difficult to explore ecological mechanisms.
- Long time series containing multiple variables available in the East Pacific Sector of the SO: (Palmer LTER, Rothera Rats; Brasier et al. 2019) which could be used to identify some, coarse-scale mechanisms.
- Concurrent tracking and mounting of video loggers on predators (Thiebot et al. 2016), with diet data, which is increasingly available (e.g. from DNA metabarcoding of faeces, McInnes et al. 2017), offer advances for identifying mechanisms.
- More targeted data collection from the breadth of trophic levels within the same spatial and temporal domain is required.
- Experimentation is challenging, but models are being developed which could be used to explore potential ecological mechanisms (Brasier et al. 2019).

Q5. Can the system be guided towards a ‘safe operating space’?

Unknown. Ensemble modelling to predict responses to change, combined with expert opinion and precautionary approaches to management is the best hope in the absence of understanding of thresholds and ecological mechanisms for regime shifts.

- ‘Safe operating space’ is unknown and feedback mechanisms poorly understood.
- Fishing pressure is the main manageable driver, the many climate-related drivers cannot be controlled on relevant time-scales.
- The precautionary catch limit set for Antarctic krill is an attempt to maintain the system within a safe operating space, in the absence of understanding of thresholds in the system (Constable et al. 2000).
- Continued development of ecosystem models will enable exploration of management options and outcomes (Brasier et al. 2019).

Q6. When will the system shift?

This is not currently predictable given lack of information on thresholds.

- Ecosystem models (M10 & M11) that could be used to explore this question are under development (Brasier et al. 2019), but information on drivers, thresholds, mechanisms, and likely pathways is required to parameterise them.
- Order in which different drivers will become important is still uncertain (Deppeler and Davidson 2017).

Q7. What is the future state of the ecosystem?

Not yet predictable due to high number of unknown factors (e.g. timing of shift and available species pool and environmental conditions at that time).

- There are few appropriate ecological time series data that could be explored to predict future state from flickering (M2) or for multivariate autocorrelation (M1), except potentially from the WAP (Brasier et al. 2019). In the future, predator dietary data (e.g. DNA metabarcoding of faeces) could be used to detect shifts in availability of lower trophic levels, but these time-series are currently too short.
- No similar system to compare with, but changes in different regions (e.g. WAP) may indicate future changes in other regions.
- Past changes (e.g. M7) could be explored (to gain an understanding potential future states) in a few paleo records, e.g. predator paleo guano time-series reconstruction, ancient DNA (e.g. Younger et al. 2016), diatoms in sediment cores; however, it is not clear if these capture a different regime, and driver trends are unlikely to return to previous state.
- Several Southern Ocean ecosystem models (in different regions and at different scales) exist or are being developed which could be used to explore possible future states (Brasier et al. 2019), in combination with expert judgement.

Capacity to predict ecological mechanisms and thresholds in Southern Ocean ecosystems is challenged by issues of scale and accessibility. The Southern Ocean is a harsh, and high-risk

environment in which to operate, making it challenging to conduct *in-situ* experiments to identify thresholds. Experiments that have been conducted have necessarily been small scale, considering relatively few drivers and on lower trophic levels with relatively fast generation times (e.g. Hancock et al. 2018) and/or are conducted in *ex-situ* with organisms isolated from their ecological context (e.g. Boyd et al. 2015a). However the system is facing concurrent changes in multiple drivers (e.g. temperature, wind patterns, salinity, sea-ice, pH, etc.) that can act synergistically, will affect different organisms and trophic levels differently, and are changing over longer time scales (Constable et al. 2014; Deppeler and Davidson 2017; Gutt et al. 2015). Modelling studies can be used to fill this capability gap (e.g. Clark et al. 2013; McNeil and Matear 2008), but these need to be informed by understanding of ecological relationships (and physiological limits) developed through experimentation, long time-series observations and expert opinion. Planned advances in observational capability (Newman et al. 2019) will be essential in extending the understanding of ecological processes and relationships in the Southern Ocean, and for predicting thresholds arising from them.

2.5.3 Detection of past regime shifts in Southern Ocean ecosystems

Capacity for detecting past regime shifts in the Southern Ocean ecosystems is also limited by data availability. For example, given the multifunctional, ecosystem-engineering role of whales (Roman et al. 2014) it is possible that their past near-extirpation from the Southern Ocean caused a regime shift, but a lack of baseline data means this cannot be definitively assessed (though with the right models some assessment might be possible) (Chapter 1.2.3). Southern Ocean ecosystems encompass several habitats, sectors, environmental gradients and boundaries, and data from different trophic levels are frequently not associated with concurrent timeseries of other trophic levels from the same domain (Brasier et al. 2019). This makes it challenging to identify system-wide shifts (as opposed to shifts in individual species or functional groups). For example, more recent (1980's and 1990's) changes in higher predator populations (Reid and Croxall 2001; Weimerskirch et al. 2003) suggest the possibility of shifts in the system, but paucity of concurrent data from lower trophic levels limits capacity to determine the system-scope of the change. In the Atlantic sector there are indications that it was related to changes in krill availability (Reid and Croxall 2001), but the nature of the change is less clear. These data sets are candidates for the application of change-point analyses described earlier. For benthic habitats, there is the potential to use camera, AUV or SCUBA transects to identify regime shifts using the 1D-CLS method (Ward et al. 2018, Chapter 4), and in the pelagic zone this method could be applied to underway transects during voyages (e.g. Appendix E), however in this latter case the system scale is likely to be ecological-oceanographic rather than being purely ecological. Remotely sensed chlorophyll-*a* data could be explored using 2D-CLS methods (Habeeb et al. 2005) but may

be hampered by missing data caused by cloud cover.

2.5.4 Summary for Southern Ocean ecosystems

Application of this assessment framework to Southern Ocean ecosystems highlights both the likely vulnerability of benthic and sea-ice communities to regime shifts, as well as the need for targeted data collection using new technology as it becomes available. Step-changes in drivers and altered disturbance regimes are likely to alter the dominance of habitat-forming species in Antarctic shelf benthic ecosystems, making benthos particularly vulnerable to regime shifts. Positive feedback in sea-ice growth means that beyond a threshold temperature, sea-ice growth will be inhibited. This will affect sea-ice algal communities at the local scale, but the importance of sea-ice for the whole system means loss of sea-ice is likely to cause regional scale shifts. While pelagic communities are likely to be affected by shifts in the sea-ice, the intrinsic vulnerability to regime shifts is less clear, highlighting the need for greater understanding of the importance of different feedback processes. Future targeted collection of time-series data from multiple trophic levels within the same spatial and temporal domains will increase capacity both to develop a better understanding of ecological mechanisms and feedbacks, and to predict and detect regime shifts.

The application of this framework to Southern Ocean ecosystems has identified a number of data sources that could be used to address key questions posed (Section 2.3.1, Box 2; see also Brasier et al. 2019), and the process has additionally identified data gaps limiting capacity to identify and understand regime shifts in this system. In general, the taxonomic, spatial and temporal patchiness of ecological data available from the Southern Ocean limits possible evidence of ecosystem-level regime shifts (e.g. Brasier et al. 2019; De Broyer et al. 2014). Key strategies recommended to advance capacity to assess for regime shifts include: i) identifying spatial domains (at different scales) which behave consistently (e.g. Trebilco et al. 2019), and which can be feasibly sampled regularly; ii) selecting a range of ecological variables which could provide signals of shifts, including shifts in dominant ecological mechanisms, processes and feedbacks within each spatial domain; and iii) identifying and monitoring variables that can provide links between spatial domains and across scales to evidence broader-scale shifts. Judicious selection of areas for longer-term research programs, use of technological advances for sampling, and prudent selection of ecological variables could advance current capacity to predict, detect and characterise regime shifts in Southern Ocean ecosystems, despite the physical challenges the environment engenders. Collaborative expert opinion and ecological modelling exercises are key to designing and refining such a program (e.g. Constable et al. 2016; Newman et al. 2019).

This has been a first, broad-scale assessment of the vulnerability of Southern Ocean ecosys-

tems to regime shifts, and the capacity for predicting and detecting such shifts. Future work will be required to conduct more formal risk assessments and to develop processes for incorporating these assessments into management procedures. Implementing or updating ecosystem management procedures (e.g. in response to predictions of regime shifts) could occur through the Commission for the Conservation of Antarctic Living Resources (CCAMLR) or might require joint decision-making across multiple agreements, such as between CCAMLR and the International Whaling Commission (IWC). Generally, adaptive management that combines annual measures and within-season provisions with assessments of future ecosystem trends and shifts will help reduce the risks of negative impacts on Southern Ocean ecosystems (IPCC 2019a).

2.6 Conclusion

This review has presented a variety of approaches to assessing different aspects of ecological regime shifts and synthesised these into a general framework. This framework is intended to assist both researchers and ecosystem practitioners to ascertain the status and nature of regime shifts in their ecosystem, and to proactively adapt management to address changes before or as they occur. To increase the accessibility of this information to a broader range of ecosystem stake-holders and policy decision makers, it could usefully be translated into a risk assessment protocol (e.g. Hobday et al. 2011).

A key overarching consideration is the spatial and/or temporal scale at which to consider and observe for regime shifts and features that make ecosystems vulnerable to them (Box 1). Recent analyses highlight the interconnectedness of many regime shifts - with regime shifts in different systems being connected by not only shared drivers, but also hidden feedbacks and cascading changes (Rocha et al. 2018). What is clear is that ecosystems will increasingly reach and cross thresholds as the climate and other pressures on ecosystems reach levels beyond what present-day ecosystems have experienced. Ecosystem practitioners and policy-makers will need to be able to proactively assess for and respond to impending and detected regime shifts. A broad suite of tools and approaches, such as those presented here, will be required to achieve this.

Interleaf 1

The previous chapter highlighted the importance of feedbacks, higher-order interactions and the distribution of non-trophic interactions over a community network for determining stability and vulnerability to regime shifts. The next chapter explores these features more in depth using the example of a Southern Ocean community. To do this, I use and present a novel application of simulation-based qualitative network modelling combined with machine learning classification.



CHAPTER 3

Trophic mediation and ecosystem stability: an assessment using qualitative network models

3.1 Abstract

Regime shifts are fundamental changes in ecosystem structure, function and dynamics and the presence and relative importance of positive feedbacks in an ecosystem strongly influences its stability and the likelihood of regime shifts. A potentially important positive feedback in the Southern Ocean ecosystem involves production of a chemical cue, dimethyl sulfide (DMS), by some phytoplankton. Production of DMS can promote phytoplankton growth by attracting predators of phytoplankton-grazers, and nutrients released as faeces from those predators help fertilise the water column. Here I used a qualitative modelling approach to explore how uncertainties in the nature of this feedback affect community stability in a set of small, community models. I found that stability varied substantially depending on how the community was modelled, but that the interactions most important for determining stability were consistent across all models. Community stability was sensitive to the strength of phytoplankton competition, controls on phytoplankton, DMS production and release, and predator attraction to DMS, suggesting that the community could be destabilised by perturbation affecting these interactions. Incorporating DMS-mediated feedbacks into a larger Southern Ocean network had a moderate impact on stability characteristics and altered the trophic level at which the system would be most vulnerable to perturbation.

3.2 Introduction

The possibility of regime shifts – fundamental changes in ecosystem structure, function and dynamics – occurring in ecosystems is of concern, and tools for assessing their likelihood

are required by researchers and decision-makers (Scheffer et al. 2001). Regime shifts are difficult to predict and manage and to do so requires a deep understanding of underlying mechanisms. One feature that consistently arises as important for regime shifts is the presence of net positive feedbacks which can destabilise a system (Marzloff et al. 2011; Scheffer et al. 2009). Positive feedbacks can cause unsustainable growth or decline of species, which beyond a threshold destabilises the community. This can trigger the system to transition to an alternative stable state (e.g. consisting of different abundances of the same species), or it could also trigger a complete collapse and replacement by a completely different community, with different network configurations. In fact, the strength of net positive feedbacks in a system determines the degree of hysteresis between forward and reverse transitions (Kéfi et al. 2016b).

Positive feedbacks often involve higher-order interactions as well as positive, non-trophic interactions, which are themselves also implicated in system stability (Grilli et al. 2017; Kéfi et al. 2016a; Kéfi et al. 2016b; Kondoh and Mougi 2015; Levine et al. 2017). These types of interactions are typically challenging to study, and to incorporate into ecosystem models, particularly into food web models (Berlow et al. 2004). Nevertheless, in some ecosystems, such as plant-pollinator communities, non-trophic relationships are well studied and recognised. In pelagic ecosystems, the nature of many of the higher-order and non-trophic interactions (that could potentially be involved in positive feedbacks) are uncertain because community structure is generally reconstructed from trophic data (i.e. ignoring non-trophic interactions), and non-trophic interactions are difficult to observe at sea. Consequently, the strength and importance of non-trophic interactions and feedbacks in the pelagic system are often poorly understood. This makes it difficult to assess whether they are likely to be involved in regime shifts, or how important they are for the emergent dynamics of ocean ecosystems.

An interesting proposed positive feedback in the Southern Ocean pelagic ecosystem involves the production of the infochemical dimethyl sulfide (DMS) by some phytoplankton and sea-ice algae (Savoca and Nevitt 2014). This chemical is released by some phytoplankton as they are grazed and is an attractant for many predatory species (e.g. birds, seals, fish) (DeBose et al. 2008; Kowalewsky et al. 2006; Nevitt et al. 1995). It is thought that the phytoplankton producers of DMS benefit from reduced predation as their grazers are consumed by the predators attracted to the DMS (Savoca and Nevitt 2014). Additionally, predators, particularly large predators such as whales, can contribute to phytoplankton productivity by fertilizing the water column with nutrients from their faeces (Nicol et al. 2010; Ratnarajah et al. 2014; Savoca and Nevitt 2014).

The importance of DMS as an infochemical among lower trophic levels in pelagic systems has been explored by Lewis et al. (2012, 2013) who used quantitative models to explore the effects of DMS production by phytoplankton in simple predation and competition models,

using attraction to DMS as a ‘tuning’ parameter. They found that attraction of predators to DMS stabilised system dynamics in a predator-prey model (and even promoted phytoplankton blooms) (Lewis et al. 2012), and that attraction of grazers to DMS promoted coexistence of phytoplankton groups in a competition model (Lewis et al. 2013). In the Southern Ocean, the strength and configuration of DMS-mediated interactions are largely unknown. Moreover in this region, DMS-mediated interactions are thought to involve much larger species (megafaunal rather than planktonic predators) than modelled by Lewis et al. (Amo et al. 2013; Nevitt et al. 1995; Savoca and Nevitt 2014).

One approach to assess for potential regime shifts is to construct a stability landscape (e.g. range of parameter values for which the regime is stable) of the ecosystem (Beisner et al. 2003). However, doing this quantitatively for systems in which the strength and configuration of the interactions are uncertain is difficult. When interaction strengths are unknown, an alternative approach is to construct qualitative network models (Levins 1974). Qualitative network models are codified conceptual models that enable exploration and interrogation of the conceptual understanding of a system (Dambacher et al. 1999; Levins 1974; Melbourne-Thomas et al. 2012). The method is particularly useful for data-poor systems because no assumptions are required about the strength or shape of relationships between species - only the sign and direction of interactions are modelled. Strengths of the qualitative approach include that different types of interactions can easily be accommodated in within a single model, and that it facilitates exploration of alternative network structures where uncertainty exists (Dambacher and Ramos-Jiliberto 2007; Dambacher et al. 2007; Melbourne-Thomas et al. 2012).

Qualitative network models have been used to explore the role of feedbacks in determining network stability (Dambacher et al. 2003), to assess alternative persistent states (Marzloff et al. 2011), and to predict ecosystem response to perturbation (e.g. Melbourne-Thomas et al. 2013). Here I am primarily interested in ecosystem stability, and whether the presence of DMS-mediated feedbacks might make the system more vulnerable to collapsing or shifting towards a different ecosystem structure. I carefully make a distinction between alternative stable states (of the same network structure) and other types of regime shifts that could occur when a community moves into an unstable parameter space (and focus interpretations on the latter case). I combined two different qualitative approaches, simulation and symbolic analysis of community matrices, to explore the implications of the uncertainties in DMS-mediated interaction networks for evaluation of system stability. I first explored stability feedback configurations in a set of alternative, small ‘motif’ versions of the network, and then explored how these interactions could be incorporated into larger Southern Ocean trophic networks. For each model I aimed to identify the interactions most influential in determining stability, and how these related to the patterns of feedback present in the network.

3.3 Methods

3.3.1 Qualitative network modelling

Qualitative network modelling is a useful tool for exploring ecosystem structure and stability when the exact strengths of interactions are uncertain (Dambacher et al. 2002, 2003; Melbourne-Thomas et al. 2012). The interaction network is represented as a signed directed graph (digraph) of nodes (interacting entities) connected via edges (their interactions). Edges represent the sign (\bullet is negative; \rightarrow is positive) and direction, but not the magnitude, of pairwise interactions. The approach for incorporating mediated interactions (where the interaction between two nodes is modified by a third node) into the pairwise framework has been formalized previously (Dambacher and Ramos-Jiliberto 2007). Mediated interactions were modelled following Dambacher and Ramos-Jiliberto (2007) such that: if a trophic interaction ($\bullet \rightarrow$) is enhanced by a third node, then it results in a negative pairwise effect from the mediating node to the node of the prey, and a positive effect on the predator (and only the net pairwise interactions arising from this mediation are included in the community matrix). If the mediating node suppresses a trophic interaction, then there is a positive effect on the prey and a negative effect on the predator from the mediating node. From the model network, a community matrix of interaction coefficients is constructed, with each pairwise edge in the network model represented in the community matrix. Mediated interactions are reduced to their net pairwise effects, as described above, and represented in the community matrix as pairwise effects. In the symbolic approach the community matrix is analysed symbolically through analysis of feedbacks, but weights are not assigned to interactions (see Section 3.3.5 for more detailed description of the symbolic approach). In the simulation approach a large number of community matrices are constructed with randomly assigned edge weights, such that the underlying qualitative model is identical (see Section 3.3.3 for details of the simulation approach).

3.3.2 Alternative model structures

I constructed three groups of models based on the models of Lewis et al. (2012, 2013) (Figure 3.1). The first group of models are predator-prey models and have a DMS-producing phytoplankton group that is consumed by grazers. The second group of models include an additional phytoplankton group which competes with the DMS producers for nutrients. The third group of models is similar to the second, but the presence of the other phytoplankton group is beneficial to the DMS producers by being the favoured prey of the grazers (Haberman et al. 2003b). In the model of Lewis et al. (2013), both predators and grazers show attraction to DMS, but in our example the importance of grazer attraction to DMS is less clear. Antarctic krill initiate and increase their search behaviours in response to phytoplank-

ton odours (Hamner et al. 1983; Weissburg et al. 2019), but the possible responses of these grazers are likely to be less important when compared to the great distances over which some predators may respond to DMS. This uncertainty in structure is explored in different models.

There are both direct costs and benefits of DMS production to DMS producers. For these models I assume that these costs and benefits balance out so that there is no direct effect of DMS on DMS producers, except in Model 3 and Models 6-9 where DMS mediates the trophic interaction between DMS producers and grazers. Other uncertainties in the sign of edges are not explored in this paper. QPress accepts constraints on edge weights, and in all cases when using the simulation modelling approach, the strength of the direct DMS impact on nodes (resulting from mediated interactions) was constrained to be weaker than the trophic edge which it mediates (individuals gain more by consuming other prey than by being attracted to DMS; see Section 3.3.3 for details). I imposed negative self-effects on all nodes to represent a suite of effects not otherwise captured in the models (such as intraspecific competition for biotic nodes and dissipation for DMS). For each model, I also consider an alternative configuration involving a proposed feedback from predators (via defecated nutrients) to phytoplankton (Savoca and Nevitt 2014) (hereafter when discussing specific models, an ‘n’ is shown after the model number to indicate that it includes nutrient feedbacks). For these models it could be argued that the magnitude of the gain to predators from grazers is minimal in comparison to the negative effect of predators on grazers. I chose to include the positive effect of grazers on predators because grazers are an important component of predator diet, and in the bigger picture I am interested in the potential importance of DMS in predator foraging success and population growth in the Southern Ocean. In the Southern Ocean many predators are central place foragers (e.g. seabirds, seals) and for these organisms even few prey items are important for offspring survival. Nevertheless, I also explored the effect of leaving out predator gain from feeding on grazers and present these results in the appendices (Table B.1, Appendix B).

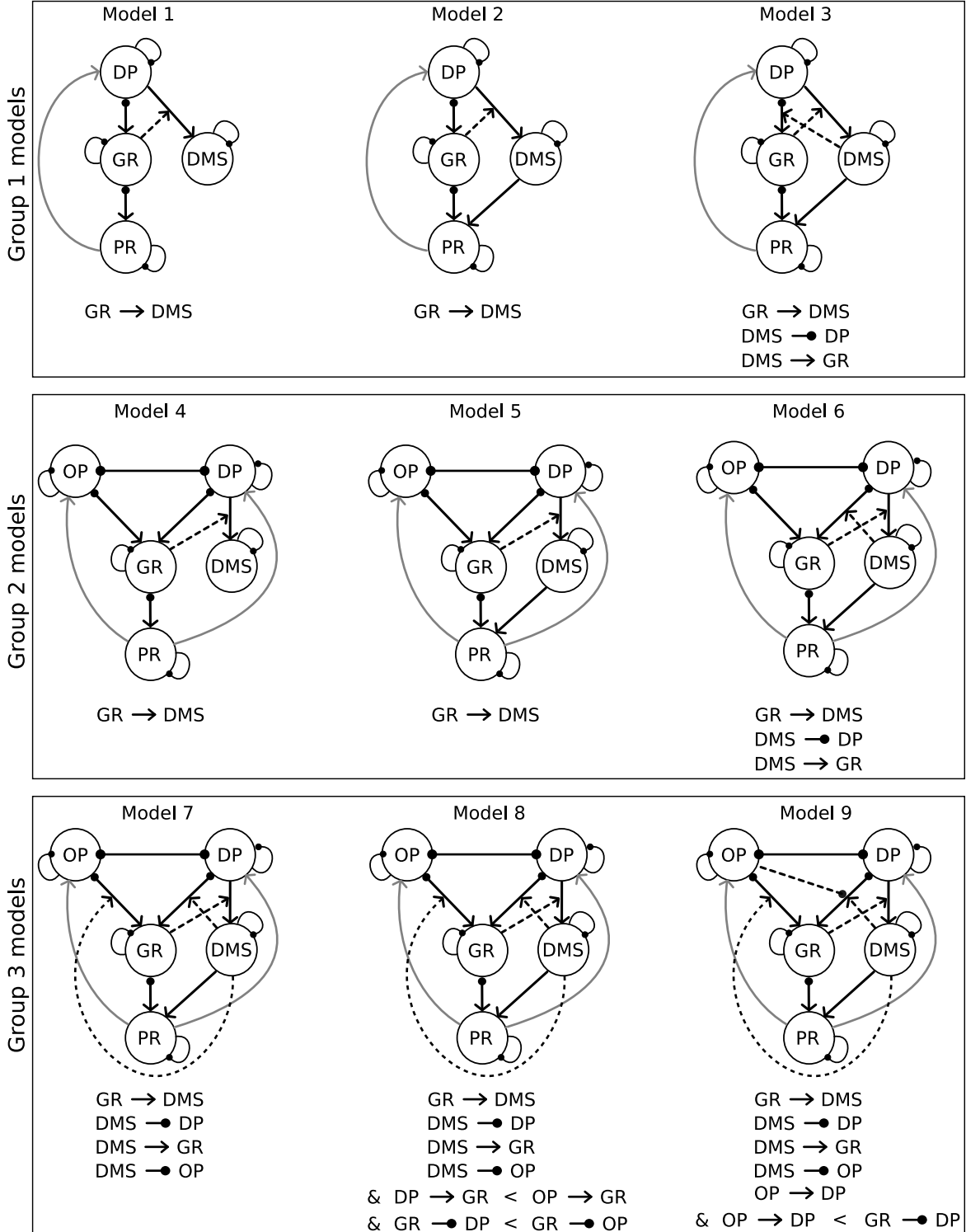


Figure 3.1: Alternative model configurations examined. Abbreviations are: DMS = dimethyl sulfide; DP = DMS-producing phytoplankton; GR = grazers; PR = predators; OP = other (not DMS-producing) phytoplankton. See the text for explanations of the different model structures. Arrows signify positive effects and circles negative effects. Dashed edges represent those that mediate another edge, while solid edges are direct effects. Listed below each model are the pairwise effects resulting from the mediated edges. Additionally, below Models 8 & 9 are indicated the edges that are constrained (in addition to the constraints on DMS mediated edges and attraction). Grey edges represent nutrient addition from predators to phytoplankton, and are only present in the nutrient versions of the models.

Basic predation model

The first group of models (M1-3) comprises predator-prey type model with grazers (**GR**) eating DMS producers (**DP**) and being consumed by predators (**PR**), based on the model of Lewis et al. (2012)). Model 1 is a control, in which phytoplankton produce DMS (**DMS**), but DMS has no mediating effect on trophic interactions. Model 2 includes the attraction of predators to DMS. In these models, which represent the scale of a ‘hotspot’ of productivity, the attraction of wide-ranging predators to DMS brings more predators into the arena of the model, but does not alter the encounter rate of prey by the predators. Thus, I modelled predator attraction to DMS as a direct effect, rather than having DMS mediate the trophic interaction between grazers and predators. Model 3 is similar, except in this model grazers are attracted by DMS (and thus to phytoplankton prey) at the local scale, so DMS enhances the trophic interaction between DMS producers and grazers, resulting in a positive edge from DMS to grazers, and a negative edge from DMS to DMS producers.

Competition model

The second group of models (M4-6) includes a second phytoplankton node, other phytoplankton (**OP**), which does not produce DMS (as per Lewis et al. 2013). In this group of models, the two phytoplankton nodes compete for nutrients (nutrients are not included as a node in the interests of keeping our models simple), and both are consumed by grazers, which in turn are consumed by predators. A similar set of alternative configurations are explored in this group of models as in the first. Model 4 represents a control, where DMS is produced but does not mediate any other edges. Model 5 is equivalent to Model 2 in that DMS attracts predators into the model arena, but has no direct effect on grazers. Model 6 is equivalent to Model 3: DMS both attracts predators and mediates the trophic interaction between grazers and DMS producers.

Other phytoplankton benefit DMS-producers

In Antarctic waters, the main DMS-producer is *Phaeocystis antarctica*, which is a substandard prey item for most grazers (Haberman et al. 2003a,b; Turner et al. 2002). The third set of models (M7-9) present different ways of representing a scenario where the presence of the other phytoplankton node benefits the DMS producers by being the preferred prey of the grazers (i.e. the presence of ‘other phytoplankton’ triggers the grazers to switch prey targeted from DP to OP). In each of these models, both phytoplankton groups are assumed to be in a mixed assemblage, and grazers are attracted to the area of increased DMS concentration containing both groups of phytoplankton. In Model 7, DMS mediates (strengthens) the trophic interaction between OP and GR, but this model does not represent a grazer preference

for OP. Model 8 has the same network structure as Model 7, but additionally increases prey preference for OP by constraining the trophic interaction between OP and GR to be stronger than that between DP and GR. Model 9 is the same as Model 7, but additionally, the presence of OP mediates (suppresses) of the trophic interaction between DP and GR, and, as with the DMS-mediated interactions, the magnitude of the resultant pairwise effect of OP on DP is constrained to be smaller than the magnitude of the effect of GR on DP.

3.3.3 Stability analysis with QPress

I used the R package ‘QPress’ (Marzloff et al. 2016a; Melbourne-Thomas et al. 2012), which is available from <https://github.com/SWotherspoon/QPress>. This package uses a Bayesian framework to simulate a set of community matrices (Figure 3.2). In each community matrix, each edge is randomly assigned an interaction weight drawn from a uniform distribution of $[0$ and $1]$, such that each different matrix represents different quantitative configurations of the same qualitative community structure (determined by the existence and sign of edges). The exception to edges being randomly assigned a weight between $[0$ and $1]$ is when the strength of an edge relative to that of another is constrained (as described in Section 3.3.2 and Fig. 3.1). In this case, a topological sort is applied to the edges, and they are indexed according to their relative strength. Then a set of random values are drawn a uniform distribution between $[0$ and $1]$, and the values assigned to the edges according to their index, such that edges that are constrained to be smaller than another are assigned a smaller weight value (closer to 0). So for example, if $a < b$, then the weight assigned to edge a will be closer to 0 than that of edge b .

Unlike previous uses of this framework (e.g. Marzloff et al. 2016a; Melbourne-Thomas et al. 2013; Reum et al. 2015), I retained the unstable as well as the stable formulations of the community matrix to enable comparisons between them. In QPress, matrix configurations are stable if the real roots of its characteristic polynomial equation are all negative. In ecological terms this means that the community does not head away from equilibrium following a press perturbation.

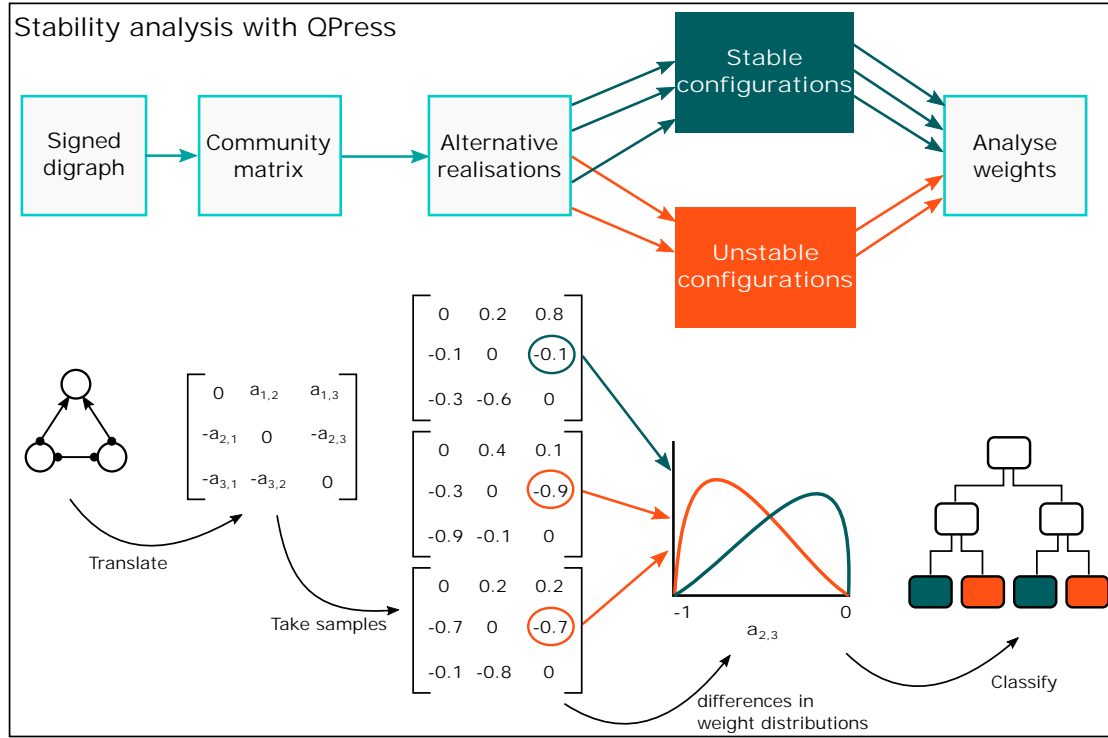


Figure 3.2: Stability analysis in QPress. Diagram illustrating the process for building alternative realisations of network configuration. Stable realisations of the community matrix are those for which the real roots of the characteristic equation are negative. Classification to identify edges which differ in strength in stable versus unstable matrices is carried out with machine learning algorithms, such as random forest as used here. Adapted from Melbourne-Thomas et al. (2012).

For each model, 10,000 random community matrices were simulated. QPress takes criteria for validating community matrices to ensure realistic responses to perturbations. I only retained simulated matrices in which a decline in grazers would lead to a decline in predators (predators leave the model ‘arena’ in the absence of prey). Each simulated community matrix was then tested for stability. The percentage of simulated matrices that are stable are reported for each model.

3.3.4 Edge importance

I used random forests (Breiman 2001) to explore differences in the edge weights of the stable and unstable community matrices simulated in QPress. Random forests are a machine learning classification technique involving the construction of an ensemble of random classification trees that are used together to make stronger predictions than are possible with single trees (Breiman 2001). The importance of different variables can be assessed by removing variables from the classification, and calculating the difference in the error rate of predictions. For each model, I used the *randomForest* function from the R package ‘randomForest’ (Liaw and Wiener 2002) to compare the edge weights of the stable versus unstable community

matrices. Having unbalanced sample sizes is a problem when using random forests because there is little penalty for incorrectly classifying minority classes. I balanced the classes by down-sampling the majority group with replacement, and also increasing node size (to 20) so that classification error rates were similar for stable and unstable matrices. Each random forest contained 3000 trees. I ranked edges according to their importance in determining stability by considering how much removing each edge from the classification decreased accuracy and the Gini Index. For each model, I plotted partial dependence plots of each of the most important edges to determine whether it tended to be weak or strong in stable matrices. I then synthesised this information to enable comparison of the importance of different edges in determining stability across different model structures. I present only the most influential edges in the random forest, with the cut-off for inclusion being based on the pattern of edge influence, and whether the accuracy and Gini Index metrics both ranked the relative importance of each edge in the same order.

3.3.5 Stability analysis and feedback identification with symbolic loop analysis

Using QPress it is not easy to identify all the feedback cycles contained in each model, or explain how the edges identified as being important affect model stability. Thus, I conducted symbolic analysis of the community matrix for each model using the Maple software, following (Dambacher et al. 2002, 2003). In brief, feedback cycles contained within the model were determined from the symbolic qualitative community matrix (i.e. including the sign, but not magnitude of interactions). Each model was assessed according to the Hurwitz criteria for Lyapunov stability (Dambacher et al. 2003). The first Hurwitz criterion states that to be stable, the roots of the characteristic equation of a system must have negative real parts, and further, that their polynomial coefficients must all be of the same sign (Dambacher et al. 2003). Systems that fail this criterion are destabilised by positive feedbacks and are called Class I systems. The second Hurwitz criterion states that the Hurwitz determinants of the system are all positive. Systems that fail this criterion are destabilised by weak low-level feedbacks and are termed Class II systems. Systems that pass both criteria are sign stable (Dambacher et al. 2003), and only Class I systems could potentially have alternative stable states. For interest, I also present the connectance of each model. Connectance is a measure of complexity sometimes used to infer stability and is the proportion of realised versus possible interactions (edges/nodes²) (Dunne et al. 2002, Glossary). The Maple code for conducting these symbolic analyses is available in the supplementary information of Dambacher et al. 2002.

3.3.6 Southern Ocean models

In the small motif networks described earlier, DMS attracted predators into the realm of the model, and so had a direct effect on predators (increases predator numbers as opposed to encounter rate). However over the scale of the Southern Ocean, DMS affects the encounter rate of predators, and so in this context (Southern Ocean scale), DMS mediates (enhances) the interaction between predators and grazers.

I aimed to investigate the possible stability implications for incorporating DMS related feed-backs into larger Southern Ocean ecosystem models. Given uncertainty about which Southern Ocean species are attracted to DMS, there are many possible alternative configurations to model DMS attraction in the system. I explore three of these alternative configurations, based on a simple model developed to represent the food webs in the eastern sector of the Southern Ocean (Figure 3.3) (Constable et al. 2017):

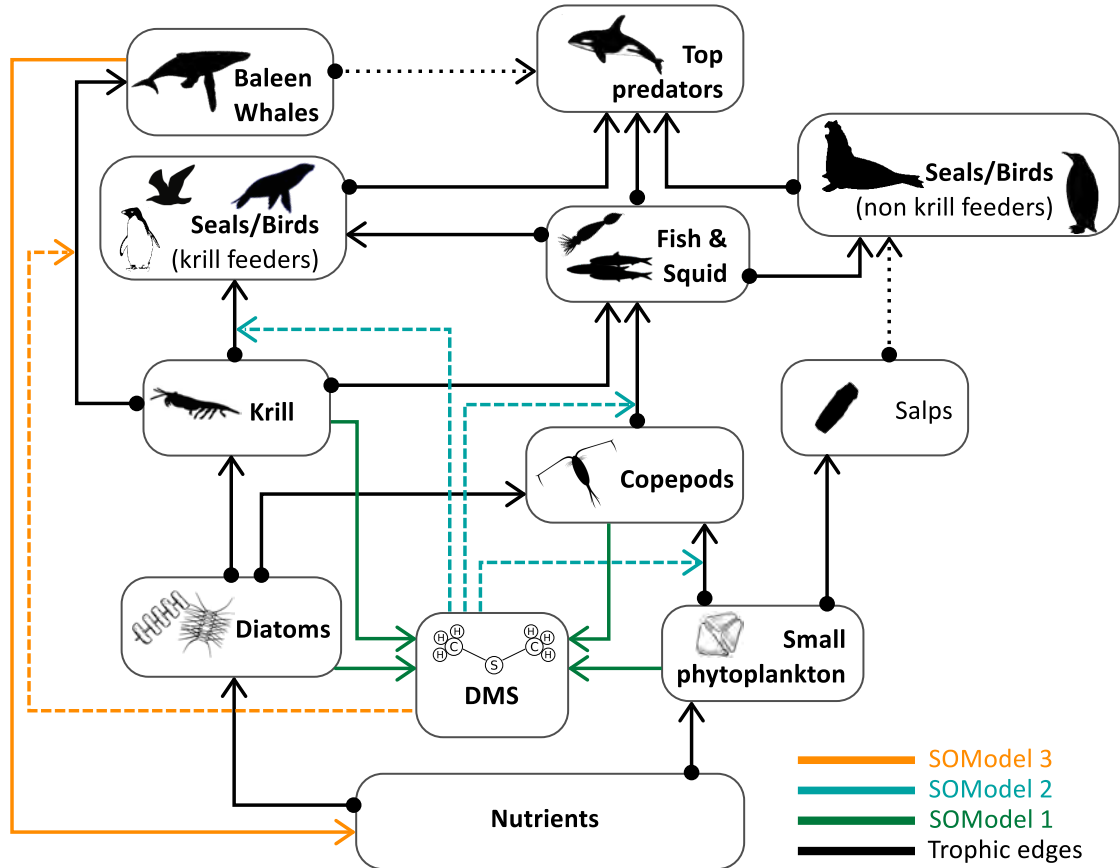


Figure 3.3: Simple Southern Ocean trophic network model used as a basis for exploring implications of DMS-mediated interactions and feedbacks. SOM1 includes trophic edges plus release of DMS shown in green; SOM2 additionally includes blue edges and SOM3 additionally includes orange edges. Solid edges indicate direct effects and dashed edges mediation of other edges. Black dotted edges indicate uncertain trophic links (included in 50% of simulations). Arrows signify positive effects and circles negative effects. All nodes have negative self-effects (not shown in diagram). Thanks to Rowan Trebilco for assistance with this figure.

- SOM1: Trophic control only –This model includes all trophic edges in Figure 3.3, plus release of DMS by grazing on diatoms and small phytoplankton by copepods and krill. However, because *P. antarctica* (a small phytoplankton) produces more DMS per capita than diatoms (Stefels et al. 2007), the contribution of diatoms and copepods to the DMS pool is constrained to be smaller than the contribution of small phytoplankton, and the contribution of krill to be smaller than that of copepods. In this model DMS does not mediate any interactions.
- SOM2: This model is the same as SOM1, except that DMS attraction is included for those types of organisms for which there is a demonstrated response to DMS, viz. copepods, seals, birds (krill-feeders), and fish. Although DMS attraction of Southern Ocean copepod, fish or seal species has not been investigated, species of these groups in other ocean basins have demonstrated attraction to DMS (DeBose et al. 2008; Kowalewsky et al. 2006; Steinke et al. 2006). Thus, in this model, DMS mediates the trophic interactions between these organisms and their prey (shown in blue in Fig. 3.3), resulting in a positive effect towards the predator and a negative effect towards the prey. Because copepods and their predators are both attracted to DMS, I assume for this model that these costs and benefits balance and there is no net direct effect of DMS on copepods. All DMS-mediated effects are constrained to be smaller than the trophic links they mediate. Nutrient addition by higher predators is not considered in this model.
- SOM3: This model is the same as SOM2, but additionally, baleen whales are attracted to DMS (DMS→Baleen, DMS→•Krill), and contribute to the nutrient pool (Baleen→N). This configuration is more hypothetical, because although there is some evidence that baleen whales may detect and orient themselves towards DMS (Berta et al. 2014; Torres 2017), as far as I am aware no studies have definitively shown DMS-attraction in cetaceans. However, there is growing evidence of their contribution to nutrient recycling in surface waters through defecation (Ratnarajah et al. 2014).

All three models contain 12 nodes. For each of these three models, 20,000 community matrices were simulated in QPress. As for the smaller motif models above, all nodes have negative self-effects and all pairwise edges resulting from DMS-mediation of interactions were constrained to be weaker than the trophic interaction they mediated. The two uncertain trophic interactions were included in 50% of simulations. No validation criteria were applied as there was no obvious expected response for any node. Random forests were used to distinguish edges which had the greatest influence on the stability. For each forest, 12,000 trees were built and were balanced by down-sampling the larger group and increasing the node size to 70. Symbolic analysis in Maple was used to classify the models according to the Hurwitz criteria, but no exploration of model feedbacks was conducted.

3.4 Results

3.4.1 Stability of simulated matrices

The percentage of simulated community matrices that were stable varied across the models (Figure 3.4). The first group of models with 3 trophic groups were generally stable over a wide range of interaction strength combinations, while the competition models were stable over a smaller range of configurations. In the 3rd group of models, the stability depended on how the prey-switching and preference was represented in the model; the two models that included competition between the phytoplankton groups were stable over a smaller range of configurations than the model that did not include competition. The inclusion of an edge representing nutrient addition from predators benefiting phytoplankton typically only made a small difference to the stability of the models. The model in which inclusion of nutrient feedbacks had the greatest impact was Model 2, for which the percentage of simulated matrices was 15% lower in the model including nutrient addition. Stability was slightly higher when nutrient feedbacks were included in Model 7n, and similar when included in Model 3n. There was no relationship between connectance and stability for our models (Fig. B.1, App. B).

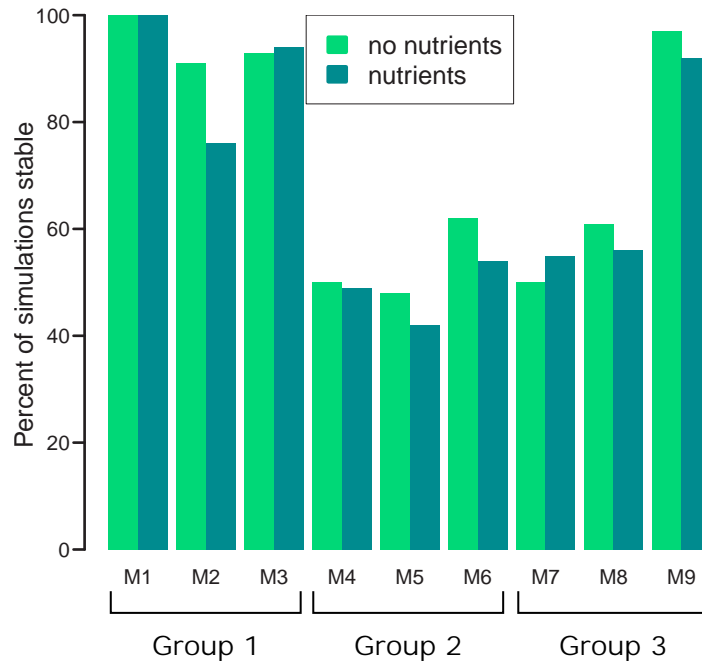


Figure 3.4: Percentage of simulated community matrices (of 10,000) that were stable for each model. Dark blue-green bars correspond to models including predator contribution to a nutrient pool (via faeces), realised as a positive effect from predators to phytoplankton (grey edges in Fig. 3.1); light green bars correspond to models without that edge. Group 1 models are predator-prey models, Group 2 are the same but include an additional phytoplankton node and competition between the two phytoplankton nodes, and Group 3 represent prey-switching (by grazers) in different ways.

3.4.2 Edge importance for stability

Stable and unstable matrices of a model can be distinguished based on the strengths of their component edges. Weak edges have values closer to 0, whereas strong edges have values closer to 1 or -1. The strength of an edge can affect its stability, but it is important to note that the presence of an edge (even when weak) can create feedback loops and so may have a greater influence on stability. Below I discuss the effect of edge strength on relative stability of different community matrices with the same network structure (but the importance of edge presence/absence is considered separately through different model versions above).

The edges that were most influential in distinguishing between stable and unstable matrices were consistent across model structures (Figure 3.5). Community matrices with weak self-limitation of, and strong competition between, phytoplankton groups tended to be unstable for most model structures, while the reverse was true of stable matrices. Self-limitation of other nodes, other controls on DMS producers, release of DMS and predator attraction to DMS were also important in distinguishing between stable and unstable matrices in some model structures. For some models there was a clear distinction in the importance of some edges over others, whereas for other models there was a ‘gradient’, of importance – where each edge had some influence in distinguishing between stable and unstable matrices, and the importance of some edges was clearly dependent on the strength of other edges within the matrices. For example, for M4, there were four edges that were highly influential, and each of the remaining edges had minimal influence in determining stability. Conversely, for M2, nearly all edges had some usefulness in distinguishing between stable and unstable matrices.

3.4.3 Symbolic analysis of stability and feedbacks

When nutrient feedbacks were not included, Model 1 was the only sign-stable model. All other models were Class 1 models, with either net negative or net neutral feedbacks at the highest level (Table 3.1). Models that included nutrient feedbacks were either Class 1 or Class 2 models (none were sign-stable), and one model (Model 3n) had positive net feedbacks at the highest level (Table B.2, App. B). Model 1n QPress matrices were all stable, but loop analysis identified this as a Class I model. This discrepancy is due to the use of the validator (that predators must decline when grazers decline) used to eliminate ecologically unrealistic matrices in QPress; without the validator, 50% of community matrices were unstable (Table B.3, App. B). The lower level feedbacks tended to be common to several models, while some of the higher-level feedbacks were unique to one or two models. In most models, low level positive feedback sequences also contributed to higher level feedbacks when combined with sequences of the opposite sign, for example with negative self-effects. Models with a higher proportion of positive feedbacks tended to be less stable (Fig. B.2, App. B).

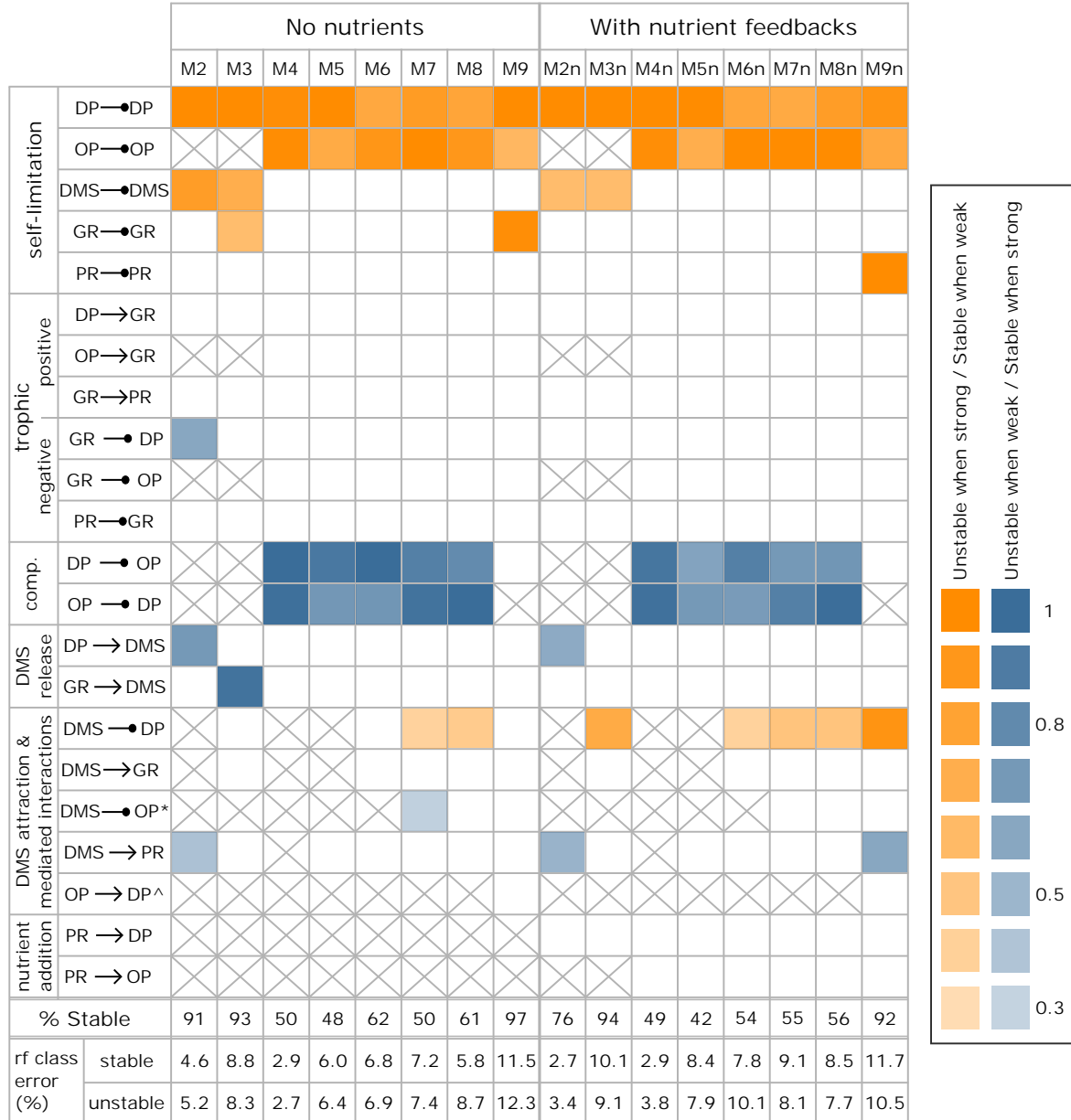


Figure 3.5: The importance of edges in distinguishing between stable and unstable matrices is consistent across model structures. Here each column represents one model structure and each row an edge. Random forests were used to rank the importance of each edge in classifying stable and unstable matrices. The most influential edges are denoted with a coloured square. Edges that tended to be weak (values closer to 0) when the simulated community matrices were unstable are shown in orange. Edges that tended to be strong (values closer to 1 or -1) when the simulated community matrices were unstable are shown in blue. Shading indicates relative importance of the edges for stability within that model (where shading value 1 - strongest colour - indicates the most important edge in that model, and shading value 0.3 indicates an edge whose importance is 30% that of the most important edge in that model, based on the relative decrease in accuracy from the random forest). Boxes with grey crosses indicate interactions not represented in that model. The bottom rows show the proportion of simulations that were stable for each model and the class error rates for that random forest model. Phytoplankton and DMS limitation, and phytoplankton competition were particularly important in determining stability across all models. Abbreviations: DMS, Dimethyl sulfide; DP, DMS-producing phytoplankton; OP, other phytoplankton; GR, grazers; PR, predators.

Table 3.1: Symbolic loop analysis results for models not including nutrient feedbacks (results for models including nutrient feedbacks are provided in Appendix B Table B.2). Reported for each model is the connectance (C), class (based on Hurwitz criteria for Lyapunov stability; weighted feedback at highest level wFn, weighted determinant wDn, and ratio of the weighted determinant to a control model C, as per Dambacher et al. 2003), net sign of feedbacks (at highest level), total number of feedbacks with total positive feedbacks in parentheses. The unique positive feedback sequences at each level of feedback are listed, with the total number of times each sequence is repeated in higher positive feedback cycles in the model stated in parentheses.

Model	C	Class	Sign at highest level	Feedbacks, total and (positive)	Positive feedback sequences			
					Length 2	Length 3	Length 4	Length 5
M1	0.625	Sign stable	negative	24 (0)	none	none	none	NA
M2	0.688	Class I, wF ₄ =-0.60, wD ₃ =0.16, ratio to model C=1.8	negative	27 (1)	none	none	DP → DMS → PR—●GR—●DP (1)	NA
M3	0.75	Class I, wF ₄ =-0.43, wD ₃ =0.16, ratio to model C=1.8	negative	33 (5)	GR→DMS→GR (4)	none	DP → DMS → PR—●GR—●DP (1)	NA
M4	0.6	Class I, wF ₅ =0, wD ₄ =0.04, ratio to model C=4.3	neutral	74 (18)	DP—●OP—●DP (10)	DP → GR—●OP—●DP (4) DP—●OP → GR—●DP (4)	none	none
M5	0.64	Class I, wF ₅ =0, wD ₄ =-0.037, ratio to model C=4	neutral	82 (21)	DP—●OP—●DP (11)	DP → GR—●OP—●DP (4) DP—●OP → GR—●DP (4)	DP → DMS → PR—●GR—●DP (2)	none
M6	0.72	Class I, wF ₅ =-0.14, wD ₄ =0.017, ratio to model C=1.8	negative	116 (33)	DP—●OP—●DP (11) GR → DMS → GR (8)	DP → GR—●OP—●DP (4) DP—●OP → GR—●DP (4)	DP → DMS → GR—●OP—●DP (2) DP → DMS → PR—●GR—●DP (2) DP—●OP → GR → DMS—●DP (2)	none
M7/8	0.76	Class I, wF ₅ =0, wD ₄ =0.016, ratio to model C=1.7	neutral	129 (42)	DP—●OP—●DP (11) GR → DMS → GR (8)	DP → GR—●OP—●DP (5) DP → DMS—●OP—●DP (5) DP—●OP → GR—●DP (3)	DP → DMS → GR—●OP—●DP (2) DP → GR → DMS—●OP—●DP (2) DP → DMS—●OP → GR—●DP (2) DP → DMS → PR—●GR—●DP (2) DP—●OP → GR → DMS—●DP (2)	none
M9	0.76	Class I, wF ₅ =-0.46, wD ₄ =-0.03, ratio to model C=3.2	negative	129 (21)	GR → DMS → GR (10)	DP—●OP → GR—●DP (4)	DP→DMS—●OP→GR—●DP (2) DP → DMS → PR—●GR—●DP (2) DP—●OP → GR → DMS—●DP (2)	DP→DMS→PR—●GR—●OP→DP (1)

3.4.4 Larger Southern Ocean models

All three Southern Ocean models contain positive feedbacks and are Class I models (Table 3.2). The proportion of stable community matrices decreased across the models as more interactions were added. The number of both negative and positive feedbacks increased as DMS-mediated interactions were added to the models, but the increase in the number of positive feedbacks was greater relative to the negative feedbacks. In the trophic model, SOM1, 16% of the total number of feedbacks are positive. In SOM2 and SOM3, positive feedbacks comprise 26% and 30% of the total feedbacks respectively. The trophic level at which the ecosystem would be most vulnerable to perturbation depended on how the DMS-mediated interactions were arranged in the food web. For SOM1, matrices tended to be more unstable when controls on higher trophic levels were weaker and inputs stronger, while SOM2 matrices tended to be unstable when lower level controls were weaker. The most influential edges for stability in SOM3 are a mix of controls on the lower levels and baleen whales, and contribution of baleen whales to nutrients.

Table 3.2: Results of qualitative analysis of the larger Southern Ocean models. Refer to the main text for detailed description of the models. In brief, SOM1 is a trophic model, SOM2 includes DMS-mediated interactions involving organisms with recognised DMS attraction, and SOM3 includes hypothetical DMS attraction by baleen whales as well as their contribution to the nutrient pool via defecation. Colours as per Fig. 5: orange edges are those that tend to be weak, and blue edges strong in unstable matrices. Abbreviations: Baleen = baleen whales; DMS = dimethyl sulfide; N = nutrients; SBkf = krill-feeding seals & birds; TP = top predators. Class is based on Hurwitz criteria for Lyapunov stability and wF_{12} is the weighted feedback at highest level (as per Dambacher et al. 2003).

	SOM1	SOM 2	SOM 3
class	Class 1	Class 1	Class 1
wF₁₂	-0.33	-0.15	-0.10
Net feedback sign	negative	negative	negative
# positive feedbacks	11940	36742	49379
# negative feedbacks	63580	104179	116911
Connectance	0.33	0.36	0.375
Stable matrices (of 20,000)	92%	89%	82%
Important edges for stability	SBkf—●SBkf, Fish&Squid → TP, TP—●TP, SBkf—●Fish&Squid, TP—●SBkf	Diatoms—●N DMS—●DMS Diatoms—●Diatoms	Diatoms—●N Diatoms—●Diatoms DMS—●DMS Baleen → N Baleen—●Baleen N—●N
Random forest class error rate	Unstable= 0.27 Stable= 0.26	Unstable= 0.25 Stable= 0.24	Unstable= 0.24 Stable= 0.24

3.5 Discussion

In this study I used qualitative modelling approaches to explore how uncertainty in network structure might affect conclusions in assessment of ecological stability, and thus the likelihood of a community persisting or shifting to a different community structure. Overall, I found that while there were substantial differences in the stability of the alternative configurations amongst the smaller network motifs that I investigated, the interactions that were most influential in determining stability were consistent across models. For the larger ecosystem models, introducing DMS mediated interactions decreased stability slightly, but the most prominent effect was to alter which interactions were most influential in determining stability.

3.5.1 Network stability patterns

In general we would expect that networks with low stability would rarely be observed in nature, or may exist mainly as a transitional state. Low stability networks have a smaller range of possible interaction strength configurations compared to the more stable network structures. Low stability networks would be more easily perturbed towards an unstable state, and then reorganise into a different network structure. In comparison, network structures with a greater proportion of stable matrices are less sensitive to perturbation so may not exhibit regime shift type behaviour. However, it should be kept in mind that not all of the community matrices that are mathematically stable, will be ecologically viable, and that using QPress I have used a validator (that predators decline – i.e. leave the model arena – if grazer populations decline) and constraints (costs and benefits of DMS to other nodes are weaker than the trophic interactions they mediate) to eliminate ecologically unrealistic matrices. This affects the resultant stability of the models because there may be biased elimination of stable or unstable matrices (e.g. the ecologically unrealistic matrices may tend to be more stable or unstable - in this case eliminating ecologically unrealistic matrices resulted in a higher proportion of stable matrices being retained; see Figure B.3 for comparison).

Of the smaller network motif models, only the first control model, M1, was stable over all of its parameter space. Each of our remaining alternative representations of the network contained destabilising positive feedbacks. Similarly high proportions of the community matrices for Models 2 and 3 were stable, but inclusion of competitive edges in Models 6-8 reduced stability, most likely through exclusion of one phytoplankton group (Lewis et al. 2013; Tilman 1976). Whether DMS stabilised the competitive networks (compared to the control Model 4) depended on how it was connected to other nodes. Attraction of both grazers and predators to DMS (Model 6) stabilised the network, whereas attraction of predators alone (Model 5) reduced stability. All simulated community matrices were stable for M1n, but this was identified as a Class I model (containing positive feedbacks) via loop analysis.

Exploring this disparity, removing the validator resulted in 50% of the community matrices being unstable (Fig. B.3). This indicates that 50% of the matrices would have had predators remaining, or increasing, even as their prey numbers dwindled, which is ecologically unlikely (especially in this model where predators are not attracted by DMS). In most cases, including nutrient feedbacks from predators to phytoplankton decreased stability slightly, but in Models 3n and 7n, it resulted in slightly higher stability. Though only marginally different, this result is somewhat unexpected as the models including nutrient feedbacks contain a higher proportion of positive feedbacks, and Model 3n is the only model with net positive feedbacks at the highest level. This pattern was not present in the absence of validators or constraints, suggesting that making the models more realistic also made them more stable in this case. In some other cases, adding nutrient feedbacks changed the network from a Class I to a Class II model, meaning that they may be destabilised by having weak lower level feedbacks.

3.5.2 Comparison with quantitative models

Four of the model motifs presented here are based on quantitative models presented elsewhere: Models 1 and 2 (Lewis et al. 2012), and Models 5 and 6 (Lewis et al. 2013). Interestingly, while our Model 1 was stable, the quantitative representation of the system in Lewis et al. (2012) contained an unstable focus point with stable limit cycles. Oscillatory behaviour is not dealt with well in the qualitative modelling framework: in QPress a community matrix is stable if it returns to an equilibrium, so an oscillatory system would be unstable (Justus 2006). It is interesting but unclear why the qualitative representation of the same system is stable. Lewis et al. (2012) found that including DMS induced mortality of grazers into this model (equivalent to our Model 2) resulted in a number of stable and unstable equilibria, depending on the degree of attractiveness of DMS to the predators. Our results are broadly consistent; Model 2 was stable under most configurations of the community matrix (92% of matrices stable), though it was not possible to tease out different stable equilibria. Nevertheless, our results do show that this network has the potential to be destabilised by positive feedbacks.

Lewis et al. (2013) found that when grazers were not attracted to DMS (and thus the DMS-producing phytoplankton), DMS-producing phytoplankton were outcompeted by the other phytoplankton, and driven to extinction. This was due to the cost involved in DMS production which resulted in lower growth rates. Our version of this (Model 5) was different; because the relative strength of the direct costs and benefits of producing DMS (and precursor compounds) are difficult to quantify (e.g. Stefels et al. 2007; Verity et al. 2007), for the purpose of this exercise I assumed that they balanced out, such that there was no net direct effect of DMS on DP. I found that only half of the Model 5 community matrices were stable, but consistent with the findings of Lewis et al. (2013) and others, I found that the unstable matrices tend to have strong competition between the phytoplankton, and weak self-

limitation. In their model, when grazers were attracted to DMS (equivalent to our Model 6) the phytoplankton groups stably coexisted because increased attraction to DMS (and therefore DMS-producing phytoplankton) led to increased grazing, increased DMS release, increased attraction of predators and therefore increased mortality of grazers. Our Model 6 was also stable in comparison to Model 5, but was not stable over all of its parameter space.

3.5.3 Interactions and feedbacks important for stability

In systems which contain a mix of positive and negative feedbacks, the relative strength of negative versus positive feedbacks will determine stability (Dambacher et al. 2003). Our two qualitative approaches for investigating the importance of feedbacks (QPress with random forest to identify edges important for stability, and symbolic loop analysis to identify feedbacks) produced consistent results, which together highlight the importance of particular edges in strengthening negative and weakening positive feedbacks in stable matrices. For each of the models, the most influential edges identified in the random forests that tended to be strong in unstable matrices were ones contained mostly (or only) in positive feedbacks, and those that tended to be weak in unstable matrices were only or mostly present in negative feedbacks. Detailed examples exploring the relationship between the results of the two qualitative approaches can be found in Appendix B. In brief, competition between the phytoplankton groups created low-level positive feedback (which was amplified at higher levels of feedback, i.e. in longer feedback loops), whereas attraction of predators to DMS contributed to positive feedback only at higher levels (i.e. in long loops; Table 3.1).

Despite some differences in the nature of the positive feedbacks present in each model, there is a consistent pattern across all the models for self-limitation (particularly of phytoplankton) to be strong and competition to be weak in stable matrices. Other interactions also arise as being important in some models, for example, negative effects of DMS on DMS producers and predator attraction to DMS. While the alternative motifs are exploratory rather than definitive representations of the community, there is still interest in exploring how sensitive the community might be to changing climate or human pressures. These interactions could also usefully be targeted for monitoring and better quantification given their potential importance in this type of community.

A future increase in competition strength, decrease in negative control strength, increase in DMS production and release or increase in predator attraction to DMS would destabilise the community represented in these models, as outlined below.

Competition: In the Southern Ocean iron is the main limiting nutrient, but how well phytoplankton can compete for this resource depends on a range of other factors including light (Deppeler and Davidson 2017; Strzepek et al. 2012). Climate changes such as increased ocean

acidity and temperature are likely to alter the relative competitive fitness of phytoplankton species and sensitivity to changes in other drivers (e.g. Boyd et al. 2015b; Hancock et al. 2018). Changes in iron and light availability (e.g. driven by changes in mixed layer depth (MLD), or cloud cover) are expected to differ among different regions and habitats of the Southern Ocean (Deppeler and Davidson 2017). *Phaeocystis antarctica* is well adapted to low light, and so may do better where MLD increases (Deppeler and Davidson 2017). Interestingly, DMS also acts as a cloud condensation nucleus, so *P. antarctica* could potentially also be promoting their own competitive advantage by triggering cloud formation, as well as creating feedbacks to climate (Charlson et al. 1987; Wang et al. 2018).

Dimethyl sulfide production and release: Predictions of future trends in DMS production and release are contradictory and depend on the species, habitat and scenarios tested (e.g. Sunda et al. 2002; Vogt et al. 2008; Webb et al. 2016; Wingenter et al. 2007). Producing DMS (and its precursors) has an energetic cost for phytoplankton, but the compounds have a number of direct benefits for phytoplankton (reducing oxidative stress, e.g. from UV exposure, nutrient limitation and cold stress, and as a grazing deterrent) (Nejstgaard et al. 2007; Stefels et al. 2007; Sunda et al. 2002). Climate change is likely to alter the balance of costs and benefits, and if costs consistently outweigh combined direct and indirect benefits, then there will be strong selection pressure against DMS production. Assuming cellular DMS production continues, the spatial distribution of DMS is likely to change in the Southern Ocean. Under warmer climate conditions DMS flux to the atmosphere is predicted to increase close to the continent, but decrease in other regions (especially between 50° and 60° S), driven by pole-ward shifts of ecological communities (*P. antarctica*) and changes in sea-ice (Cameron-Smith et al. 2011). Decreasing sea-ice extent is likely to reduce DMS production and release (Stefels et al. 2018). Predicted future trends in *P. antarctica* are variable (Hancock et al. 2018; Kaufman et al. 2017), although their high genetic diversity may enable them to evolve to changing conditions (Gäbler-Schwarz et al. 2015).

Other controls on phytoplankton: Colony formation could reduce intraspecific competition, and this would have substantial consequences for stability in this framework. The colonial life stage of *Phaeocystis* is thought to be a means of avoiding predation mortality, and increasing competitive advantage for nutrients, but the triggers for colony formation are poorly understood so predicting the response to future change is difficult (Bender et al. 2018; Verity et al. 2007). In these models the negative effect of DMS on DMS-producing phytoplankton resulted from DMS mediating the trophic interaction between the phytoplankton and grazers. This effect could reduce in the future if grazers become less responsive to DMS. For example, ocean acidification alters the behavioural response of fish to chemical cues, but whether zooplankton exhibit a similar behavioural response is yet to be investigated (Draper and Weissburg 2019).

Predator attraction to DMS: Attraction of Southern Ocean aquatic predators to chemical foraging cues may reduce as ocean acidity increases, as has been shown for some tropical fishes (Cripps et al. 2011; Dixon et al. 2015; Munday et al. 2009). Attraction of air-breathing predators depends on the DMS flux to the atmosphere, and the strength and direction of winds to carry the scent. Therefore, attraction of air-breathing predators will be sensitive to changes in wind patterns and DMS flux.

3.5.4 Incorporating DMS-mediated interactions into Southern Ocean networks

Including DMS-mediation of interactions in more complex Southern Ocean models (i.e. with more nodes) increased the proportion of positive feedbacks relative to negative feedbacks. Consequently, the range of parameter space over which SOM2 and SOM3 are stable is reduced compared to SOM1. These models are too large for detailed investigation of feedbacks using symbolic analysis, but it was possible to identify edges most influential in determining stability using QPress and random forests. Most importantly, the change in the level at which the network is most sensitive to perturbation has strong implications for predicting changes in this ecosystem. In particular, the high-level feedbacks created from the inclusion of baleen whale contribution to the nutrient pool, removes the system from both top-down and bottom-up control. This highlights the importance of understanding the nature of these feedbacks for predicting likely responses to changing pressures on this ecosystem.

There are many different possible configurations of DMS attraction in this ecosystem, and here I have just considered three. Nevertheless, in contrast to the smaller motif models, the results from these more complex models highlight how lack of understanding of the importance of DMS attraction by different organisms is likely to limit the capacity to predict how the ecosystem will respond to altered interaction strengths amongst different nodes. As the ecological role of DMS becomes better understood, the uncertainty in the nature of the associated feedbacks will be reduced. Qualitative modelling - symbolic loop analysis in particular - is useful for predicting and understanding dynamics that could lead to a shift, but not necessarily the future beyond that shift. The approach is less useful for characterising the likely alternative regimes unless there are clear positive and negative correlations between nodes in responses to press perturbations, or, where the alternative regime is already known (e.g. Marzloff et al. 2011). However, based on the results of Lewis et al. (2012), we could predict that an alternative regime might be one with lower productivity. Importantly, this approach has clarified the relative interaction strengths that could tip the community towards a different regime which is often more difficult to achieve in quantitative ecosystem models, where limited combinations of interaction strengths are explored.

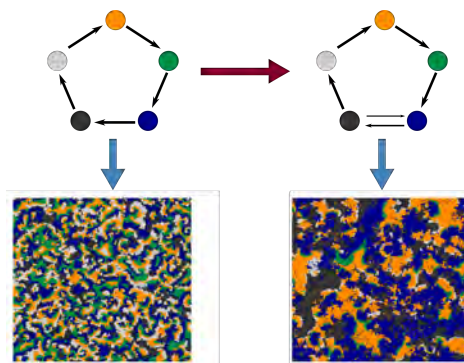
Qualitative models such as these represent snapshots of a system, but in the Southern Ocean

and other ecosystems, the inherently spatial and temporal nature of interactions is likely to impact the overall stability of the system (DeAngelis and Yurek 2017; Lurgi et al. 2016). While the small motif models represent local ‘hotspots’, the larger Southern Ocean models were intended to represent the whole ecosystem. However, lags induced by spatial and temporal features of interactions (e.g. time taken for predators to detect and arrive at an area of high DMS concentration) are not included in these models. The spatial scale of DMS-attraction is likely to vary greatly, from quite local benefits for zooplankton to long-distance benefits for predators (with the actual scale dependent on mobility and sensitivity of the predator to DMS as a cue). On the other hand, there are likely to be fewer predators than zooplankton grazers overall, so DMS could be an important mechanism for concentrating both groups (and thus potentially enhancing productivity of the whole system). Spatial components of the interactions cause temporal lags, which cannot be captured in these qualitative models. Additionally, in the Southern Ocean, DMS concentration and flux to the atmosphere is highly seasonal (Lana et al. 2011) so the strength of these interactions, and consequently the stability of the network, is also likely to vary seasonally (e.g. Ushio et al. 2018). How these factors interact to modify the potential importance of DMS (and DMS-producing phytoplankton) in structuring and enhancing productivity in the Southern Ocean will need further exploration, i.e. in spatially and temporally explicit, quantitative models. Targeted studies quantifying the strength and spatial scale of DMS-attraction in the Southern Ocean will be required to support these analyses.

In conclusion, the use of qualitative modelling approaches to assess the stability of a community with uncertain network structure and interaction strengths is a relatively rapid means of exploring the consequences of structural uncertainty on conclusions of stability. While this approach does not enable identification of precise thresholds, it does enable useful exploration of the feedbacks that may result in threshold behaviours, and can be used to help guide future data collection on important interactions. If the key interactions identified are perturbed such that they change in strength, then the balance of feedbacks within the system can change, destabilising the community and leading to a regime shift. Use of the symbolic loop analysis approach is powerful in identifying these feedbacks, but is difficult to carry out for models with more than 5 nodes. In this case, use of a simulation qualitative modelling approach, such as QPress, combined with machine learning classification algorithms, such as random forest, is valuable for identifying key interactions. Overall, this exercise is valuable as a sensitivity analysis for understanding consequences of decisions made in constructing and parameterising quantitative ecosystem models, in terms of model stability.

Interleaf 2

The previous chapter focused mainly on the importance of network structure and interactions for ascertaining vulnerability to regime shifts. Feedbacks of the sort explored in that chapter can give rise to emergent spatial patterning of ecosystems. As discussed in Chapter 2, identifying change in emergent spatial pattern is an alternative means (rather than change in temporal dynamics) for detecting regime shifts. The following chapter addresses the need for methods for detecting regime shifts (after they occur) by developing a method of regime shift detection for 1-dimensional spatial data.



CHAPTER 4

Detecting ecological regime shifts from transect data

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4.1 Abstract

Timely detection of ecological regime shifts is a key problem for ecosystem managers, because changed ecosystem dynamics and function will usually necessitate a change in management strategies. However, currently available methods for detecting regime shifts depend on having multiple long time series data from both before and after the regime shift. This data requirement is prohibitive for many ecosystems. Here, we present a new approach for detecting regime shifts from one-dimensional spatial (transect) data from just a single time step either side of the transition. Characteristic length scale (CLS) estimation is a method of attractor reconstruction combined with nonlinear prediction that enables identification of the emergent scale at which deterministic behaviour of the system is best observed. Importantly, previous studies show that a fundamental change in ecosystem dynamics, from one domain of attraction to another, is reflected in a change in the CLS, i.e., the approach enables distinguishing regime shifts from variability in dynamics around a single attractor. Until now the method required highly resolved two-dimensional spatial data, but here we adapted the approach so that the CLS can be estimated from one-dimensional transect data. We demonstrate its successful application to both model and real ecosystem data. In our model test cases, we detected change in the CLS in cases where the shape (topology) of the interaction network had changed, leading to a shift in community composition. In an examination of benthic transect data from four Indonesian coral reefs, changes in the CLS for two of the reefs indicate a regime shift. This new development in estimating CLSs makes it possible to detect regime shifts in systems where data are limited, removing ambiguity in the interpretation of community change.

4.2 Introduction

Increased anthropogenic pressure is driving change in most ecosystems (Hughes et al. 2017a; Pecl et al. 2017; Walther 2010; Walther et al. 2002). Yet as the drivers and nature of ecosystem change are varied and interdependent, characterizing and quantifying the degree and type of change remains a challenge. Ecosystem change can take many forms. Losses and invasions of species with particular qualities can completely disrupt the dynamics of some ecosystems, but have little observable impact in others (Ricciardi et al. 2013). Changes in the frequency or type of disturbance events can force changes in any number of directions and can interact with other ecological changes in complex ways (Pascual and Guichard 2005; Sousa 1984; Turner 2010). While some ecosystem changes may be straightforward to detect (for example, the addition or loss of species), whether an observed change constitutes a fundamental change in system structure and dynamics, a transition from one regime to another, is much more difficult to determine (deYoung et al. 2008; Litzow et al. 2016).

The distinction between ecosystem state and regime is important. The state of an ecosystem is essentially its status at a point in time, for example, the population sizes (or other state variable) of component species (Biggs et al. 2012). Ecosystem state changes dynamically and continuously; for example, seasonal oscillations between high and low biomass states, or multiannual cycles in population sizes. However, a change in regime constitutes a fundamental change in the dynamics of the ecosystem, such that the system functions in a different way than previously (Biggs et al. 2012; Scheffer and Carpenter 2003). Importantly, there may be many possible ecosystem states within the same regime. For example, Figure 4.1 shows a well-studied example of a system that has large changes in state within a single regime. This type of intrinsic system behavior complicates the detection of regime shifts based on changes in state. Consequently, changes in ecosystem state alone are not evidence of a change in regime. A shift from one regime to another is difficult to demonstrate because it requires evidence that fundamental dynamics, e.g., the nature of species interactions, or more formally, the underlying attractor for the system (see Glossary), have changed. Harnessing information about system dynamics inferred from emergent spatial pattern is likely to be one practical means of overcoming this challenge (Hammond and Kolasa 2014; Marcos-Nikolaus et al. 2002).

Regime shifts can have significant consequences for ecosystem function and service delivery (Ainsworth and Mumby 2015; Graham et al. 2013; Nystrom et al. 2012; Selkoe et al. 2015; Travis et al. 2014). Thus, identification of regime shifts is vital for effective ecosystem management, managing an ecosystem according to the dynamics of a previous regime may result in further deterioration of ecosystem state, or even further regime shifts. Growing awareness of the importance of early detection of regime shifts, soon after they have occurred, has led to increased effort in developing methods to detect them (Andersen et al. 2009; Rodionov 2005; Scheffer et al. 2001). Parallel efforts have considered methods to predict regime shifts prior to their occurrence (as distinct from detection after a shift has occurred; e.g. Biggs et al. 2009; Dakos et al. 2012; Kéfi et al. 2014; Scheffer et al. 2015); here we focus on the detection aspect only.

Most methods currently used to detect regime shifts only describe change in ecosystem state, using time series data to identify sustained shifts in state (Biggs et al. 2012, but see Habeeb et al. 2005; Johnson 2009). These methods rely on having time series of multiple ecosystem variables from both before and after the suspected transition, to allow clear identification of system state both before and after the shift, and to distinguish sustained shifts in mean ecosystem state from stochastic fluctuations away from a steady state or deterministic cycles (Beaugrand et al. 2002; Mantua 2004; Rodionov and Overland 2005; Rodionov 2004). These approaches can identify significant change in ecosystems where sufficient long time-series data exist (e.g. Beaugrand et al. 2015; Möllmann and Diekmann 2012; Reid et al. 2015), but they

have limitations. Firstly, the requirement for long time series data of multiple variables from both before and after the transition delays possible detection of regime shifts until long after they have occurred (as opposed to soon after they occur). Secondly, the data requirements are prohibitive for many ecosystems. Finally, because these methods track ecosystem state over time, any interpretation of changes in regime will be ambiguous since there could be sustained changes in state within the same regime (Di Lorenzo and Ohman 2013; Doney and Sailley 2013). The goal is therefore to develop capacity to distinguish changes in ecosystem state within the same regime or “basin of attraction,” from a regime shift representing change to a different system attractor (Johnson 2009; Johnson et al. 2017).

An attractor is the region of multivariate phase space (values of state variables) to which a system (ecological system) of interacting entities (species) tends to return. A regime shift involves the transition of the system to a different attractor, with a consequent change in the structure and functioning of the system (Biggs et al. 2012; Scheffer et al. 2001). Transitions between attractors can occur when the ecosystem is pushed from one basin of attraction to another in response to pulsed or sustained perturbations, and can also relate to a change in stability of an attractor (Scheffer et al. 2001). The behaviour of the system as a whole may differ around different attractors. For example, a system may remain fairly stable, it may oscillate around an attractor (cyclical changes in ecosystem state), or it may move around the attractor in a haphazard manner in the face of multiple pulsed forcing events (Scheffer and Carpenter 2003; Scheffer et al. 2012b). This complicates the detection of regime shifts and the characterization of observed change as regime shifts, and emphasizes that ecosystem state alone is insufficient to detect regime shift from one attractor to another.

Developing methods based on consideration of ecosystem attractors rather than ecosystem state provides a more objective means to detect regime shifts. Takens (1981) showed that it is possible to reconstruct the attractor of a system of interacting components from the time series of a single component of that system. This is based on the theory that the behaviour of any one component is related to the behaviour of the rest of the system and thus information about the system should be contained in the history (time series) of that component’s behaviour (Fig. 4.1). This is important because if the attractor of an ecosystem can be reconstructed, then it becomes possible to detect when the system shifts to an alternative attractor. This makes it possible to distinguish cases where changes in ecosystem state are due to oscillations around a single attractor, from cases where a change in system state reflects transition from one attractor to another. However, a key issue is that most methods of attractor reconstruction require very long, continuous time-series data, making them impractical for detecting change from one point in time to another.

Habeb et al. (2005) provided a solution to the problem of unrealistic data demands by largely substituting space for time to reconstruct the system attractor, which they used to

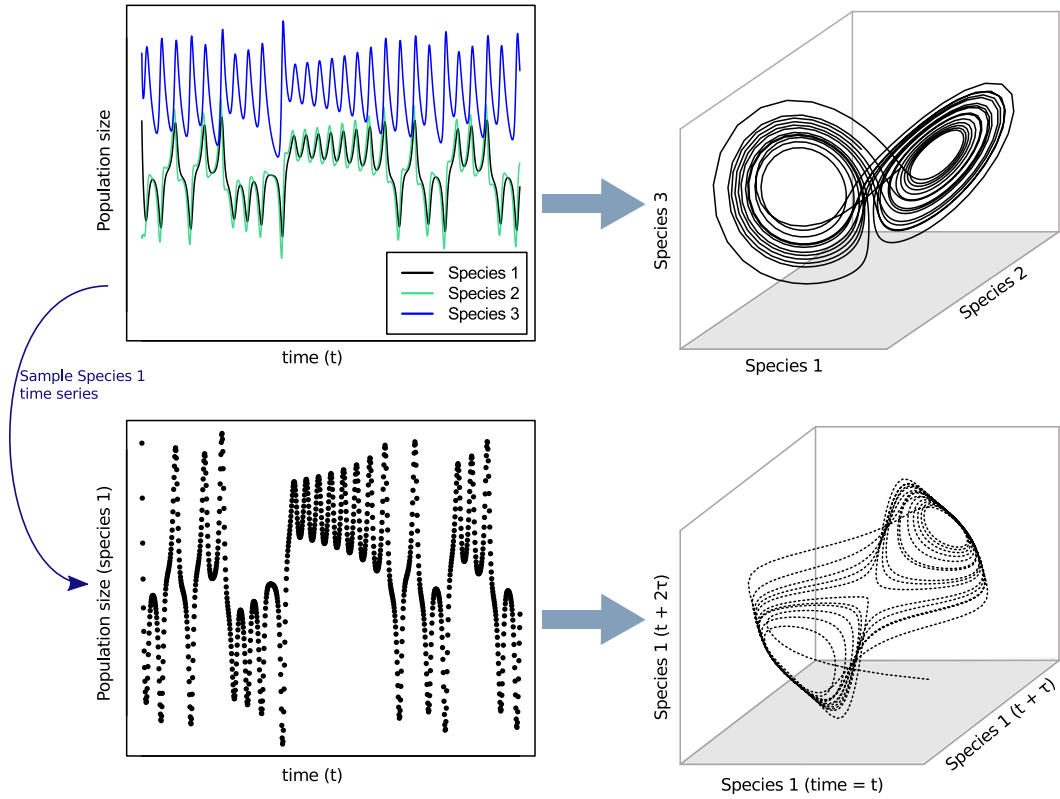


Figure 4.1: Schematic representation of attractor reconstruction from time series data. The top panel shows how time series of three interacting “species” relate to the ecosystem attractor, using the Lorenz attractor as a hypothetical example. The bottom panel shows how a topologically equivalent shadow of the real system attractor can be reconstructed from the time series of a single species, by delay embedding its time series on itself. The Lorenz system typifies a time series that has large swings in state within a single attractor.

estimate the characteristic length scale (CLS) of ecological systems. The concept of CLSs was originally developed to determine the optimal spatial scale at which to observe the deterministic dynamics of an ecosystem, which is the scale of observation at which the signal to noise ratio is maximal (Keeling et al. 1997; Pascual and Levin 1999). Importantly, if a system shifts from one domain of attraction to another, i.e., there is a fundamental shift in space–time dynamics, then the shift is reflected as a change in the CLS (Johnson 2009). Conversely, there is no change in the length scale when the fluctuations in system state are within a single attractor even though the fluctuations may be large (Johnson 2009). Applications to real (marine) ecosystems show that CLSs can be calculated by considering space–time dynamics at the habitat (Habeeb et al. 2007) or species (Johnson et al. 2017) level and that, as the theory predicts, the CLS of the system can be estimated from attractor reconstruction based on the dynamics of a single component habitat or species, provided that components are connected directly or indirectly in an interaction network. However, a limitation of the approach is that to date it has only been applied using highly resolved two-dimensional spatial data (Habeeb et al. 2007, 2005; Johnson 2009; Johnson et al. 2017),

which can be difficult to obtain for some ecological systems.

One-dimensional spatial data (transects) are collected far more commonly for a wide range of ecosystem types (e.g., grasslands, forests, reefs), and in marine systems is the form of data streams that emanate from autonomous underwater vehicles (AUVs), towed instruments, and acoustic information collected along ship tracks. Thus, adapting the CLS method to estimate characteristic length scales (and changes in these scales) using one-dimensional transect data would constitute a significant step forward in terms of detecting regime shifts in a much broader range of ecosystem types. This paper aims to (1) test whether the methods described by Habeeb et al. (2005) can be adapted to estimate the CLS of ecological systems using transect data; (2) use model systems to explore the types of ecological changes that can be detected as a change in the CLS; and (3) test the utility of the method applied to data obtained from one-dimensional transects on coral reefs in Indonesia.

4.3 Methods

The CLS of an ecosystem is the emergent spatial scale that arises from the dynamics between interacting species (see Glossary for definition). Characteristic Length Scale estimation involves reconstruction of the system attractor by delay embedding spatial data, then using nearest neighbour trajectories (see Glossary) to predict subsequent points in the data series (Keeling et al. 1997; Pascual and Levin 1999), similar to the methods introduced by Sugihara and May (1990) for purely temporal data. Habeeb et al. (2005) adapted the long timeseries approaches of Keeling et al. (1997) and Pascual and Levin (1999) by substituting variation in space for variation in time to estimate the CLS of a system from a two-dimensional landscape based on either a single time step (“sliding window” method) or very few (4) time steps (“short time series” method). Here we describe how these two methods can be applied to one-dimensional transect data. Application of these approaches to a system assumes that the system has underlying deterministic dynamics resulting in emergent spatial pattern, and that spatial data can be obtained from the system. For more detailed information about the techniques described here, please refer to Kantz and Schreiber (2003).

4.3.1 CLS estimation process

The sliding window and short time-series approaches to CLS estimation primarily differ in how the delay embedding is constructed. We first describe the steps in detail in relation to the sliding window approach, following Figure 4.2. Then we give an overview of the short time-series approach, highlighting how the steps differ in that approach.

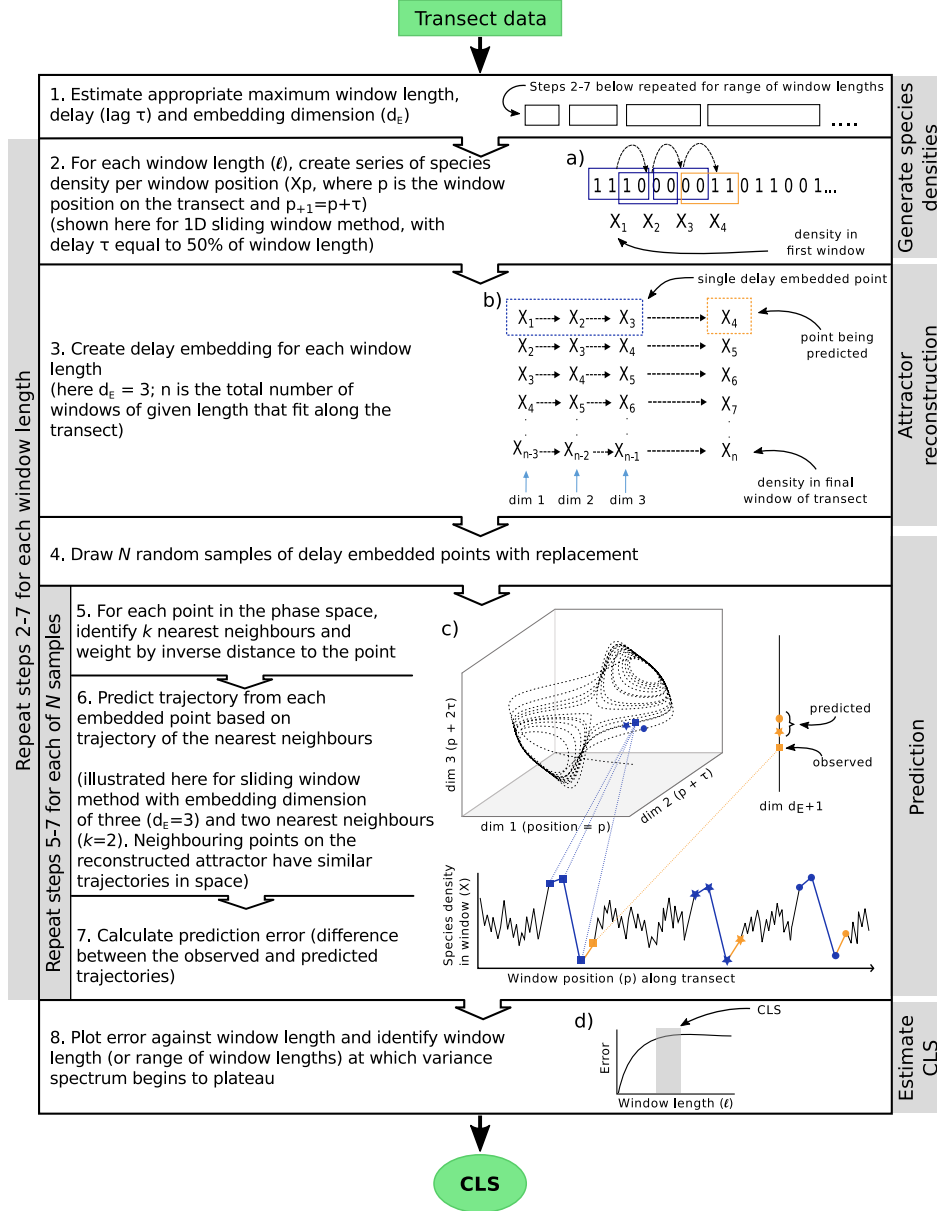


Figure 4.2: Flow diagram showing the steps in the characteristic length scale (CLS) estimation method. Panels a–c illustrate the process for the one-dimensional sliding window approach. A similar diagram is provided for the one-dimensional short time-series approach in Appendix C.1. For more detailed descriptions of the techniques, see Kantz and Schreiber (2003). (a) Slide the 1D window of observation along the transect and calculate mean number (density) of the target species in each window (0 = absent, 1 = present). (b) Delay embed the spatial data series so that the trajectory over d_E sequential windows becomes a single point on the reconstructed attractor (shown in panel c). (c) Identify k nearest neighbours of each point in the reconstructed attractor space and predict density X in the subsequent window based on the trajectory of neighbouring points. Here, the blue square represents the three-dimensional point of interest in the attractor space, and the star and circle its nearest neighbours. The orange square is the point being predicted, based on the orange star and circle. The lower plot illustrates how each d_E dimensional point in the reconstructed attractor maps to a d_E trajectory of densities in space, and that nearest neighbours in the attractor space have similar trajectories in space but are not neighbouring in space. (d) The characteristic length scale (CLS) is the window length at which prediction error begins to plateau.

Sliding window approach: prediction in space

The “sliding window” approach can be used to estimate the CLS of a system from purely spatial data in a single time step (Figure 4.2). In our case the base data is a transect of species inhabitancy recorded over regularly spaced intervals. Here we use presence–absence data, but note that the method could also work with count or concentration data.

i Generate species densities From the transect data, we need to create series of species densities in one-dimensional windows of different sizes (with side length l). The minimum window size has a length that is two times the spatial resolution of the transect (e.g., if resolution is 1 cm, the minimum window size will be 2 cm). The choice of maximum window size is a trade-off between being large enough to capture the CLS, and small enough to achieve sufficient replication along the transect. The species density series are generated by sliding windows of observation along the transect. A new vector of species densities is created for each window size. The window of observation slides along the transect by one-half the window length to each new window position (p) (Fig. 4.2a). The density X of the target species is then calculated for each window position.

ii Attractor reconstruction The system attractor is reconstructed multiple times by delay embedding each vector of species densities generated for each window length (l) into d_E embedding dimensions. For the sliding window approach, the delay (τ) is a spatial delay. Habeeb et al. (2005) found that, for the sliding window method, a proportional delay works better than a fixed delay, such that $\tau = \alpha \times \text{window length } l$. We found 1D CLS estimates to be robust to choices of α , and here we set α to 50% of the window length, as described above in section 4.3.1. One representation of the attractor is reconstructed per window size by delay embedding the vector of densities generated for that window size. To do this, a matrix is constructed where the original vector of species densities forms the first column. The second column is the same vector of densities, delayed by one spatial step (minus the density in the initial window; see Figure 4.2b for illustration of delay embedding). Each column of the resultant matrix is one dimension of the reconstructed attractor, and each row is a single delay embedded point. Each embedded point therefore captures the trajectory of the species density forward in space by d_E number of window positions. We found 1D CLS estimates to be robust to choice of d_E , and here use a d_E of 3.

In theory, observations of any of the interacting species in a system can be used to reconstruct the system attractor (Abarbanel 1996), though Habeeb et al. (2005) found some sensitivity to choice of species when estimating the CLS from long time series. We use observations of a number of species to reconstruct separate representations of the attractor of each system.

iii Prediction Many more small windows fit along the transect than large windows so there will be many more points in the attractor reconstructed from small windows than those reconstructed with large windows. To avoid resultant bias in predictive power, N equally sized samples (we used $N = 20$) of delay embedded points are generated for each window size by randomly sampling with replacement from the delay embedding of each window length.

The aim is to predict the next point in space (which is effectively the $d_E + 1$ dimension from the reconstructed attractor). To do this, k nearest neighboring points to each sample point in the attractor space are located using the *nn2* function from the ‘RANN’ package (Arya et al. 2017) in *R* (R-Core-Team 2017). The trajectory from each embedded point is predicted from the trajectories of the nearest neighbours (see definition in Glossary), with the prediction being weighted toward the trajectories of the closest neighbours (inverse distance weighting) (Fig. 4.2c). To illustrate, in Figure 4.2c, the blue square on the reconstructed attractor is the delay embedding of the three blue squares (representing species densities) in the spatial series in the panel below. The point to be predicted is the species density in the following window position (the orange square). The two nearest neighbours are represented by a blue star and circle in the reconstructed attractor, and represent similar sequences of species density in space. The trajectories from the two nearest neighbours (the orange star and the circle on the lower panel) are used to predict the next species density (the value of the orange square). To calculate the prediction error, the predicted value (the weighted average of the orange star and circle) is then compared with the observed species density (the value of the orange square). Initial testing showed that 1D CLS estimates were robust to the choice of k (we set k equal to 7).

There are two available measures of prediction error: *Error X* (Keeling et al. 1997) and *Prediction r^2* (Pascual and Levin 1999). Previous work (Trebilco 2002) showed that *Error X* produces the most interpretable curves when using the sliding window method (but that *Prediction r^2* was the better metric when using the short time series approach), and our initial testing supported that finding. We therefore use *Error X* as the metric to identify the CLS using the sliding window method, but present examples of both metrics.

Error X For two-dimensional data, *Error X* is calculated as follows:

$$\text{Error } X = l \sqrt{E_p[(X_l^p - \hat{X}_l^p)^2]} \quad (4.1)$$

where X_p is the observed and \hat{X}_p species X in a window of length l at window position p , and E_p is the expectation of their difference for that window length (mean difference over different window positions). For one-dimensional data, a window of length l contains less information than a two-dimensional window of the same length because the area contained

in the two-dimensional window is l^2 . Thus for one-dimensional data, *Error X* is given by:

$$\text{Error } X = \sqrt{l E_p[(X_l^p - \hat{X}_l^p)^2]} \quad (4.2)$$

Prediction r^2 The *Prediction r^2* metric of Pascual and Levin (1999) is given by:

$$\text{Prediction } r^2 = 1 - \frac{E_p[(X_l^p - \hat{X}_l^p)^2]}{\text{Var}(X_l^p)} \quad (4.3)$$

Estimate the CLS Finally, the prediction errors are plotted against window length, to produce a variance spectrum showing how prediction error varies with the scale of observation (Fig. 4.2d). For both *Error X* and *Prediction r^2* , the CLS is defined as the window size at which the variance spectra begin to plateau (following Habeeb et al. 2005; Johnson 2009). In practice, the precise window size at which the curve begins to plateau can be difficult to pinpoint. Accordingly, the CLS is given as a range of possible window sizes.

Short time-series approach: prediction in time

This approach to CLS estimation involves reconstructing the system attractor from short-time series of observations from multiple window positions placed along the transect (see Appendix C.1 for figures illustrating this approach). As in the sliding window approach, each window is placed one-half a window length along the transect from the previous window. The density of a given species in each window position is then tracked for a small number of time steps (four or five), where each time step acts as one dimension of the embedding and the final time step is the one being predicted. Unlike in the sliding window approach above, this delay τ is a temporal lag. We use a delay of ten time steps, as per Habeeb et al. (2005) and Johnson (2009). The attractor of the system is then reconstructed for each window size from the multiple short time series. Then, for each point, the density in the next time step is predicted from the trajectories of k neighbouring points on the attractor. This is the key difference between the two approaches: in the short time-series method the density in the same window position in the following time step is being predicted, whereas in the sliding window method the density the next window position in space (in the same time step) is being predicted.

4.3.2 Detection of regime shifts

Regime shifts can be detected by comparing the CLS of the system from time to another. A change in the CLS of a system from one time to another indicates that there has been a regime shift (Johnson 2009; Johnson et al. 2017). When the CLS of a system is identified, it is given as a range of possible window sizes (see 4.3.1: ‘Estimate the CLS’). A regime shift

can only be detected when the CLS range in one time step does not overlap the CLS range from the other time step.

4.3.3 Model test systems

To create test cases, we planned to run ecosystem models for 5,000 time steps, change the model parameters to simulate different types of ecosystem change, then continue the model run for a further 5,000 time steps. The test systems we used are two-dimensional toroidal probabilistic cellular automata of interacting species, programmed in *Python*. In the model simulations, the initial cover of species over the model landscape is set by randomly selecting a species to inhabit each cell (pixel) within a $2,000 \times 6,000$ -pixel landscape. Species interactions are governed by a set of overgrowth probabilities, where each species has a set probability of overgrowing each other species. At each time step, the species in each cell interacts with one randomly selected neighbouring cell. To determine the outcome of each interaction, a random number between 0 and 1 is generated. If the random number is less than the probability that the cell would be overgrown by the species in the neighbouring cell, then the cell is replaced by the species in the neighbouring cell when the landscape is updated in the next the step. Otherwise, the species inhabiting the cell continues to inhabit that cell into the next time step. To avoid artefacts of sequentially updating the landscape, after each individual cell interacts with one neighbour at time t the result is written to a “new” working landscape matrix representing time $t + 1$, and once the whole landscape is updated the new landscape at $t + 1$ replaces the landscape at t before the next new time step begins. The competitive dynamics of each system and the changes to those dynamics are described in test cases of ecosystem change.

Test cases of ecosystem change

To evaluate whether the 1D CLS estimation methods could detect a change in system dynamics, we used the test cases previously described by Johnson (2009). Johnson’s model systems were run in the Compete software package (Johnson 2002) (and analysed using the two dimensional CLS methods) (Johnson 2009). The simulations in this paper were run in Python to be able to consider larger landscapes (from which long transects could be extracted) than is possible with Compete. A summary of test cases, species considered, metrics and figures presented is provided in Table 4.1.

Table 4.1: Summary of all the analyses performed on each system and the species analysed.

System	Test case	Regime	1D methods	Species analysed	Figures
5-Species model	Test case 1	1 and 2	SW Error X; SW Prediction r^2 ; STS Error X; STS Prediction r^2	2, 3, 4	Figs. 4.3 & 4.4
	Test case 2	1 and 2	SW Error X; <i>SW Prediction r^2</i> ; <i>STS Error X</i> ; <i>STS Prediction r^2</i>	2, 3, 4	Fig. 4.5; App. Figs. C.2 & C.3
20-Species model	Test case 3	1 and 2	SW Error X; <i>SW Prediction r^2</i> ; <i>STS Error X</i> ; <i>STS Prediction r^2</i>	3, 10, 19	Fig. 4.6; App. Fig.C.4
	Test case 4	1	SW Error X; <i>SW Prediction r^2</i> ; <i>STS Error X</i> ; <i>STS Prediction r^2</i>	3, 10, 19	Fig. 4.7a, b; App. Fig.C.5a-c
		2	SW Error X; <i>SW Prediction r^2</i> ; <i>STS Error X</i> ; <i>STS Prediction r^2</i>	3, 10, 19, 21	Fig. 4.7c, d; App. Fig. C.5d-f
Coral reef benthic community transect data from Wakatobi Marine NP	Blue Bowl reef slope	2007, 2010, 2011	SW Error X	foliose, branching, and soft corals, algae, dead coral (2007 only), and dead, algae-covered coral (2010 and 2011 only)	Fig. 4.8
	Coral Gardens reef slope	2007, 2010, 2011	SW Error X	soft coral, sponges, branching coral, encrusting coral	Fig. 4.9a, c, e; App. Fig.C.6
	Sampela 1 reef slope	2007, 2010, 2011	SW Error X	soft coral, sponges, massive coral, encrusting coral	Fig. 4.9b, d, f; App. Fig. C.6
	Hoga Buoy 2 reef slope	2007, 2010, 2011	SW Error X	massive, branching, laminar, encrusting and soft corals, coralline algae and sponges	Fig. 4.10; App. Fig. C.7

Note: Tests in shown in italic typeface (short time-series [STS] methods and sliding window [SW] prediction r^2 for all except Test case 1) were performed and included in Appendix C but are not presented in the main text. Detailed description of models and test cases are provided in test cases of ecosystem change.

Four test cases based on two model systems were considered. The first model system is a five-species intransitive loop, where each species is able to overgrow just one other species, and does so in 100% of occasions in which they interact. This system is structured so that Species 1 overgrows Species 2, which overgrows Species 3 and so on: Species 1 > Species 2 > Species 3 > Species 4 > Species 5 > Species 1. After this model system runs for 5,000 time steps, the system dynamics change and the model runs for a further 5,000 time steps (continuing from the final landscape of the previous “regime”). The change in dynamics brought about in this second regime were as follows:

- 1 Test case 1: A change in the environment results in the growth rate of Species 5 being reduced to 75% of its original growth rate. This is achieved by reducing the probability that it overgrows Species 1 from 100% to 75% of occasions in which they interact.
- 2 Test case 2: A change in the environment causes a change in the way Species 1 and Species 2 interact, such that Species 1 now only over grows Species 2 in 60% of interactions and Species 2 overgrows Species 1 in the other 40% of occasions in which they interact.

In the second set of test cases, the initial system is a 20-species system interacting according to a random interaction matrix. The system initially has open recruitment, meaning that no species can become permanently extinct from the landscape, regardless of how poorly competitive it might be. At each time step, 0.0001% of cells suffer random mortality (disturbance) events, so that those cells become empty space in the following time step. Any of the species are then able to recruit to one of these empty cells, where each species has a 1% chance of being recruited to each empty cell at each time step. After 5,000 time steps, the dynamics change as follows:

- 3 Test case 3: The system changes such that open recruitment stops. According to these new rules, empty space can only be filled by the overgrowth of a species from one of the four neighbouring cells.
- 4 Test case 4: An invasive species arrives. Open recruitment is maintained; however, a 21st species of a highly invasive nature enters the system. This invader overgrows three randomly selected species in 80% of occasions in which they interact, and is overgrown by those same species in the other 20% of interactions. Interactions between the invader and any of the other 17 species result in standoff, i.e., it neither overgrows, nor is overgrown by, any of those 17 species.

For each test case, we chose to present the spectra estimated from three species. For Test cases 1 and 2, spectra estimated from Species 2, 3, and 4 are presented. For Test Cases 3

and 4, three species were chosen to analyze based on their abundance in regime 1: Species 19 was the most abundant, Species 10 was the third most abundant, and Species 3 was the fifth most abundant. The spectra from Species 21 was also analysed and presented for Test Case 4, regime 2. For each test case, three transects were extracted from each of the final landscapes (of the first and second regimes) to test the sliding window method. We present the spectra of all three transects for each species together to demonstrate variability amongst transects. To test the short-time series method, transects were taken from four landscapes separated by ten time steps at the end of each regime for Test Cases 1–3. However for Test Case 4, transects for the short time-series method were taken from landscapes separated by 50 time steps because regime 2 of this test case evolved so slowly that there was very little difference between landscapes separated by only 10 time steps.

4.3.4 Real world test case

We applied the sliding window 1D CLS estimation method to pre-existing coral reef benthic community transect data from four sites within the Wakatobi Marine National Park, Sulawesi, Indonesia (Haapkylä et al. 2016). The collection of these data is described in Haapkylä et al. (2015, 2016, 2007, 2009). Briefly, three replicate line-intercept transects of 20 m length and 1 cm resolution were recorded from the slope, crest, and flat of each of these sites in 2007, 2010, and 2011. The three replicate transects at each site followed a fixed depth contour in each habitat, and were separated by 5 m. When the 20 m coral reef replicate transects were analysed individually, the CLS sometimes appeared to be larger than the maximum window size we were able to consider. Accordingly, the coral reef transects from each site were treated as a single transect to maximize the maximum window size that could be considered. The maximum window size and transect length were kept consistent (100 cm and 60 m, respectively) between sites to ensure CLSs were comparable.

Here we present the CLS estimated from each of the reef slopes (Blue Bowl, Coral Gardens, Sampela1 Reef, Hoga Buoy2 Reef), and discuss both temporal and spatial differences in the estimated CLSs within and among the sites. Initial testing of the short time-series method on this data set showed that this method was inappropriate for the data set, because of the nature of the data set and the number of time steps available (only three time steps). We therefore only estimated CLS using the sliding window approach. The CLSs presented for each reef are based on morphotypes rather than species. Decisions on which morphotypes to investigate and present for each reef were based on whether morphotypes had sufficient coverage to produce an interpretable curve in each of the three years, so that comparisons could be made between years.

4.3.5 Analyses

All model test case simulations were run using the NumPy and Numba packages in Python (Python Software Foundation, version 3.5.2, available at <http://www.python.org>) Anaconda (Anaconda Software Distribution, version 4.2.0, <https://anaconda.com>) on a Ubuntu (16.04.1 LTS x86_64) system hosted by NeCTAR. NeCTAR is a cloud computing research environment supported by the Australian Government through the National Collaborative Research Infrastructure Strategy. Landscape data were exported in NumPy format and read into RStudio using the RcppCNPY library (version 0.2.6; Eddelbuettel and Wu 2016). Transects were sampled, data formatted, and analyses performed in the RStudio (version 1.1.383, RStudio Team 2015) environment and *R* (version 3.4.1; R-Core-Team 2017) using version 2.5.1 of the ‘RANN’ package (Arya et al. 2017). All code for test case simulation and analysis is available online as supplementary material in ‘Data S1’ associated with the publication Ward et al. (2018), and all coral reef transect data are available through Australian Ocean Data Network (Haapkylä et al. 2016). The 1D CLS estimation R package is available through GitHub (<https://github.com/DelphiWard/CLS1D>; Appendix D; Ward and Wotherspoon 2018).

4.4 Results

4.4.1 Model test cases

Test case 1

The estimated CLS of the first regime in Test case 1 was 15–20 pixels. After the Species 5 growth rate was reduced, Species 1 increased in abundance, Species 2 and 4 decreased in abundance, and the abundance of Species 3 and 5 increased very slightly. Despite these observed changes in abundance, there was no clear change in the estimated CLS between the two regimes, with the CLS in the second regime also being estimated at 15–20 pixels (Fig. 4.3). The lack of change in CLS indicates there was not a regime shift in this test case. Although the estimated CLS did not change, the shape of the sliding window *Error X* spectra from Test case 1 differs between the two regimes. The main difference in the spectra is that while the magnitude of *Error X* was equivalent between species in the first regime, the height of the curve (magnitude of *Error X*) for species 2 and 4 were smaller in the second regime, coinciding with declines in the numbers of those species observed within the landscape. Despite this, the emergent CLS of the system remained consistent when estimated from the different species, as expected from the theory, indicating that the species are indeed interacting within the same community (Habeeb et al. 2005; Keeling et al. 1997; Pascual and Levin 1999; Rand and Wilson 1995).

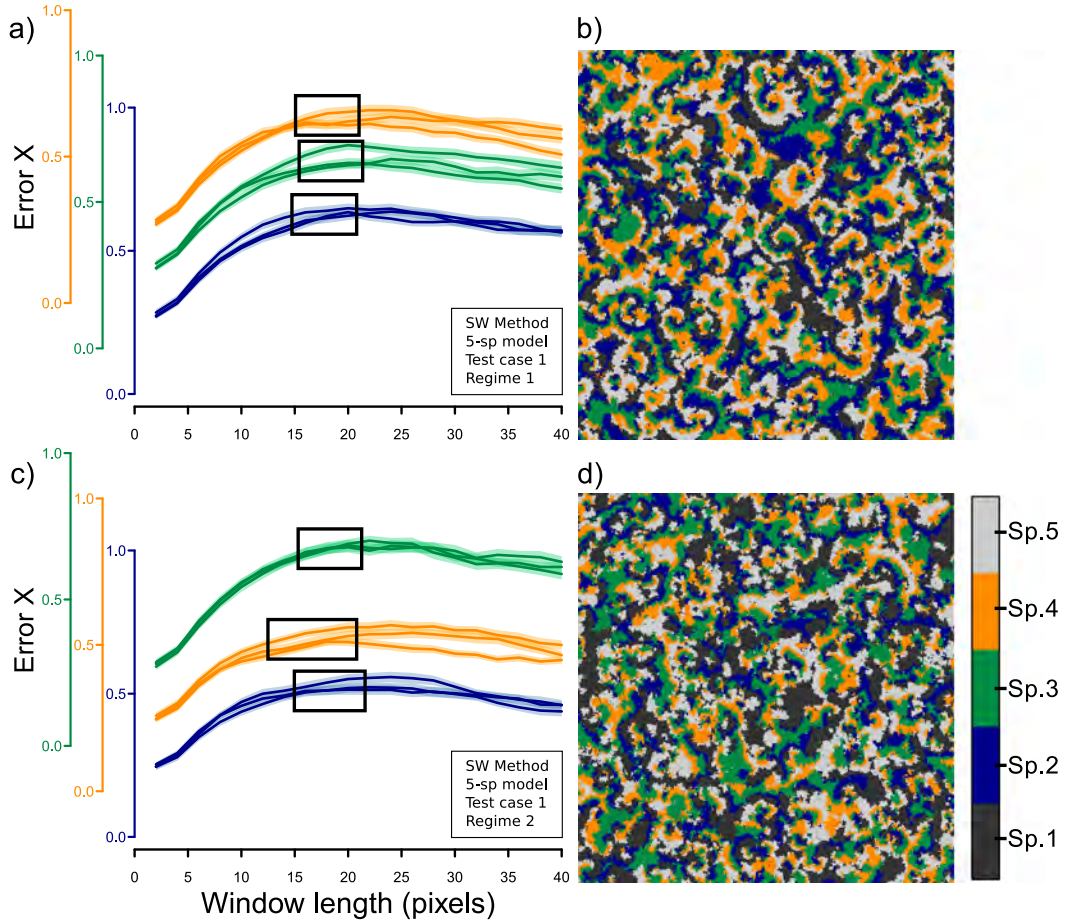


Figure 4.3: Test case 1 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes as indicated by the color bar. For each of three species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. The reduction of the growth rate of Species 5 in regime 2 did not result in a change in the CLS in this test case.

Prediction r^2 spectra proved more difficult to interpret than the *Error X* spectra. The sliding window *Prediction r^2* spectra appear inverted (Fig. 4.4a, d), as had been previously reported by Trebilco (2002). Similarly, the CLS is not estimable from the short time-series *Prediction r^2* spectra for Test case 1 (Fig. 4.4c, f). These spectra continue to increase with window length and do not appear to reach a plateau. The short time-series *Error X* spectra in both regimes for Test case 1 indicated a CLS of approximately 5–10 pixels, which is smaller than that of the sliding window spectra (Fig. 4.4b, e). Interestingly, these spectra exhibit a decline in *Error X* after a peak is reached. Given the difficulty interpreting the 1D *Prediction r^2* spectra, and the ultimate goal for this method to be used to detect change between time steps, we hereafter only present sliding window *Error X* spectra (the other spectra are available in Appendix C).

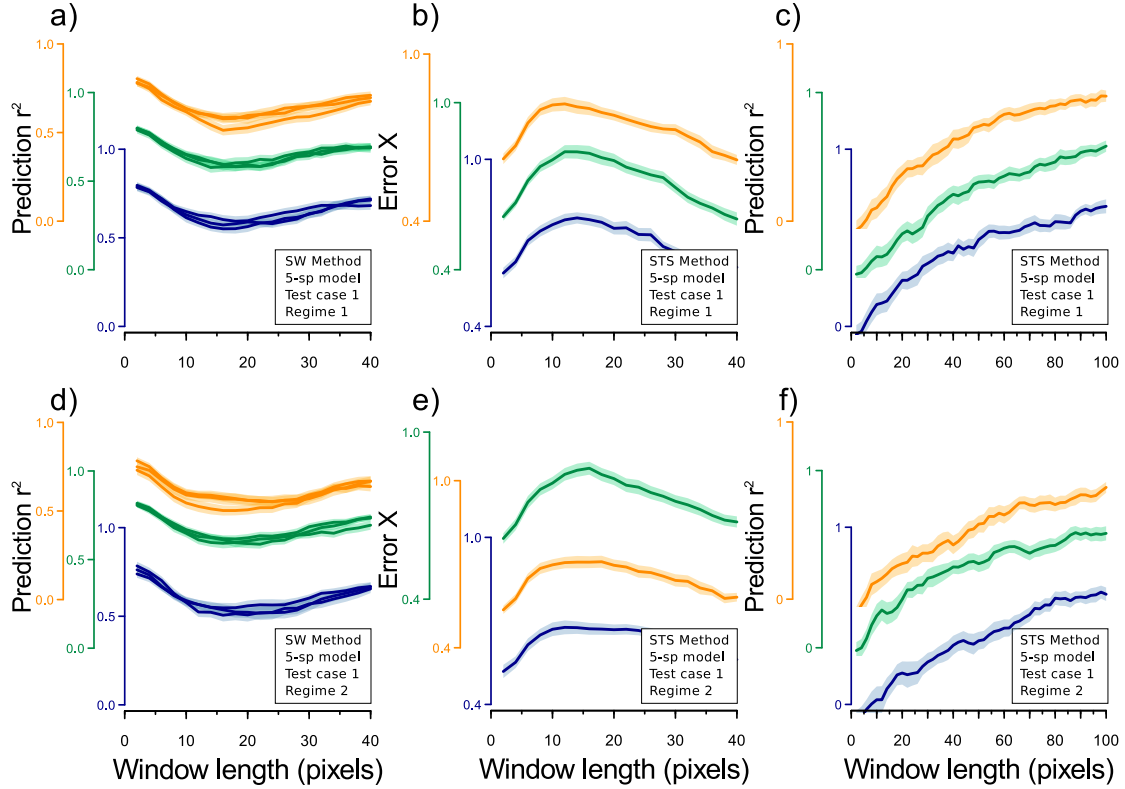


Figure 4.4: Further Test case 1 spectra obtained from one-dimensional “transect” data. Sliding window (SW) *Prediction r^2* spectra for (a) regime 1 and (d) regime 2; short time series (STS) *Error X* spectra for (b) regime 1 and (e) regime 2 and short time-series *Prediction r^2* spectra for (c) regime 1 and (f) regime 2. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. Colors as per Fig. 4.3.

Test case 2

All three species considered in Test case 2 indicate a CLS of approximately 15–20 pixels in the first regime (Fig. 4.5a, b). After the interaction between Species 1 and Species 2 changed, the

abundance of Species 1, 2 and 4 increased in the landscape, while Species 3 and 5 decreased (Fig. 4.5d). In this second regime, the CLS estimated from spatial patterns of Species 2 and 4 increased to 25–30 pixels (Fig. 4.5c). For Species 3, the CLS in the second regime was difficult to interpret (when considered on the same y-axis scale) because its *Error X* curve was very shallow, seemingly a consequence of its low abundance. Nevertheless, the estimation of the CLS as 25–30 pixels was supported when the *Error X* spectra was considered over a smaller y-axis range (App. C.2). The CLS of this system changed so we detected a regime shift in this test case.

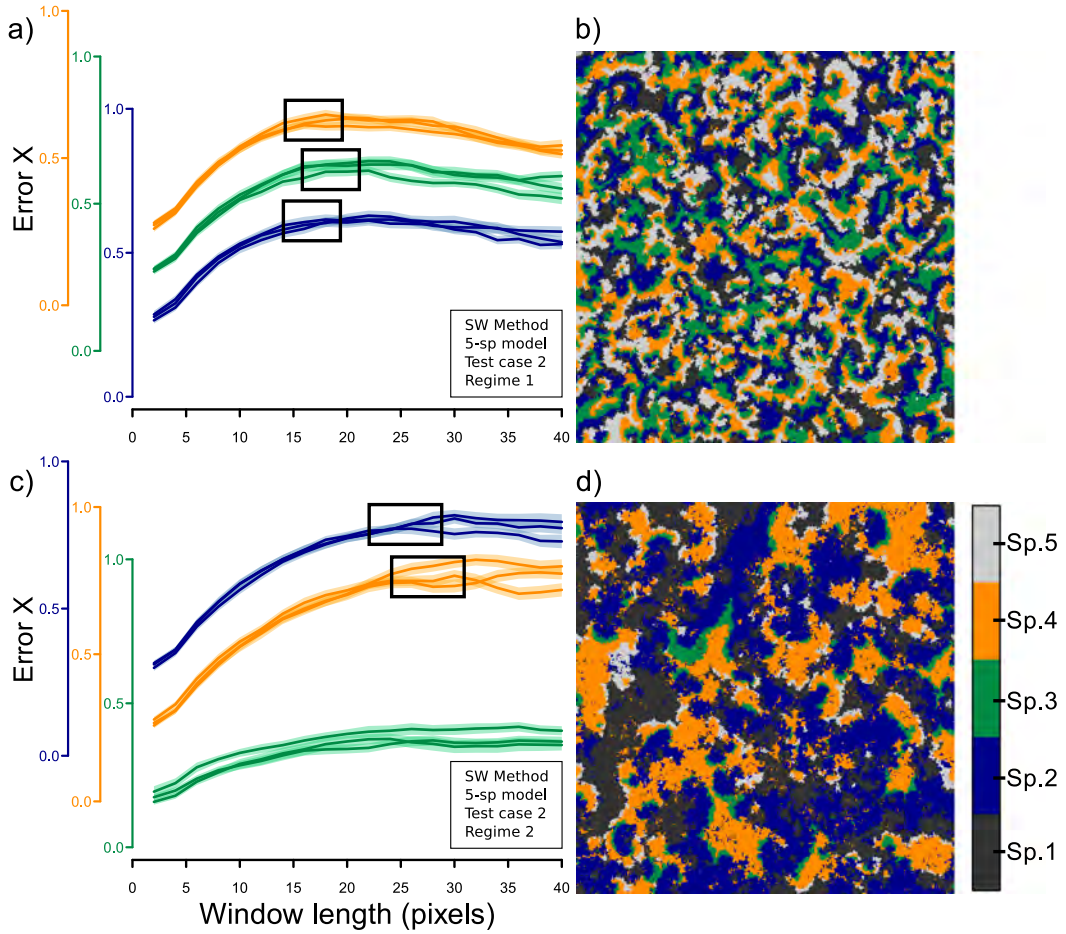


Figure 4.5: Test case 2 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes, as indicated by the color bar. For each species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. In this test case, the CLS increased from 15 to 20 pixels in the first regime, to 20–25 pixels in the second regime following a change in the interaction between Species 1 and 2. See Appendix C.3 for spectra of Species 3 from regime 2 on a smaller y-axis scale.

Test case 3

Species 10 and 19 indicated a CLS of around 20 pixels in the first regime of Test case 3, while the CLS indicated by Species 3 is larger: between 20 and 30 pixels (Fig. 4.6a, b). In the randomly determined interaction matrix, Species 3 typically had low probabilities of either overgrowing or being overgrown by other species, so its dynamics may be somewhat more independent than those of species with strong interaction probabilities. In the second regime, the CLS indicated by each species remains unchanged after the cessation of open recruitment, suggesting that scale of this system is dominated by interaction outcomes rather than by recruitment (Fig. 4.6c, d). Accordingly, we did not detect a regime shift in this test case.

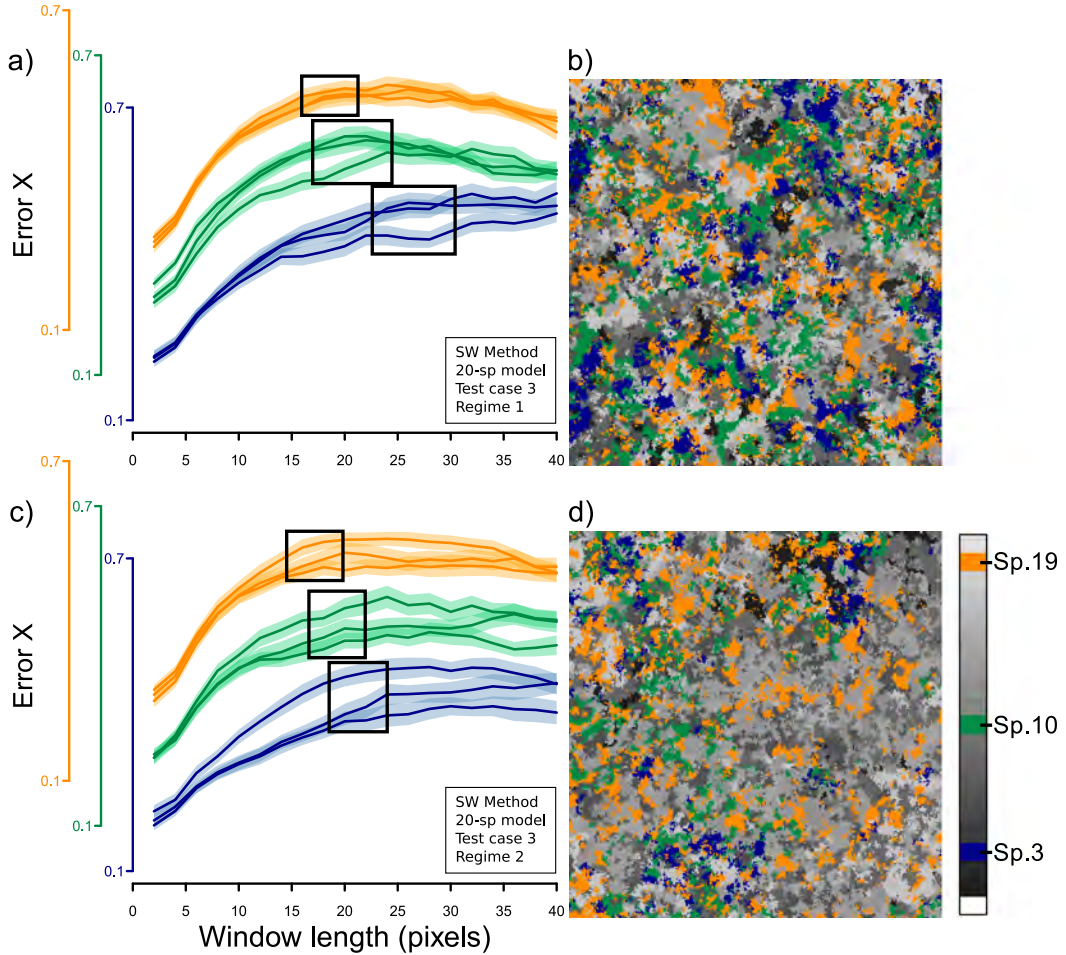


Figure 4.6: Test case 3 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes, as indicated by the color bar. For each species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (3 windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. There was no change in the CLS following the cessation of open recruitment in this test case.

Test case 4

The CLS estimates from Species 10 and 19 in the first regime of Test case 4 are 15–20 pixels, similar to those of Test case 3 (Fig. 4.7a, b). Again in this test case, Species 3 indicates a slightly larger CLS, but the curves are more difficult to interpret, and are more variable between transects than for the other species. Following the invasion of a new, highly competitive Species 21 in the second regime, the landscape became dominated by that invasive species while the abundances of other species fell (Fig. 4.7d). This is reflected in much shallower *Error X* spectra for Species 3 and 19 (Fig. 4.7c). For both of these species, the spectra became harder to interpret. Species 19 appears to indicate a CLS of 10–15 pixels in regime 2, and Species 3 possibly indicates a CLS of 20–25 pixels, though this is difficult to estimate. Neither Species 3 nor Species 19 interacted directly with Species 21. Species 10 was one of the three species that directly interacted with Species 21. Although Species 10 was still present in very low numbers on the final landscape, it was absent from all three transects and so *Error X* could not be calculated from this species. In the final landscape, the Species 21 spectra indicate a clear CLS of 10–15 pixels. The changes in CLS observed in this test case indicate that there was a regime shift.

4.4.2 Coral reefs

Blue Bowl reef

Blue Bowl reef exhibited large changes in CLS over the time period 2007 to 2011 (Fig. 4.8, Table 4.2). In 2007, this reef was dominated by foliose coral, which indicated a CLS of the order of 55–70 cm. Other morphotypes considered were branching coral, which indicated a CLS of about 65 cm, soft coral showing a CLS of about 45 cm, and algae, which indicated a CLS of about 25–30 cm. These length scales had changed markedly in 2010. In 2010, the CLS indicated by foliose and branching corals had declined to 30–35 cm, and that indicated by soft coral had declined to around 35 cm. The CLS determined from cover of algae is harder to distinguish in 2010, but appears to be around 45 cm. Interestingly, the CLS of dead, algae-covered-coral was about 60 cm in 2010, similar to that of foliose coral and dead coral in 2007 (though with a much higher abundance than the latter). This probably reflects the spatial patterns of (now deceased and overgrown) foliose coral. In 2011 the CLSs were largely similar to those of 2010. The CLS indicated by cover of foliose coral was 35–50 cm, while that estimated from branching coral appeared to increase slightly to 40–55 cm. CLSs determined from cover of algae and dead, algae-covered-coral remained unchanged at 40–55 cm and 60 cm respectively. The changes in CLS on this reef indicate that a regime shift occurred between 2007 and 2010 and that the new regime persisted into 2011.

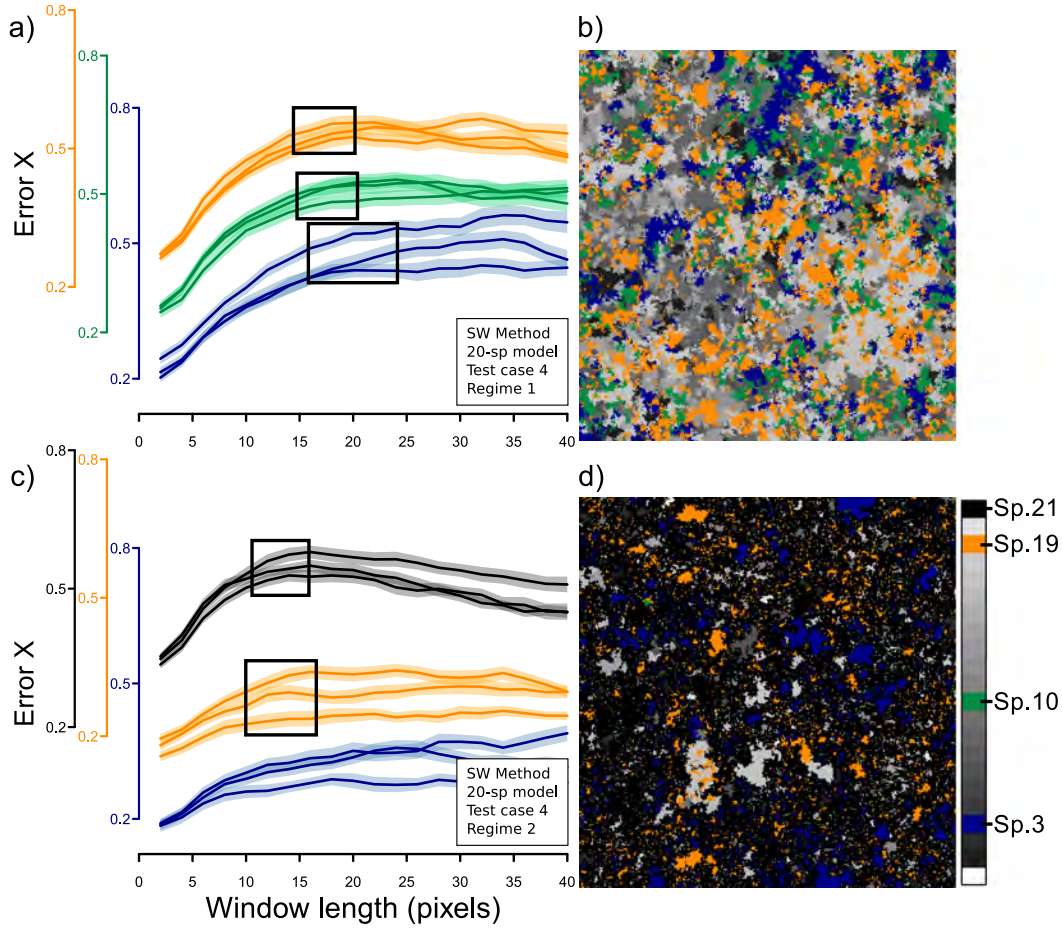


Figure 4.7: Test case 4 *Error X* spectra from the one-dimensional sliding window method for (a) regime 1 and (c) regime 2 and corresponding model landscape sections of 400×400 pixels from (b) regime 1 and (d) regime 2. Species are shown in the same colors in both the spectra and the landscapes; the invasive species is Sp.21 in black. For each species, spectra from three replicate transects are shown together to demonstrate variability due to transect position. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each species. In this test case, there was a decline in CLS from 15 to 20 pixels in regime 1 to 10–15 pixels in regime 2 following the invasion of a new species to the landscape.

Table 4.2: Blue Bowl reef characteristic length scale (CLS) estimates from one-dimensional sliding window *Error X* spectra, and percent cover of each morphotype (in the 60-m transect).

Morphotype	CLS (cm)			Cover (%)		
	2007	2010	2011	2007	2010	2011
Foliose coral	55-70	30-50 (50)	35-50 (35)	60.6	7.5	9.3
Branching coral	60-70 (65)	30-40 (30)	40-55	12.0	9.6	5.0
Dead coral (DC)/dead algae-covered coral (DCA)	55-70 (55)	55-70 (60)	55-65 (60)	6.1 (DC)	58.3 (DCA)	61.9 (DCA)
Soft coral	45-65 (45)	35-45 (35)	30-40 (30)	7.9	5.8	2.9
Algae	25-30	35-45 (45)	40-55	3.6	5.7	16.5

Note: The CLS estimated from the *Error X* spectra is stated as range of possible scales, but where possible, the most likely CLS is also given in parentheses.

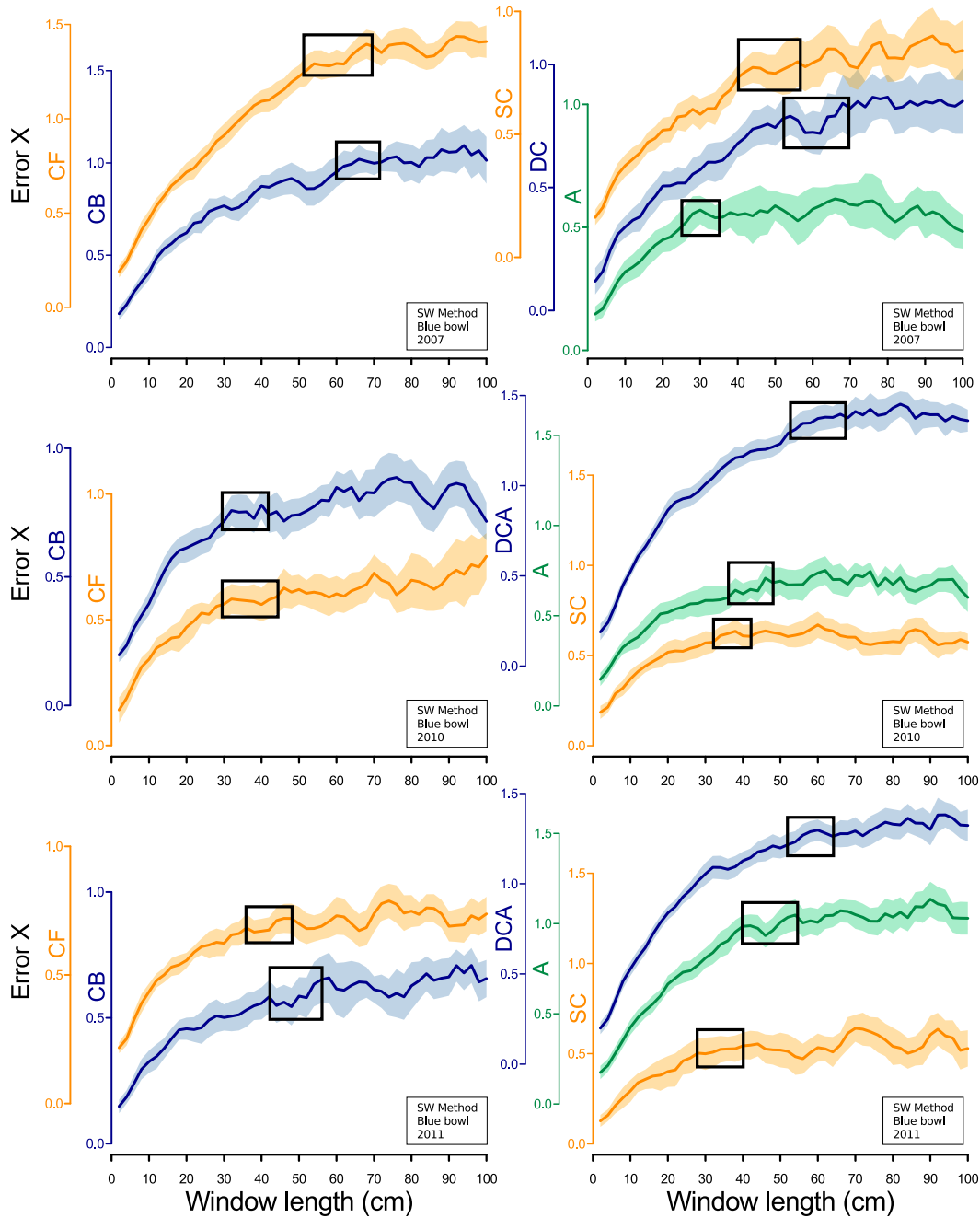


Figure 4.8: *Error X* spectra determined from cover of five morphotypes from Blue Bowl reef in 2007, 2010, 2011. Solid lines are a rolling mean (three windows) of the *Error X* estimates from the 20 sets of random samples for each window size, and shading indicates the 95% pointwise confidence intervals. The black boxes indicate the CLS range estimated from each spectra. CLSs indicated by hard corals (left column, foliose coral [CF] in orange, branching coral [CB] in blue) declined markedly from 2007 (top row) to 2010 (middle row). In the right column, spectra from soft coral (SC) is shown in orange, algae (A) in green, and dead coral (DC) (2007), and dead, algae-covered-coral (DCA) (2010 and 2011) are shown in dark blue.

Coral Gardens

For the most part, the CLSs determined from the cover of morphotypes on the Coral Gardens reef slope remained unchanged between 2007 and 2011 (Fig. 4.9a, c, e, Table 4.3). Coral Gardens was dominated in coverage by soft coral, and in 2007 the CLS of this morphotype was 60–80 cm. In 2007, encrusting coral and sponges both indicated a CLS of about 30 cm, while that derived from branching coral was slightly larger. In 2010, the CLSs indicated from the latter three morphotypes were largely unchanged, but that shown by soft coral had declined. The spectra for encrusting coral in 2010 appears shallower, despite having similar cover and CLS in both years. In 2011, the CLS indicated by encrusting coral had declined slightly, but soft coral indicated a similar CLS to 2007. Sponges indicated a similar CLS to the previous years. The CLS was difficult to estimate from branching coral for 2011, but was possibly around 35 cm. The lack of clear changes in CLS mean that there is no evidence of a regime shift at this reef.

Table 4.3: Coral Gardens reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).

Morphotype	CLS (cm)			Cover (%)		
	2007	2010	2011	2007	2010	2011
Encrusting coral	20-35 (30)	20-35 (25)	10-20 (15)	3.0	3.6	1.8
Soft coral	60-80 (60)	40-55 (45)	45-65 (65)	20.6	31.8	16.6
Sponge	20-40 (30)	20-35 (30)	35	1.6	6.6	6.1
Branching coral	35-50 (40)	25-45 (40)	30-50, or 70+ (35)	2.7	2.7	2.7

Note: The CLS estimated from the Error X spectra is stated as range of possible scales, but where possible, the most likely CLS is also given in parentheses.

Sampela1 reef

Sampela reef slope only exhibited small changes in CLS between 2007 and 2011, despite experiencing declines in cover of all morphotypes considered except encrusting coral (Fig. 4.9b, d, f, Table 4.4). In 2007 the CLS indicated by massive coral, soft coral, and sponges was around 50 to 60 cm. The CLS was harder to determine from encrusting coral, but appeared to be about 40 cm. In 2010, the CLS indicated by encrusting coral was slightly smaller, at around 35 cm, but that shown by the other morphotypes was either unchanged (sponges) or had declined (soft coral and massive coral). The CLS ranges estimated from soft coral do not overlap between 2007 and 2010; however the CLS range estimated in 2011 overlaps both the previous years. Between 2010 and 2011 there was no change in CLS estimates from encrusting coral or massive coral, but there was a slight increase in that indicated by soft coral, and there was a decline in the CLS indicated by sponges to 25–45 cm. The CLS estimated from sponges declined enough in 2011 to be detected as a regime shift; however the lack of a consistent pattern from the other morphotypes at this reef mean we would not

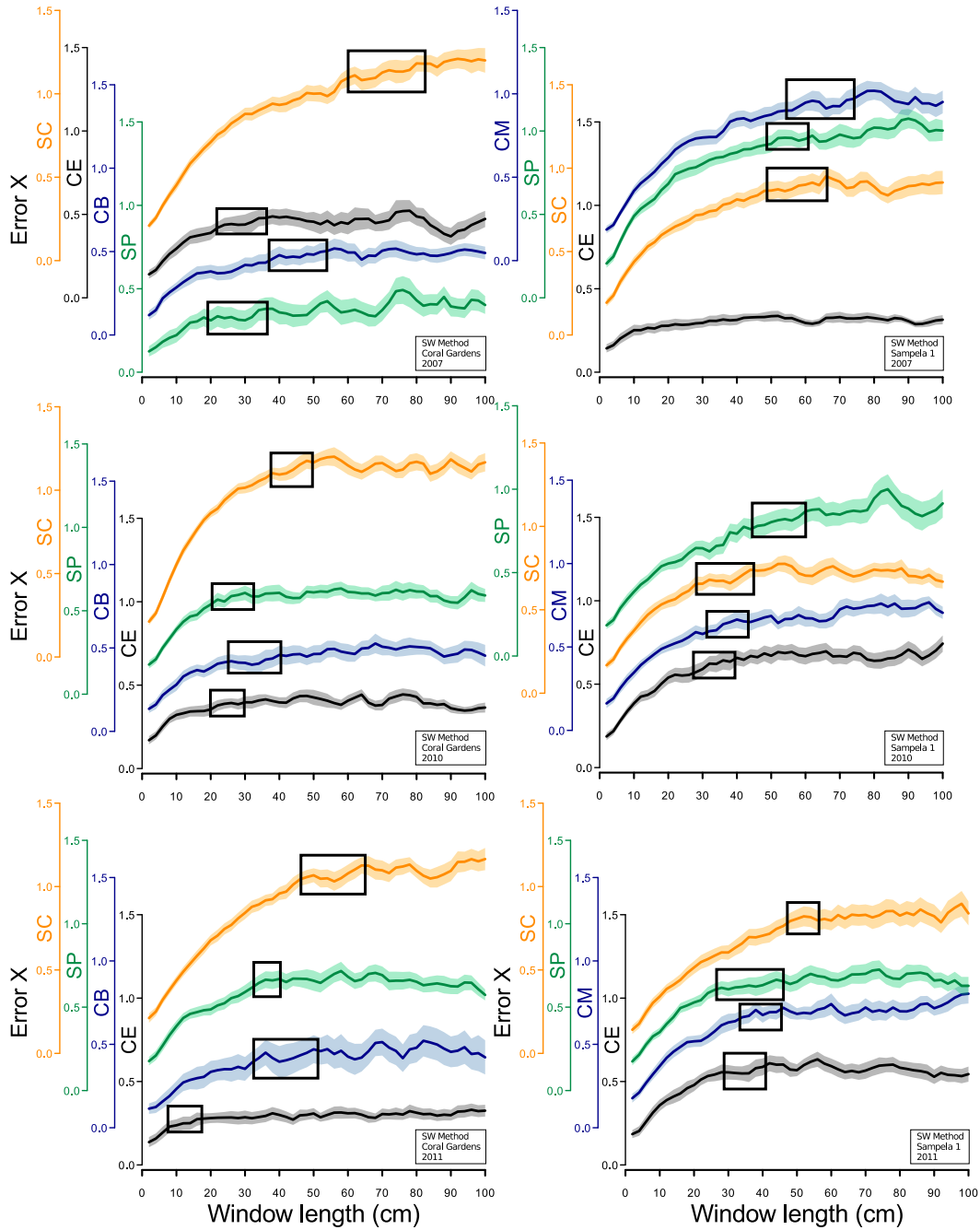


Figure 4.9: *Error X* spectra determined from cover of four morphotypes for each of Coral Gardens (left) and Sampela (right) reef slopes in 2007 (top), 2010 (middle), and 2011 (bottom). Soft coral (SC) spectra are shown in orange, sponges (SP) in green, encrusting coral (CE) in black. Blue lines are branching coral (CB) at Coral Gardens and massive coral (CM) at Sampela. The black boxes indicate the estimated CLS range from each spectra.

be confident in identifying a regime shift here.

Table 4.4: Sampela1 reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).

Morphotype	CLS (cm)			Cover (%)		
	2007	2010	2011	2007	2010	2011
Encrusting coral	30-50 (40)	30-50 (35)	30-40 (40)	2.3	6.3	5.4
Soft coral	50-65 (50)	30-45 (40)	45-55 (50)	11.2	7.6	6.6
Sponge	50-60 (50)	50-60 (50)	25-45 (25)	14.3	8.1	6.3
Massive coral	50-70 (60)	30-50 (35)	30-40 (35)	12.0	6.4	6.5

Note: The CLS estimated from the Error X spectra is stated as range of possible scales, but where possible, the most likely CLS is also given in parentheses.

Hoga Buoy2 reef

At Hoga Buoy 2 reef slope, there were a number of large changes in CLS derived from cover of hard corals over the period 2007 to 2011 (Fig. 4.10, Table 4.5). The CLS indicated by branching coral declined from 90 cm in 2007, to about 50 cm in 2010. The next year (2011) it appeared to indicate multiple length scales: one at about 30 cm and possibly another at 60 cm or over. The CLS from cover of laminar coral declined by a similar magnitude: falling from around 65 cm in 2007 to around 15–20 cm in 2010, and then remained low in 2011. Conversely, the CLS indicated by massive corals increased over the study period, from 40 cm in 2007 to 60 cm in 2011.

Table 4.5: Hoga Buoy2 reef characteristic length scale (CLS) estimates from one-dimensional sliding window Error X spectra, and percent cover of each morphotype (in the 60-m transect).

Morphotype	CLS (cm)			Cover (%)		
	2007	2010	2011	2007	2010	2011
Branching coral	90+	40-50 (50)	30-60 (30 or 60+)	11.3	11.1	4.4
Laminar coral	60-70 (65)	15-20	15-30 (15)	6.9	0.95	1.2
Massive coral	20-40 (40)	60	50-60 (60)	3.5	7.1	10.5
Coralline algae	45-55 (50)	40-55 (45)	50-60 (55)	12.0	28.7	13.4
Encrusting coral	40-55 (50)	45-60 (60)	40-50 (45)	10.5	17.6	15.0
Soft coral	20-30 (30)	15-35 (30)	15-30 (15)	3.7	2.3	1.5
Sponge	20-40 (20)	25-40 (40)	30-50 (40)	3.0	6.1	5.1

Note: The CLS estimated from the Error X spectra is stated as range of possible scales, but where possible, the most likely CLS is also given in parentheses.

There appeared to be a slight increase in the CLS estimated from sponges from 20 cm to 40 cm between 2007 and 2011 at Hoga Buoy reef; however, the overlap in the estimated CLS ranges between years makes this uncertain. There was little apparent change in CLS determined from coralline algae, despite large changes in its cover. Similarly, there was no change in the CLS indicated by encrusting corals between 2007 and 2010, despite a large increase in the cover of this group, but there was a very small decline in the CLS estimated from it between 2010 and 2011. Finally, the CLS range estimates determined from soft coral were overlapping between years, making it difficult to confidently identify any change. Nevertheless, it appears likely that there was a decline in the CLS when estimated from soft

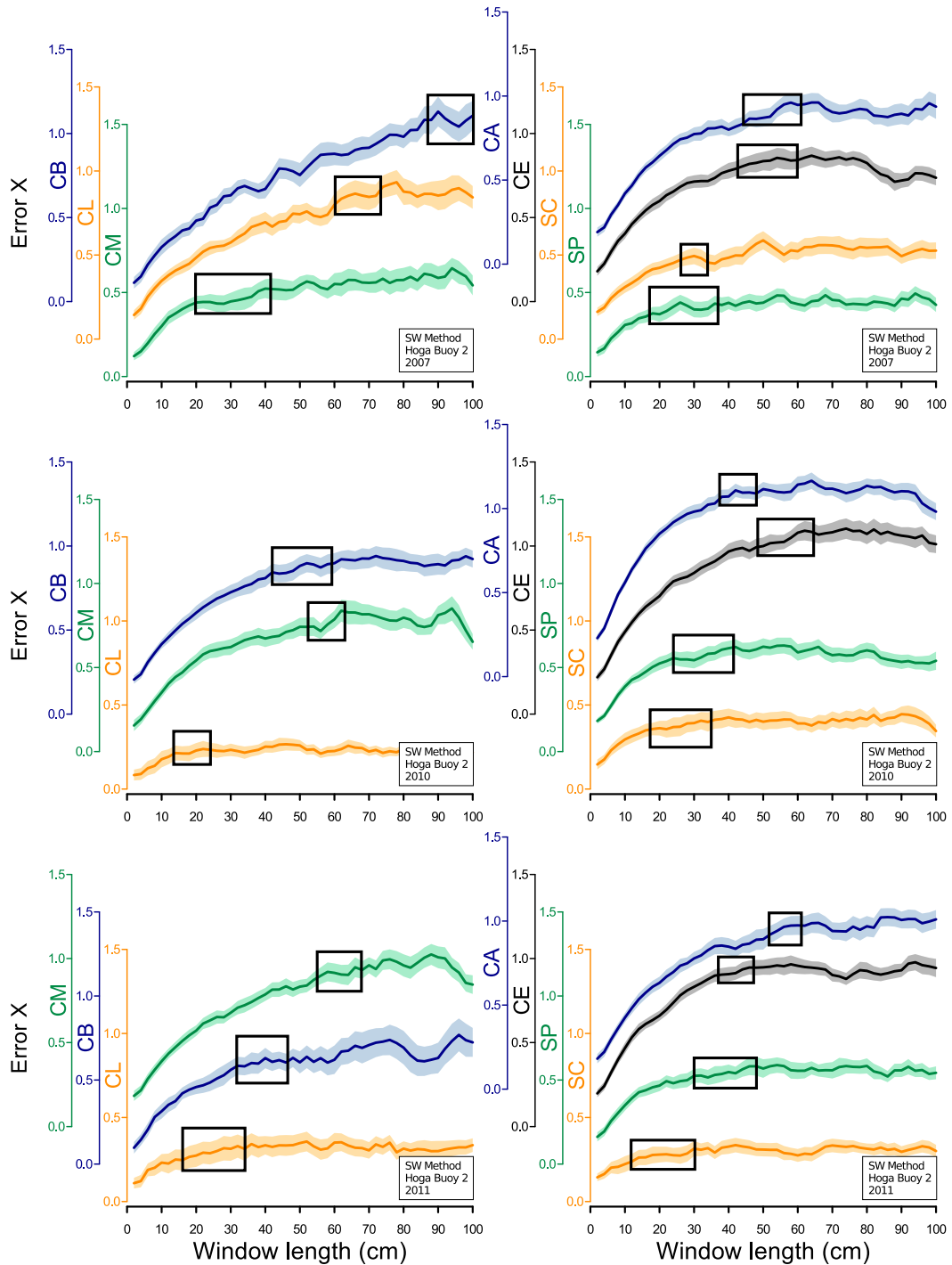


Figure 4.10: *Error X* spectra determined from cover of seven morphotypes Hoga Buoy 2 reef slope for 2007 (top row), 2010 (middle), and 2011 (bottom row). Spectra from cover of hard coral morphotypes are presented in the left column: massive (CM, green), branching (CB, blue), and laminar (CL, orange), and other morphotypes (coralline algae [CA, blue], encrusting coral [CE, black], sponges [SP, green], and soft corals [SC, orange]) are presented on the right. The black boxes indicate the CLS range estimated from cover of each morphotype.

coral between 2007 and 2011. Consistent changes in the CLS estimated from cover of hard corals between 2007 and 2010 mean that a regime shift was detected at this reef, despite the

lack of clear change in CLS estimated from other morphotypes.

4.5 Discussion

We have successfully adapted the method for estimating the CLS of ecological systems (Habeeb et al. 2005; Johnson 2009; Johnson et al. 2017; Keeling et al. 1997; Pascual and Levin 1999) so that it can be used with one-dimensional spatial data (transects). Using this approach, we were able to estimate the 1D CLS for real and model systems based on the cover of most species or morphotypes that we tested. The results demonstrated that 1D CLSs are sensitive to the changes in network topology that we instigated. Using 1D CLS *Error X* estimates, obtained with the sliding window method, we detected changes in ecological regimes in both the model and real world ecosystems examined. However there are caveats in the application of the method, which we detail in following sections.

The results of this study contribute important findings to ongoing discussion about what defines regime shifts and how to detect them (Andersen et al. 2009; Doney and Salliey 2013; Mantua 2004; Rodionov 2005). In our model test cases, it was circumstances where the structure of the interaction network changed (Test case 2 and Test case 4) that exhibited the clearest change in CLS. Conversely, in Test cases 1 and 3, where the network topology of the system was not changed, there was no clear change in CLS. The model test cases presented here provide a range of examples of ecosystem change, but it is not exhaustive. Further studies are necessary to determine whether these observations hold true in other test systems. Among the four coral reef sites, two had clear changes in the CLS, while the other two did not.

4.5.1 Model test systems

In the five-species model, the abundances of species changed in both test cases between the first and second regime, but only in the second test case did the changes manifest as a change in CLS. In Test case 1, although the reduction in growth rate of Species 5 did affect the abundances of other species, the form of the interaction network was still an intransitive loop, and there was no apparent change in CLS. However there was a change in magnitude (asymptote) of *Error X* estimates obtained from Species 2 and 4. This difference in magnitude suggests a change in the system, but it is beyond the scope of this study to explore what kind of change it indicates.

In Test case 2, the interaction network began as an intransitive loop, but the interaction between Species 1 and 2 changed so that each could overgrow the other, changing the network topology. A feedback developed such that, as Species 2 had more opportunities for

overgrowth, its numbers increased, which gave more overgrowth opportunities to Species 1. Species 3 became scarce as Species 2 had more opportunities to overgrow it. This in turn meant Species 4 did well, and overgrew more of Species 5. Consequently, the cover of Species 1, 2, and 4 increased while that of Species 3 and 5 decreased, and patch sizes increased overall. Thus, the change in the structure of the interaction network had significant implications for the scale of spatial self-organization in the system, which changed the CLS and, by definition, the shape of the attractor describing the dynamic (consistent with previous work; Habeeb et al. 2005; Johnson 2009; Johnson et al. 2017).

In the 20-species model, both test cases had the same randomly determined interaction network and had open recruitment to empty cells that were created by a low background level of disturbance. In Test case 3, the cessation of open recruitment did not change the form of the competitive interactions, but did result in the loss of the less competitive species from the landscape. The numbers of these species were originally low and their presence in the landscape was maintained solely by open recruitment to empty spaces. Their loss did not result in an observable change in the spatial scale of the system dynamics, implying that these species had little impact on the system dynamics overall. This suggests that the dynamics of this system were dominated by direct (overgrowth) interactions of key species rather than by the low levels of ‘background’ recruitment. The lack of change in CLS in this test case means we did not detect the changes as a regime shift. We interpret this to indicate that there was no regime shift in the system (that the loss of background recruitment of rare species did not substantially alter the system dynamic), rather than as a regime shift to a new attractor where the CLS is the same as in the original regime, although this is theoretically possible.

Test case 4 involved the arrival of a new species that was highly competitive with three species in the system, but did not interact directly with the other 17 species. In this case, one of the randomly selected species with which it interacted (Species 10) was highly competitive and among the most abundant species on the landscape. Consequently, the invader (Species 21) was able to dominate the landscape to such a point that its opportunities for overgrowing more cells became limited – it had reduced the abundance of those species it could overgrow, effectively blocking its own spread. Those species that did not directly interact with Species 21 remained present in the landscape, but their opportunities for interactions were likewise limited by the spatial dominance of Species 21, which they could not overgrow. These changes in the system reduced the CLS (which we estimated from Species 3 and 19), indicating that a regime shift occurred in this dynamic.

Using 2D short time-series *Prediction r^2* spectra, Johnson (2009) found that in each of these test cases a change in dynamics resulted in a change in the CLS of the system. The CLS values presented here are not directly comparable to those of Johnson because the analytical

methods used are different (2D vs. 1D, short time series vs. sliding window, *Prediction r^2* vs. *Error X*). Moreover, Johnson’s 20-species models are not directly comparable to ours because their random interaction matrices are different. Nevertheless, for the test cases that are comparable (the five-species model test cases), and where we did detect a change in CLS using the 1D sliding window method (Test Case 2), the direction of the changes was consistent with those of Johnson (2009). It should be noted however, that while the network topology (i.e., nature of competitive interactions) of Johnson’s five species models and ours are the same, the CLSs indicated by the 1D analyses were generally smaller than those indicated by the 2D analyses. Also, the 1D analysis did not indicate a change in the CLS in both of the test cases with five species, where this was indicated by the 2D analysis. These differences in results between the 1D and 2D approaches using the same model system may reflect differences in the magnitude of variability captured by 2D and 1D windows. There is more spatial information in a 2D window than in a 1D window of the same length, and less variability between 2D windows than between 1D windows of the same length on the same landscape, and so the 2D CLS approach may be more sensitive to change. It is beyond the scope of this study to do a more in-depth comparison of 1D and 2D CLS. Future studies should aim to estimate and directly compare 2D and 1D CLS for the same system to better understand their sensitivities to changes in system topologies and dynamics.

The model test cases presented here provide examples of the kinds of changes to ecosystems that could plausibly induce a regime shift, however there are other mechanisms that can induce regime shift. Further work is required to determine whether the patterns we observed here are general to other systems. Our results do raise questions as to what constitutes a regime shift in this type of model system. The changes imposed in Test Cases 1 and 3 did not trigger changes in CLS in our model systems, but the same kind of change could have greater consequences in other systems. In our Test Case 1, the change in growth rate of a single species was not enough to change the CLS, while in other model systems changes in growth rate of a single species may have a substantial effect on the dynamics and CLS of the system (Johnson 2009), particularly if the species plays a key ecosystem role (e.g., keystone species, ecosystem engineer). Conversely, the arrival of a new ‘invasive’ species triggered a dramatic change in our model simulation (Test Case 4) since it happened to be highly competitive against very abundant species, but if a less competitive species was to arrive, or in a different system, there might be little observable impact on the system dynamics or on the CLS (Ricciardi et al. 2013).

4.5.2 Coral reefs

Coral reefs are open systems and are subject to a variety of ecological and physical processes (and stressors) operating at a wide range of spatial and temporal scales, and different reef

organisms respond to the various processes (and stressors) to different degrees (Hughes et al. 2017a). It is likely for this reason that CLSs estimated from different morphotypes at any one reef varied more than occurred in the model systems. For example, CLSs estimated from branching and laminar corals were often similar, indicating that they interact within the same dynamical subsystem of the coral reef community. The CLS estimates from coralline algae and encrusting coral were also often similar to each other, but tended to be different to the CLSs estimated from hard coral morphotypes. This indicates that different processes may determine the dynamics of these two groups, and that they interact within different subsystems, at least on the reefs examined as part of this study. Notably, for other benthic marine systems with closely interacting species, the CLSs estimated from a wide diversity of taxa representing a wide variety of life history characteristics are remarkably consistent (Johnson et al. 2017).

Changes in CLSs were evident at two of the coral reef sites (Blue Bowl and Hoga Buoy2), indicating a change not only in community structure but also in the nature of the system dynamics. The change in CLS for Blue Bowl is consistent with changes in community composition and ecosystem function described by Haapkylä et al. (2015) for this site, however the detection of a possible regime shift at Hoga Buoy2 constitutes a new observation. Blue Bowl reef was a pristine site in 2007 with high (74.4%) coral cover and a unique coral assemblage dominated by foliose corals (Haapkylä et al. 2015). However, between 2007 and 2010, there was a series of coral disease outbreaks, and consequently, a decline in coral cover. Over this time, the CLS determined from cover of hard corals decreased from 50 to 60 cm, to about 30 cm, making it similar to the CLS determined from cover of algae. This suggests a change in the system resulted in stronger interactions between hard corals and algae. At this site, filamentous algae overgrew many of the coral colonies that died completely or manifested patches of mortality (Haapkylä et al. 2015). Algal dominated reefs are widely thought to be an alternative stable state to coral dominated reefs (Done 1992; Fong and Paul 2010; Mumby et al. 2007, but see Fung et al. 2011; Mumby 2009), and given that we have observed such a clear change in CLSs at this site, it appears that this reef has transitioned to a new, algal-dominated attractor. Thus, while Haapkylä et al. (2015) were not able to ascertain whether the change they observed in assemblage structure constituted a regime shift, our results suggest clearly that it does.

At Hoga Buoy2 reef there was also a decline in the CLS coincident with a decline in cover of branching and laminar coral over the period 2007 to 2011. For branching coral in particular, the decline in CLS preceded the decline in cover, suggesting that there was a change in spatial structure and dynamics prior to the decline in cover. These declines were matched by an increase in the abundance of massive coral, and also in the CLS estimated from massive coral cover. Conversely, encrusting coral and coralline algae experienced large fluctuations

in abundance but there was little change in CLS estimated from their cover, or from that of sponges. The changes in CLS derived from different groups of organism on this reef, together with the changes in composition, suggest that the dynamics changed in favor of benthic morphotypes that are more resistant to physical damage, and so may have flow on effects for the types of organisms inhabiting the reef. A regime shift was only indicated by the hard corals at this reef, and the CLSs estimated from their cover shifted to be closer to the CLSs estimated from the other morphotypes, indicating that perhaps these groups interacted more strongly after the regime shift.

Sampela1 and Coral Gardens reef slopes exhibited little change in CLS. At Sampela reef, there was possibly a decline in the CLS estimated from massive corals and sponges, however the uncertainty around those estimates makes it difficult to interpret. Of all of the reefs, Sampela is the closest to human settlement and was the most subject to human pressures, in particular high sedimentation and nutrient input (Haapkylä et al. 2015, 2009; Salinas-de-Leon et al. 2013). However, these pressures were present throughout the period of this study and prior to it, and so the reef had most likely already responded to these pressures, i.e., if there was a regime shift at this site, it occurred prior to 2007. Although all reefs in the area are subject to fishing pressures, Coral Gardens is considered a relatively pristine reef and the lack of clear change in the CLS suggests no significant shift in the dynamics of this reef over the period of our observation.

4.5.3 Application of the 1D-CLS method

A number of considerations regarding the use and application of CLSs from 1D data arise from this study, in particular for the length and resolution of the transect data used, the species investigated, and the interpretation of change. The length and spatial resolution of a transect dictates the range of spatial scales that can be considered in CLS estimation. Characteristic length scale estimation depends on having sufficient information about the spatial patterns of ecosystem components, whether they be species, morphotypes, or even habitats (see Habeeb et al. 2007), for each window size. The higher the spatial resolution, the more information will be available about spatial patterns at smaller scales and the more the landscape or transect can be subdivided into windows. Greater resolution therefore allows for smaller scales to be considered, which can facilitate identification of the CLS. Additionally, the sliding window method in particular is limited by the need for suitable replication of the larger window sizes. Longer transects enable replication of longer 1D windows along the transect (and greater replication of all window sizes). Therefore longer transects increase the maximum scale that can be detected. Shorter and/or lower resolution transects reduce the range of scales that can be considered, and will increase the risk that the actual CLS is outside that range (and thus remain undetected).

Initial testing showed that estimation of CLSs using the 1D sliding window method for *Error X* spectra was not sensitive to choice of embedding dimension, spatial lag, or the number of nearest neighbours used in the prediction. However, we found some sensitivity to the maximum window size considered (discussed in more detail in Appendix C.1). Another issue evident from this study is that rarer species may be less suitable to estimate CLSs using the 1D approach. Using the 1D methods, rare species have a high chance of being missed altogether by a transect, and so are more likely to be represented by zeros. Thus, for CLS estimation from 1D data, sufficient information about the patterns of rare species is unlikely to be captured and we recommend that more abundant species be investigated or that species are aggregated into functional groups. It appears that for real systems, it is important to estimate the system CLS using a range of species and then compare the CLSs to determine (1) which species are likely to be part of the same dynamic community and (2) whether changes implied by observations of one species are common to the whole community.

A potential limitation in using CLSs to detect regime shifts is that a shift is only detected if there is a clear change in the CLS that emerges from the system dynamics. It is theoretically possible that a shift could occur to a different regime that has the same emergent spatial scale. Further work is required to elucidate how likely this is to occur. The detectability of a shift might also be hampered in some cases given a level of subjectivity in estimating the CLS from the spectra. Because the exact point at which a variance spectrum plateaus can be difficult to pick, it is usual to identify the CLS as a range of possible window sizes. In cases where there appears to be a change in the CLS but the ranges overlap, there can be ambiguity in interpreting the difference as a regime shift. Given these limitations, this approach is conservative in detecting regime shifts in that it is only when there is a clear change in the CLS that we can assert strong evidence of a change in the regime. Since a change in state alone is insufficient evidence of regime shift (Johnson 2009), we are unaware of any other option to unambiguously interpret whether regime shifts have occurred. This method offers the potential for greater insight into the nature of ecosystem change, where a clear shift in the CLS is a powerful indicator that a regime shift has occurred. We recommend this approach be used as part of a toolbox of techniques for studying ecosystem change.

4.5.4 Conclusion

In conclusion, we have successfully adapted the 2D CLS estimation method for 1D data, and shown that the 1D method can be applied successfully to data from both model and real-world ecological systems. It is clear that the CLS can now be estimated for systems that are monitored using transects. Our results suggest that the characteristic length scale emerges as a useful metric for detecting regime shifts because it (1) has a value that depends on the dynamics of an entire community of interacting species, (2) can be estimated from a

single, or very few, time steps, and (3) a change in the value of the CLS between time steps indicates a fundamental change in the ecosystem dynamics. Further work is required to test the generality of our observations in a broader range of model and real ecosystems.

CHAPTER 5

Managing ecological regime shifts in the context of global tipping points

In this thesis I apply multiple approaches for predicting, detecting and characterising regime shifts in ecosystems, with a goal of enhancing capacity for assessing data-poor ecosystems for regime shifts. In Chapter 2, I developed a framework for assessing ecosystems that addresses the multifaceted nature of regime shifts and will help researchers target assessment of regime shifts towards those aspects most relevant to their system. In Chapter 3, I presented a qualitative simulation approach to assessing stability of ecological communities that can usefully be applied to explore the potential importance of interactions and feedbacks among species or functional groups in determining system stability and potential vulnerability to regime shifts. Finally, in Chapter 4, I presented a method for detecting regime shifts from 1-dimensional spatial (transect) data, which enables detection of regime shifts in the absence of lengthy time-series data and removes ambiguity in distinguishing regime shifts from variation in community structure that does not represent a regime shift.

Until now relatively little work has been done to assess the vulnerability of Southern Ocean ecosystems to regime shifts (but see Clark et al. 2013; Hancock et al. 2018), despite the global importance of the ecosystem services it provides. This thesis shows that Southern Ocean ecosystems contain features likely to make them vulnerable to regime shifts (Chapter 2 and Chapter 3), and that they may have experienced regime shifts in the past (Chapter 1). The Southern Ocean has been an interesting case study because it is generally data-poor (like many ecosystems) and is also managed by multiple sovereign states and international bodies. The approaches presented in this thesis (Chapters 2, 3 and 4) are particularly useful for Southern Ocean ecosystems as they do not require extensive data (and can make use of the data that are available). However, the added uncertainty due to data-scarcity increases the importance of using an ensemble of approaches both for assessing the risk of regime shifts, and for assessing the risk of acting on those predictions. Additionally, the complexity of management structures in this system means that a great deal of work is required in

translating data streams and regime risk assessments into management actions, and updating procedures for managing risks.

An emergent theme from this thesis is the consideration of scale in relation to regime shifts. In Chapter 2, issues of scale arose as being important in predicting and/or detecting regime shifts. The qualitative models in Chapter 3 were scale-free (though they did represent a spatial region), but the different scales at which the interactions involved occur are likely to be important (see also discussion in the following section). The application of the 1-dimensional Characteristic Length Scale (CLS) estimation method to coral reef transects that were measured at the centimetre scale highlighted the importance of the scale of observation in determining the CLS, especially when compared to the attempt to apply the method to transect data at the nautical mile scale (Appendix E). In the case of the coral reef data, the interactions being observed were most likely ecological, with the estimated CLSs being in the range of 20 – 70cm (Chapter 4). In comparison, the system scale being observed in transects of 5 nautical mile resolution would be biological-oceanographic (Appendix E). Similar mismatches between the system scale of interest and the scale being observed are likely to arise in the application of generic early warning signals (EWS) of regime shifts. Whether a signal is observed will depend on the scale at which the variable interacts with and responds to change.

5.1 Specific recommendations for Southern Ocean ecosystems

There are a number of key recommendations for targeting new research and monitoring of Southern Ocean ecosystems that arise from this thesis. Firstly, a key gap for observing and understanding regime shifts in the Southern Ocean is lack of concurrent multivariate time series data (observations of multiple species at the same time and space). Access to such data would allow better characterisation of the nature of change, including understanding the scope of change (single species or community level change) and possible ecological mechanisms (Chapter 2). Future studies could also usefully aim to increase understanding of community- and biophysical-level feedbacks, including those that involve non-trophic interactions. Given the challenges in accessing the Southern Ocean, comprehensive monitoring of all ecosystem components is not feasible; however strategically targeting certain locations and variables could significantly enhance capacity to detect and characterise regime shifts.

Secondly, the network modelling exercise in Chapter 3 highlights the lack of understanding of the importance of chemical ecology (beyond microbial communities) in Southern Ocean ecosystems, and that feedbacks caused by chemical attraction could alter the stability (and potential vulnerability to regime shifts) of pelagic communities. A key gap here includes

understanding the attraction of cetaceans and Antarctic krill to DMS, and the scales over which different organisms could be attracted to DMS. A useful future research project could be to quantify associations between different trophic levels with different natural concentrations of DMS at sea, which could elucidate how DMS affects the spatial distribution and structure of the pelagic and sea-ice communities. The qualitative approach used in Chapter 3 is useful for exploring the stability of different network structures, and thus potential vulnerability to regime shifts; however attraction to DMS needs to be incorporated into spatially explicit, quantitative ecosystem models to better explore the importance of these feedbacks in a spatial and temporal context, and to explore possible alternative regimes.

Thirdly, the 1D Characteristic Length Scale estimation method offers the opportunity to better understand the nature of change in Southern Ocean ecosystems (i.e. regime shift or not), and the CLS1D *R* package facilitates application of this method (Chapter 4, Ward and Wotherspoon 2018; Ward et al. 2018). The most obvious datasets which could be explored with this approach are benthic camera transects, particularly to identify spatial differences in regimes. Importantly, to detect changes in regime over time, there needs to be the opportunity to conduct repeat transects, and there is a need to ensure future transects are of suitable length and resolution for application of the method. Direct observations of pelagic communities are generally collected in transects along ship routes, but the spatial resolution of data (and suitability for estimating CLS) along these transects is variable. For example, it would be difficult to complete a transect of appropriate length or resolution with pelagic trawl nets as the sampling method; however data collected by active acoustics, for example, are more likely to be appropriate, if well calibrated to the variable of interest. Given CLS estimation has only been applied to benthic or terrestrial systems so far, there is a need for further work testing the suitability of the approach to pelagic communities and at what scale the CLS represents ecological versus oceanographic processes. If the approach proves suitable for pelagic systems, transect data of select variables could be included in the routine data collection of ecosystem Essential Ocean Variables for the Southern Ocean (Constable et al. 2016).

5.2 Regime shifts and stability

In Chapters 2.2 and 3 of this thesis, I have explored factors that can reduce community stability in relation to vulnerability to regime shifts. Although there are clear links between stability and regime shifts, the precise nature of the relationship between them is not straightforward, not least because there are multiple definitions and properties of stability, each with multiple metrics (Donohue et al. 2013; Grimm and Wissel 1997; Ives and Carpenter 2007; Kéfi et al. 2019; Pimm 1984, also see Glossary). For example, two stability definitions related

to regime shifts involve the number of alternative stable states (more = less stable) and how easily the system can flip from one stable state to another (more easily = less stable) (Holling 1973; Ives and Carpenter 2007). According to these definitions, stability clearly relates to vulnerability of the system to regime shifts, but for other types of stability the relationship can be less clear. Here I will discuss just a few of the stability concepts.

A common definition of stability (that mostly considered in this thesis) is the propensity of a community to return to, or remain close to, its equilibrium following a small perturbation from that equilibrium (e.g. Allesina and Tang 2012; Landi et al. 2018; Pimm 1984). To take the example presented in Chapter 3, for each of the small, motif models (Fig. 3.1), some configurations of interaction strengths are stable (won't move away from equilibrium), but other configurations (i.e. with same network structure) are unstable (Fig. 3.4). Following perturbation, unstable networks could collapse and reorganise into a different network structure, or the interaction strengths could change to become a stable configuration of the same network structure. Whether either of these changes is recognised as a regime shift would depend largely on the scale of the change in terms of biomass and function or community composition.

Another type of stability mentioned in Chapter 2.2 is persistence - i.e. maintenance of species co-existence and function over time (Grimm and Wissel 1997). According to this definition, species co-existence could be maintained through regular perturbations creating opportunities for those species which might otherwise go extinct from the ecosystem (i.e. network structure does necessarily need to be stable, but could be). But equally, a community that has low variability (constancy, another type of stability) could persist through time (Grimm and Wissel 1997). A decrease in 'stability' (persistence) in this context indicates that components of the community are being lost or going extinct. How this relates to regime shifts depends on the species or functional groups that are lost from the system - loss of species that perform important functional roles could trigger a complete reorganization of the community, but the community may continue to function in the same way if only functionally redundant species are lost. Whether the gradual loss of species from a system is considered a regime shift depends on the temporal scale at which the change is considered. Similarly, the temporal and spatial scale which is considered when measuring many types of stability is likely to affect the assessment of stability.

In summary, the concepts of stability and regime shifts are interrelated, but the correspondence between them depends on the type of stability considered, as well as the spatial and temporal environments in which changes occur. There are growing calls to better understand how different concepts of stability (and their different metrics) relate to each other (e.g. Donohue et al. 2013; Kéfi et al. 2019). Equally important is to explore how these different types of stability vary within an ecosystem through time and space and in response to different

combinations of drivers, and how changes in stability (of different types) relate to regime shifts (e.g. Kuiper et al. 2015). For example, the ecological network features presented in Table 2.1 all affect network stability (propensity to return or remain near equilibrium) but more work is needed to fully understand how these features interact with each other and spatial and temporal dynamics and pressures to modify vulnerability to regime shifts.

5.3 The importance of multifunctional organisms

One interesting observation arising from this thesis is the importance of particular species or functional groups with complex roles and adaptations in structuring ecosystems, and which could increase vulnerability to regime shifts if lost (Kéfi et al. 2016a, Chapter 2). In general, conceptual models of ecosystem processes are useful for identifying multifunctional organisms. Two examples of this type of multifunctional organism within Southern Ocean ecosystems are whales (discussed in Chapter 1.2.3) and DMS-producing phytoplankton, particularly *Phaeocystis antarctica* (Chapter 3). In the following sections I elaborate further on the multifunctional role and multi-scale feedbacks associated with *P. antarctica* and also highlight humans as important multifunctional players in the Southern Ocean and in ecosystems more generally.

5.3.1 *Phaeocystis antarctica*: a Southern Ocean example

Phaeocystis antarctica contributes to feedbacks and complexity at multiple scales, from the molecular to global (climate). For example, at the population level there is evidence that ‘cheater’ individuals exist that benefit from the DMS produced by other cells, without producing it themselves (Nejstgaard et al. 2007) and evidence from terrestrial systems shows that this type of phenotypic diversity in production of chemicals can promote species coexistence (and thus diversity) to stabilise communities over time (Lankau and Strauss 2007; Maynard et al. 2019). This highlights a gap in pelagic ecosystem research – while in terrestrial systems understanding of the way plants modify their environment to their benefit (engineer-environment feedbacks) is relatively advanced, few studies investigate the importance of phytoplankton in doing the same.

In exploring the contribution of abiotic habitat modification and facilitation to positive feedbacks and hysteresis, Kéfi et al. (2016b) hypothesised that tipping points were more likely when a) plants modify their physical environment to their own benefit; b) the effects of this facilitation extend over a considerable area of the ecosystem; and c) the effects of facilitation interact with disturbances to provide opportunities for the community to establish. It is unclear whether *P. antarctica* would meet the final condition, but it does meet the first two. *Phaeocystis antarctica* (and other DMS-producing phytoplankton) modify their habitat

by altering the chemical composition of the water, adding DMS and other molecules, which reduces their mortality rate (by attracting predators that eat their grazers), and potentially increases their growth (via extra nutrient availability from faeces of the predators) (Savoca and Nevitt 2014). When aerosolised, the released DMS molecules also act as cloud condensation nuclei - reducing irradiance levels by increasing cloud formation (benefitting *P. antarctica* which does well in low-light conditions) (Charlson et al. 1987; Cropp et al. 2007).

In modifying their habitat to their own benefit, *Phaeocystis antarctica* also contributes to climate regulation in several ways. This species (and other species in the *Phaeocystis* genus) is a major producer of DMS – it is estimated that they contribute 13% of the global DMS flux to the atmosphere (Wang et al. 2015). Coupled earth system models containing explicit parameterisations of *Phaeocystis* spp. ecology, indicate that these species contribute to a positive feedback whereby they release DMS, which increases cloud formation and albedo (reflectance) resulting in a cooling effect on the climate (Wang et al. 2018). They benefit from this by being adapted to cooler temperatures, but a predicted shift to smaller phytoplankton dominance (away from diatoms and *P. antarctica*) will alter the sign of the feedbacks and the ecosystem (Wang et al. 2018). Since *P. antarctica* contribute directly to carbon export by the sinking of their colony matrix (DiTullio et al. 2000), and indirectly by enhancing productivity through attracting predators that fertilise the water column (Savoca 2018), a replacement of *P. antarctica* by other small phytoplankton is also likely to reduce carbon export (the carbon produced by small phytoplankton is less likely to sink to the ocean floor).

5.3.2 Humans as multifunctional players in ecosystems

Considering organisms with multifunctional roles and effects on different systems, naturally leads to consideration of the role of humans in ecosystems. Humans perform many functions within ecosystems: we destroy, modify and create habitat in many ways that affect species distributions and assemblages; we act as super-predators at the top of the food chain, but also contribute to eutrophication that affects bottom-up processes; we affect disease dynamics (such as through waste and food production); we alter sound- and light-scapes; and we affect climate which impacts on all ecosystems (Darimot et al. 2015; Daskalov et al. 2007; IPCC 2014, 2019b; Millennium Ecosystem Assessment 2005). Given the fundamental importance of humans in determining the way so many ecosystems function, key actions required for managing ecological regime shifts involve understanding and modifying the way humans interact within ecosystems (e.g. Möllmann and Diekmann 2012; Osterblom and Folke 2015; Rocha et al. 2015b).

Compared to many other ecosystems, Southern Oceans are typically considered an example ecosystem relatively untouched by people, because current, direct human impacts are rela-

tively few. However, past over-harvesting has undoubtedly shaped the current state of the ecosystem (e.g. see discussion on historical whaling in Chapter 1.2.3). At a global scale, humans depend on ecosystem services provided by the Southern Ocean, including for example, for food security, climate regulation and carbon export, and medicinal products from its unique biodiversity (Grant et al. 2013; Rogers et al. 2019). Humans now act as migratory predators in the ecosystem through fisheries, but also affect Southern Ocean ecosystems through pollution, tourism, species introductions, and indirectly through our effect on climate. Whether these impacts are considered internal or external pressures on the ecosystem is a matter of perspective – the scope of the system being considered – but nevertheless, socioecological feedbacks could destabilise the ecosystem. This is especially of concern for the setting of catch limits in the Antarctic krill fishery. CCAMLR, the managing body for Southern Ocean fisheries, uses a precautionary principle in setting catch limits for krill (with current catch levels well below this limit, but has potential to become the largest single species fishery in the world) (Nicol and Foster 2016); however, the importance of Antarctic krill in the food web, especially in the areas that fishing occurs, is such that unrecognised feedbacks between the krill fishery and the ecosystem could fundamentally alter the food web (e.g. Ryabov et al. 2017). Ongoing monitoring and modelling efforts are required to ensure this does not occur. Nevertheless, the impacts of human-induced climate change on the ecosystem are likely to be more profound (Rintoul et al. 2018; Rogers et al. 2019), and will interact with other human drivers (Möllmann and Diekmann 2012).

5.4 System scope

In the following section I use the term ‘system scope’ to refer to the range of related system elements that are being considered. These elements include (but are not limited to), biophysical elements, socio-economic elements, coupled social-ecological systems, coupled (global) climatic-ecological (biosphere) systems, and finally coupled climate-socioecological systems (which might be considered at different scales). Consideration of system scope is critically important to discussions of regime shifts and tipping points (as discussed in Box 1, Chp. 2), and while this thesis has focused mostly on the biophysical scope (with some consideration of management responses), here I extend this discussion to a broader system perspective.

There is increasing recognition that a social-ecological perspective is required to manage ecosystems and societies sustainably (e.g. Biggs et al. 2018; Cumming et al. 2006; Ostrom 2009; Walker et al. 2004). Social, economic and ecological interactions can create feedbacks within and between the different system types that result in undesirable outcomes, such as the degradation of ecosystem services (e.g. Glaser et al. 2018; Lade et al. 2015; Yletyinen et

al. 2019). This is especially apparent in primary industries, where economic pressures drive over-exploitation of natural resources, such as fisheries stocks (Yletyinen et al. 2019). This human-driven development of detrimental positive feedbacks often happens where immediate economic need overwhelms the longer-term need of the ecosystem service to be maintained, or where there is a social, spatial and temporal disconnect between the main economic benefit and the people who depend on the ecosystem services in the longer term. In this context, and in order to prevent degradation of ecosystems, there is a need to explicitly frame ecosystem management in a social-ecological context to identify destabilising feedbacks, or feedbacks that are resilient but that create undesirable outcomes (e.g. Glaser et al. 2018). For example, social power imbalances can create a situation where the people exploiting an ecosystem are trapped in poverty and have little choice but to continue exploiting the ecosystem unsustainably, but gain relatively little from doing so (e.g. Glaser et al. 2018). In this case, the people who gain the greatest economic benefit from the degradation of the ecosystem are those with the greatest power, and have little interest in changing the status quo. Once undesirable feedbacks are identified, the next task is to figure out how to break those feedbacks – or modify them such that they support rather than degrade ecosystem function and services.

The qualitative approach used in Chapter 3 is useful here because it can easily be extended to social-ecological systems (e.g. Dambacher et al. 2009; Dambacher et al. 2007) or also to include abiotic feedbacks such as with climate or sea ice (e.g. Melbourne-Thomas et al. 2013). The benefit of this approach is that because it is qualitative, there is no requirement for interactions to be of the same type; thus interactions that represent energy flow, social pressure, monetary exchange and so on, can all be included within the same network. The second advantage in the context of identifying solutions for breaking undesirable feedbacks, is that while there is some skill required for accurately distilling dynamics into the network, it is relatively easy to construct alternative representations of the network. The stability and response to perturbation of these alternative network structures can then be compared to identify the most effective way to modify the feedbacks for more sustainable ecosystem management.

5.5 Managing ecological regime shifts in the context of global tipping points

As the climate changes, there is no doubt that ecosystems will be increasingly pushed across thresholds and experience regime shifts, and indications so far are that they will shift towards less productive regimes with a net loss of ecosystem services (e.g. Harris et al. 2018; Rocha et al. 2015a). Even if ecosystems are not pushed across ecological tipping points, step-changes in the global system will effectively create the same result. Evidence is mounting that Earth

has now entered its sixth mass extinction event (e.g. Barnosky et al. 2011; Ceballos et al. 2015; Fey et al. 2015; Payne et al. 2016) – indicating that a human-driven shift in the whole biosphere is occurring (Barnosky et al. 2012; Rockström et al. 2009; Steffen et al. 2018). Past evidence indicates that ecological regime shifts can also trigger social ones (Cumming and Peterson 2017; Diamond 1994). For example, fishing villages and societies collapsed following the collapse of the cod fishery (itself the result of a shift to industrialisation of fisheries) (Hamilton and Butler 2001); and collapse of ancient civilizations has been associated with over-exploitation of resources including trees and water (Diamond 1994), most likely in combination with climate variability. While social collapse resulting from ecological regime shifts has been geographically constrained in the past, the increasing global synchrony of projected ecological regime shifts has the potential to trigger broader-scale social disorder or regime shifts. If this occurs, then opportunities to effectively manage ecosystems and support ecosystem services may become limited. It is therefore imperative to proactively alter human-ecosystem interactions to maintain as many ecosystem services as possible into the future (and to avoid social collapse).

Thinking about ecological regime shifts in the context of their increasing inevitability could create a sense of despondency (especially for ecosystem practitioners that are invested in the conservation of their system); however, reframing the problem can offer hope. Specifically, management of ecological regime shifts should be viewed as an opportunity to avert global-scale climate and social tipping points. While the impact of climate on ecosystems is typically viewed as being a one-way interaction, it is also clear that there are ways in which ecosystems affect climate. Research into climatic tipping points has identified a number of ecological tipping elements in the Earth system (e.g. Bathiany et al. 2016; Lenton et al. 2008), which can then feedback to climate change. For example, Steffen et al. (2018) looked at a number of carbon cycle feedbacks that have the potential to accelerate climate change. Of these, weakening of oceanic and terrestrial physiological carbon sinks has the greatest potential impact, and together these could increase warming by an additional 0.25-2.0°C (Steffen et al. 2018). Other elements, including boreal and Amazon forest dieback and increased oceanic bacterial respiration, each have the potential to contribute an additional 0.02-0.06°C warming (Steffen et al. 2018). In this light, even though the importance of a single ecosystem in the climate system may seem negligible, collectively they play a role in regulating climate. It is clear then that maintaining ecosystem function, specifically those functions that maximise carbon uptake, is an important part of mitigating climate change. Equally important is to support those ecosystem functions that support socioeconomic resilience.

5.5.1 Some next steps towards management of ecological regime shifts

Ecological regime shifts are a multifaceted problem requiring an ensemble of approaches to predict, detect and manage. This thesis does not claim to solve the problem of regime shifts, but it does offer a range of tools that can be used to improve understanding of regime shifts and adaptation to a world where regime shifts are increasingly common.

Assessing ecosystems for evidence of past regime shifts, or for risk of future regime shifts, will invariably require evaluating multiple lines of evidence (such as in the process for assessing ecosystems against the IUCN Red List of Ecosystems criteria for risk of collapse) (e.g. Bland et al. 2017; Keith et al. 2013; Rodriguez et al. 2015). Together, the contributions of this thesis broaden the range of tools and avenues for understanding and investigating regime shifts, and increase the possible lines of evidence to inform ecological management (Table 5.1). These analytical options will be especially useful for assessment of data-poor ecosystems. These tools are equally valuable for evaluating major gaps in understanding and assessment capacity, and how future monitoring and research can be strategically targeted to maximise capacity to predict, understand, and detect regime shifts where data are few and where there is no option to monitor indiscriminately. In this case, as well as more generally, the role of expert opinion and judgement is fundamental for assessing and synthesising multiple lines of evidence into a coherent monitoring and management plan or risk assessment. Importantly, expert judgements can be biased, but the accuracy and usefulness of expert groups can be enhanced in a number of ways; this includes using a structured elicitation process, embedded training and assessment of expert judgement, and ensuring diversity amongst the experts (e.g. Burgman et al. 2011; Hemming et al. 2018; Sutherland and Burgman 2015). Unlike the Red List of ecosystems criteria, the tools and approaches from this thesis can be applied to any ecosystem – not just to those with evidence of collapse. These tools are therefore especially useful for setting research and monitoring priorities.

The review and framework developed in Chapter 2 can be used to characterise vulnerability to and the nature of regime shifts. The ecosystem attributes detailed in Tables 2.1 and 2.2 can be used to characterise the ways in which ecosystems might be vulnerable to regime shifts, but may also be increasingly useful to assess the stability of novel ecosystems that arise following species extinctions and geographic range shifts (e.g. Pecl et al. 2017) to understand whether they might experience further regime shifts and species loss. A useful future project would be to translate these tables into a risk assessment protocol or product that could be used more easily by managers and to inform policy making (e.g. Hobday et al. 2011). This will require further research to explore how the different network, spatial and dynamic features are balanced in stable systems, and how changes in one feature could be counterbalanced by forcing change in another feature to support persistence of an ecosystem. It may then

be possible to rank ecosystem features, combinations of features or combinations of features and stressors by how they affect likelihood of, and hazard posed by, regime shifts (e.g. in concert with the research recommended in Section 5.2). In the future, understanding the interplay of these ecological attributes may even assist researchers to ‘design’ more stable novel ecosystems within the goal of maintaining ecosystem functioning (e.g. Schlappy and Hobbs 2019).

Our capacity to predict future ecosystem states is becoming increasingly important, such that decisions can be made about where best to concentrate effort on managing regime shifts. Given the extent of projected ecosystem change (IPCC 2014, 2019b), it is likely that a triage approach will be required for deciding which ecosystems justify the most effort (e.g. Schlappy and Hobbs 2019). While there will need to be discussion around how ecosystems are prioritised (e.g. for greatest biodiversity conservation potential, for climate regulation services, for food production services, their likelihood of recovery following management intervention), predicting the future state of an ecosystem following a regime shift may be key to making these decisions. The challenge with this is that ecosystems and social-ecological systems are complex adaptive systems. This means there are many possible future configurations, and thus many possible futures; the configuration that eventually arises will depend on the order in which different drivers affect the system, the evolutionary capacity of organisms within it, the way ecological interactions change in response to those drivers and evolutionary changes, as well as the element of chance. It is therefore not possible to predict future state with certainty; however, with an ensemble model approach it may be possible to identify the most likely trajectory and suite of possible trajectories (Griffith and Fulton 2014; Melbourne-Thomas et al. 2017). The methods and approaches suggested in Chapters 2.3.1 and 3, and in Table 2.3.1 can be used and combined to gain an understanding of how ecosystems might respond.

Figure 5.1 illustrates potential approaches for avoiding catastrophic thresholds (discussed in Chapter 2.3.2). The Earth is already ‘locked in’ to a certain degree of future climate change, meaning that controlling these drivers to avoid a regime shift on ecologically relevant timescales is unlikely. However other pressures on ecosystems that are more responsive to management intervention can be reduced to increase resilience of ecosystems and steer systems away from regions of hysteresis or abrupt shifts (lower-right panel of Figure 5.1). Where that is not possible, or where a combination of approaches is required, understanding the ecological features and mechanisms discussed in Chapter 2 may be used to help steer ecosystems towards a smoother trajectory of change (lower left panel of Figure 5.1).

Finally, and also central to limiting the impact of regime shifts, will be the capacity to detect them when they happen. Being able to adapt management processes soon after a regime shift occurs limits the potential for management actions being applied that are maladapted

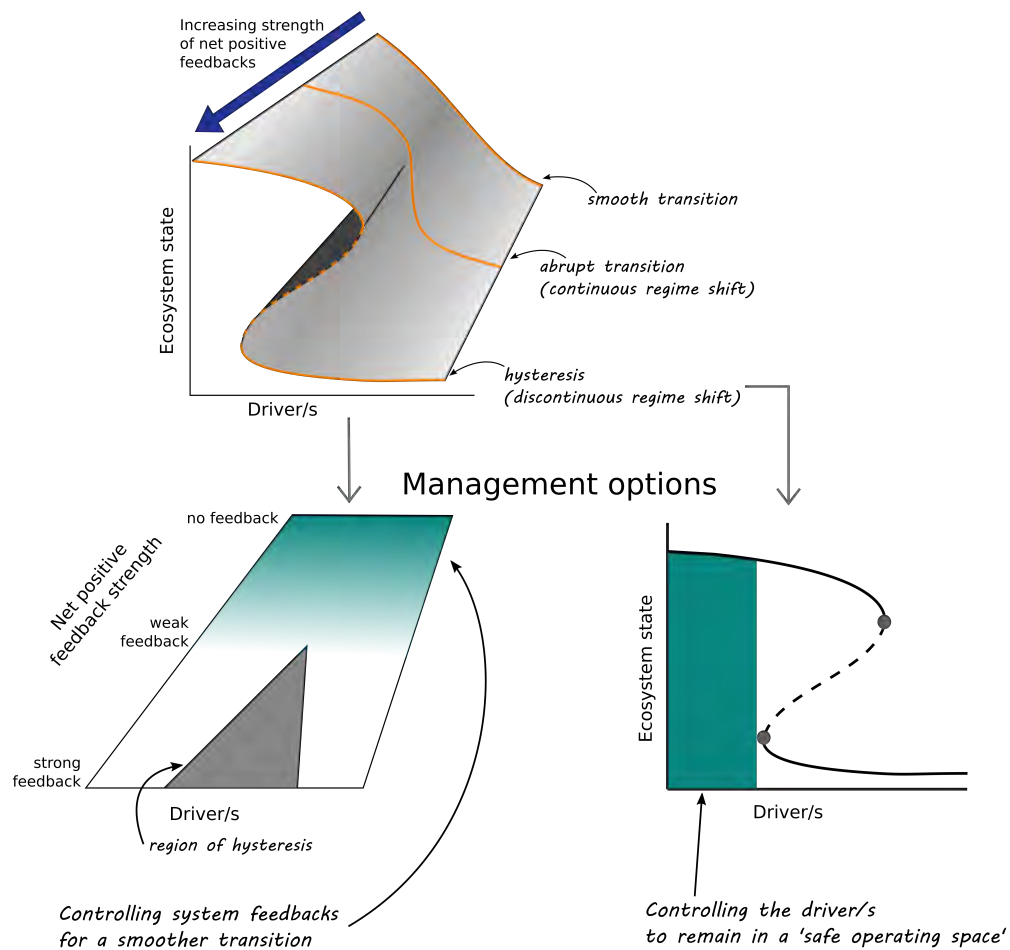


Figure 5.1: Illustration of how ecological and social-ecological (and other) systems could be managed to avoid tipping points, using the cusp diagram as a theoretical example (top panel). In the cusp diagram (top panel) the z-axis represents internal system structure or ecological-environmental feedbacks, where greater strength of positive feedbacks can increase the degree of non-linearity in the response of the system to changes in the driving parameters. In the case where hysteresis exists, to retain the system in a 'safe operating space' and avoid a change in regime altogether, one approach would be to control the drivers (on the x-axis) to avoid the region of hysteresis (to ensure stochastic events don't push the system towards the alternative basin of attraction) (lower right panel). Where controlling the drivers is not possible on relevant timescales, then an alternative approach is to change the internal structure and feedbacks (on the z-axis) to steer the system towards a smoother transition pathway and avoid tipping points (lower left panel). In both lower panels, the green area represents the more desirable operating space.

for the new regime and further erode the ecosystem state and the services it provides. The method for detecting regime shifts from spatial data that is presented in Chapter 4, provides the opportunity to detect, and therefore act promptly to adapt management processes soon after a regime shift occurs.

Chapter 5. Managing ecological regime shifts in the context of global tipping points

Table 5.1: Synthesis of advances and suggested future work. (Ticks and bullet points coloured orange for contributions to the general field of ecological regime shifts, while blue refers specifically to the Southern Ocean)

<p>Prediction of regime shifts</p> <p>This thesis</p> <ul style="list-style-type: none"> ✓ Distilled key questions to predict about regime shifts (Chp. 2) ✓ Identified and described approaches for predicting regime shifts (Chp. 2) ✓ Developed approach for predicting importance of interactions for stability and vulnerability to shifts (Chp. 3) ✓ Identified specific features that increase vulnerability of SO ecosystems to regime shifts (Chp. 2 and 3). ✓ Identified data suitable for predicting regime shifts (Chp. 2). 	<p>Future work</p> <ul style="list-style-type: none"> ● Improve capacity to predict ecological responses to synergistic interactions between drivers. ● Test available long-time series data for evidence of early warning signals ● Further explore data and ecosystem features of Southern Ocean ecosystems identified in Chapter 2, to predict regime shifts.
<p>Detection of regime shifts</p> <p>This thesis</p> <ul style="list-style-type: none"> ✓ Developed and tested a new method 1D-CLS for detecting regime shifts from 1D spatial data (Chp. 4). ✓ Applied 1D-CLS method to coral reef dataset and detected a regime shift (Chp. 4). ✓ Created an R-package, ‘CLS1D’, to increase accessibility of the method (Chp. 4, App. D). ✓ Identified and explored Southern Ocean data sets for potential application of the 1D-CLS method (Chp. 2, App. E). 	<p>Future work</p> <ul style="list-style-type: none"> ● Directly compare 2D and 1D CLS for same ecosystem/models ● Investigate whether 1D CLS works if there is a gradient along the transect, and if so, under which circumstances. ● Compare temporal and spatial methods for detecting regime shifts ● Explore relationship between spatial EWS and CLS ● Apply 1D CLS to Southern Ocean datasets.
<p>Characterisation of regime shifts</p> <p>This thesis</p> <ul style="list-style-type: none"> ✓ Described ecological features that can be used to characterise vulnerability to regime shifts (Chp. 2). ✓ Described approaches for characterising the nature of regime shifts (e.g. mechanisms, drivers, future state) (Chp. 2). ✓ Presented qualitative simulation method for exploring network stability and vulnerability to regime shifts (Chp. 3). ✓ Explored potential for DMS-mediated interactions and feedbacks to create tipping points (Chp. 3). 	<p>Future work</p> <ul style="list-style-type: none"> ● Better characterise how these ecological features work together to determine vulnerability. ● Investigate how the interplay of different ecological features of a system might affect the trajectory of the system if it does regime shift (e.g. hysteresis, relative rapidity of shift, future state). ● Extend the qualitative models presented in Chapter 3 into spatially and temporally explicit ecosystem models to better characterise the importance of the feedbacks they contain and characterise the risk that they cause a regime shift.
<p>Managing for regime shifts</p> <p>This thesis</p> <ul style="list-style-type: none"> ✓ Developed a framework ecosystem managers and researchers can follow to assess their ecosystem for regime shifts (Chp. 2) ✓ Synthesized advice for using specific ecosystem properties to improve management to avoid or reverse regime shifts (Chp. 2) ✓ Discussed implications for regime shifts on management processes and structures (Chp. 2 and 5) ✓ Discussed importance of managing ecological regime shifts in context of cross-scale feedbacks and global tipping points (Chp. 5) ✓ Identified and proposed data that should be incorporated into management decisions to enhance capacity to respond to predicted and detected regime shifts (Chp. 2). 	<p>Future work</p> <ul style="list-style-type: none"> ● Interdisciplinary research into social-climate- ecosystem feedbacks to improve management of ecosystem regime shifts ● Translate framework developed in Chapter 2 into a simpler (less academic), risk assessment document suitable for use by ecosystem managers ● Conduct more detailed risk assessments for regime shifts in Southern Ocean ecosystems ● Identify, assess and implement management actions to avoid or minimise impact of regime shifts. ● Update SO management structures and processes for better incorporation of data streams, and to be able to act proactively avert, or manage the impact of regime shifts as they occur.

Glossary

Attractor: A point or set of points in phase space to which a system is attracted, and to which it will tend to return following a perturbation.

Attractor reconstruction: Production of a representation of an attractor in phase space that is topologically equivalent to the real system attractor. The most common approach to attractor reconstruction is delay embedding (e.g. see Fig. 4.1, Chapter 4).

Carbon export: Phytoplankton take up dissolved inorganic carbon and convert it into cell structures. When they die, their cells either sink out of the surface waters (exported) or are consumed by grazing zooplankton or bacteria. Larger particles sink more quickly and are thus more likely to be exported rather than being consumed and retained in surface waters. Thus larger particles and larger-bodied organisms export more carbon. Carbon that is exported to the deeper ocean is effectively removed from the atmospheric carbon cycle for long time periods, and no longer contributes to atmospheric warming while at depth.

Characteristic Length Scale (CLS): The optimal spatial scale at which to observe a system to obtain meaningful information on its behaviour. The CLS is defined as the spatial scale at which stochastic and deterministic variation are balanced (Pascual and Levin 1999) and the scale above which windows in different regions of a landscape are statistically independent (Keeling et al. 1997). This scale emerges from the dynamics of the system and as such, a change in the CLS of a system is an indication that the dynamics of the system have fundamentally changed. Estimating the CLS involves attractor reconstruction combined with nearest neighbour prediction.

Connectance: The proportion of all possible connections that are realised in a network (where the total number of possible connections is the number of species²).

Delay embedding: A method of generating a multidimensional data set from an original data set of a single dimension. This is usually done with temporal data, but here in Chapter 4 (the sliding window approach to CLS estimation), spatial data is used. Each column in the resultant matrix will be one dimension, and each row one delay embedded point, in the reconstructed attractor in phase space.

Dimethyl sulfide: A strongly smelling compound produced by marine phytoplankton, and other organisms, via a precursor compound, dimethylsulfoniopropionate (DMSP). Dimethylsulfoniopropionate and DMS have a range of direct benefits for species that produce it, including as an antioxidant. A range of taxa - including bacteria, copepods, fish, seals, birds, turtles - are attracted to DMS and/or DMSP. When it enters the air as sea spray, DMS can become aerosolised, attract air-breathing organisms and also act as cloud condensation nuclei (CCN).

Early warning signals: Early warning signals (EWS) of regime shifts are based on emergent behaviours common to complex systems as they approach a threshold. They are generic rather than being system specific and so theoretically little understanding of the system is required to detect an early warning signal.

Feedback: A feedback is created when an organism (or a network component) affects itself through its interactions with other organisms. A feedback can be short - organism 1 affects organism two which affects organism 1, or it consist of a longer loop, e.g. organism 1 affects organism 2 which affects organism 3 which affects organism 1. When the end effect of the feedback is positive on organism 1, this is termed a positive feedback; when the end effect on organism 1 is negative, it is a negative feedback. Negative feedbacks tend to be stabilising, while positive feedbacks are destabilising.

Higher-order interactions: A higher-order interaction is when the presence of an organism alters the interaction between two different organisms (but is not involved in that interaction itself), such that the emergent outcome of the interaction cannot be predicted from the pairwise interaction alone. For example, one species may outcompete another in open grasslands, but in the shade of a tree, the other species outcompetes the first. In this case, the tree alters (mediates) the interaction between those two species.

Hysteresis: Hysteresis is typified by the presence of two different relationships between the driving and response variables, such that (at least) two different regimes are possible over a common range of the driving variable. There is a difference in the forward and reverse thresholds of a regime shift.

Interaction types: Food webs consist of networks of trophic interactions (where there is a positive effect on the consumer, and a negative effect on the prey), but many other types of interactions occur in ecosystems. Non-trophic interactions include e.g. facilitation and mutualism where one organism positively affects another, and e.g. competition and amensalism where an organism negatively affects another.

Lorenz attractor: The Lorenz attractor (also called the butterfly attractor) is based on a set of ordinary differential equations that describe and simplify atmospheric convection. I use it as a visual aid in Chapter 4 because it is a readily recognizable example of an attractor

with complex (chaotic) dynamics (Figs. 4.1 and 4.2, Chapter 4; and fig. C.1 in Appendix B). It also typifies a system that experiences large sustained swings in mean system state within a single regime.

Nearest neighbours: Nearest neighbours in a reconstructed attractor are a set of delay embedded points that represent similar local trajectories in time (or space) of the original time series (or spatial series). Nearest neighbours are adjacent in the phase space, but not necessarily proximate in the original data series (see Fig. 4.2c, Chapter 4).

Network: A network is a collection of interacting entities (e.g. individuals, species, functional groups, organisations). When represented in a network model, each entity is called a node, and they are connected by lines called edges, which represent the interactions between the nodes.

Network structure: Network structure refers to the pattern in which entities are connected with each other over the network. For example, nested structures involve generalists acting as hubs of connectivity linking more disconnected, specialised species. Modular network structures contain distinct clusters of organisms that are tightly connected within each cluster (e.g. in one habitat), but that are more loosely connected to the broader network (e.g. to organisms in other habitats).

Phase space: A space in which all possible states of a system are represented. Each state variable corresponds to one axis. Each point in phase space corresponds to a different ecosystem state.

Regime: An ecosystem regime constitutes the dynamic behaviour and functioning of a system determined by its structure and self-supporting processes and feedbacks. Because it is dynamic in nature, a system can transition through many different states within the same ecosystem regime. An ecosystem regime is associated with a single attractor.

Regime shift: A change in the structure and functioning of an ecosystem (or other complex system) involving a switch to a different attractor. Also called phase shift or phase transition. A regime shift can be classed as continuous (also called a transcritical transition, if it involves a bifurcation) or discontinuous (involving hysteresis, also called a critical transition).

Resilience: The ability of a system to return to its previous state following a perturbation, and, the time taken to do so.

Self-organised spatial patterns: Self-organised spatial patterns are those that emerge from the community interactions, rather than from spatial variability in environmental conditions or disturbance. One key feature leading to such pattern formation is the presence of organisms that facilitate growth in their local vicinity (e.g. increased moisture retention, habitat creation) but create negative effects at a greater distance (e.g. resource depletion)

(Rietkerk and van de Koppel 2008).

Southern Ocean: The Southern Ocean encircles Antarctica and extends north to the Sub-tropical Front, following one definition used elsewhere (e.g. Constable et al. 2014; Deppeler and Davidson 2017). The term as used here therefore includes waters along the coast of Antarctica, sub-Antarctic waters and islands and the sea-ice, pelagic and benthic habitats in between.

Spatially multimodal system: Over its distribution, an ecosystem can exist in different alternative states at the same time - i.e. different patches of the ecosystem are in alternative stable states. The probability distribution of such a landscape/ecosystem would have multiple modes.

Stability: There are multiple definitions of stability, reflecting the multifaceted nature of the concept (Donohue et al. 2013; Grimm and Wissel 1997; Ives and Carpenter 2007; Kéfi et al. 2019). In this thesis, particularly in Chapter 3, the definition used is Lyapunov stability: a system is stable when its characteristic polynomial has roots with negative real parts. In ecological terms, Lyapunov stability means the ecosystem will remain in the vicinity of its equilibrium following a small (press) perturbation away from that equilibrium (i.e. it will not move away from the equilibrium following perturbation). In Chapter 2 a broader range of stability qualities are considered, depending on what has been considered in the literature, this includes e.g. resistance to and recovery from perturbation, persistence, and Lyapunov.

State: An ecosystem state is the configuration of an ecosystem at one point in time (e.g., combination of population sizes, values of state variables). Importantly, there may be many possible states within an attractor, and even sustained and/or highly oscillatory changes in state (e.g., see time series in Fig. 4.1, Chapter 4).

Variance spectra: Plots of error variance (Error X or Prediction r^2) against window size, used to estimate the Characteristic Length Scale of an ecosystem. This is also referred to as a fluctuation diagram in Keeling et al. 1997.

APPENDIX A

Supplementary material to Chapter 2

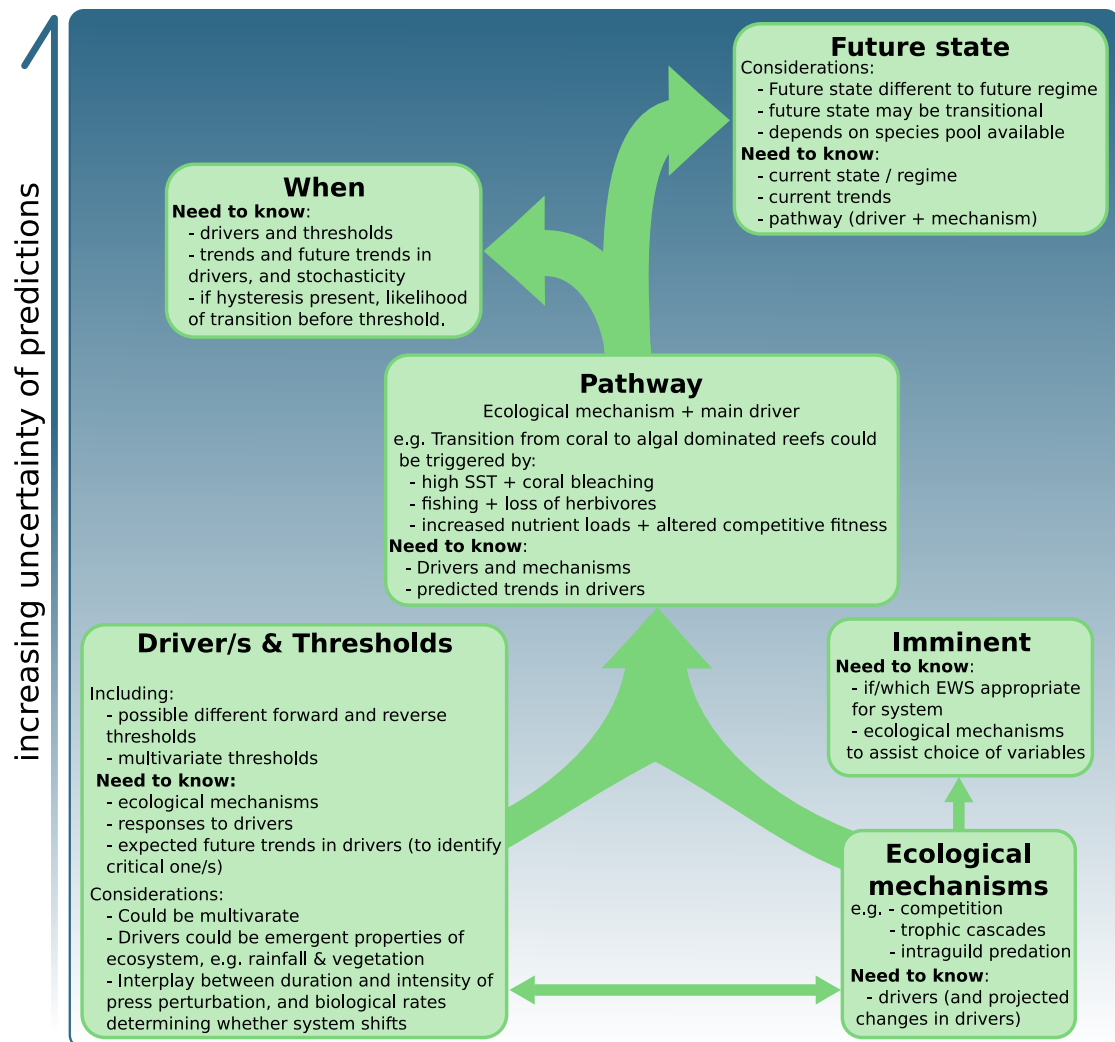


Figure A.1: Flow diagram illustrating the dependence of ecological predictions related to regime shifts on other predictions. The most uncertain predictions (when a regime shift will occur, and what the future state will be) depend on predicting and understanding the ecological mechanisms and drivers.

APPENDIX B

Supplementary material to Chapter 3

Table B.1: Comparison of results of selected model simulations in QPress between models with a grazer \rightarrow predator edge, and the same models without. Removing the $\text{gr} \rightarrow \text{pr}$ edge reduced the stability of the models, but for most models it resulted in only slight differences in the relative importance of the edges for distinguishing between stable and unstable community matrices.

Model	With $\text{gr} \rightarrow \text{pr}$		Without $\text{gr} \rightarrow \text{pr}$	
	Matrices stable %	Influential edges	Matrices stable %	Influential edges
Model 1	100%	NA	Models cannot produce stable community matrices that pass the validation criterion because predator response to decrease in grazers is uncertain. (100% stable if remove validator).	
Model 1n	100% (but class model)	NA (no unstable cases to compare)		
Model 2	91%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DMS} \rightarrow \bullet \text{DMS}$ $\text{DP} \rightarrow \text{DMS}$ $\text{GR} \rightarrow \bullet \text{DP}$ $\text{DMS} \rightarrow \text{PR}$	72%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \text{DMS}$ $\text{GR} \rightarrow \bullet \text{DP}$ $\text{GR} \rightarrow \text{DMS}$
Model 2n	76%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DMS} \rightarrow \bullet \text{DMS}$ $\text{DP} \rightarrow \text{DMS}$ $\text{DMS} \rightarrow \text{PR}$	50%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \text{DMS}$ $\text{GR} \rightarrow \text{DMS}$ $\text{GR} \rightarrow \bullet \text{DP}$
Model 3	93%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{GR} \rightarrow \text{DMS}$ $\text{GR} \rightarrow \bullet \text{GR}$ $\text{DMS} \rightarrow \bullet \text{DMS}$	80%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{PR} \rightarrow \bullet \text{PR}$ $\text{GR} \rightarrow \bullet \text{GR}$ $\text{DMS} \rightarrow \bullet \text{DMS}$
Model 3n	94%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DMS} \rightarrow \bullet \text{DP}$ $\text{DMS} \rightarrow \bullet \text{DMS}$	66%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \text{DMS}$ $\text{PR} \rightarrow \bullet \text{PR}$ $\text{GR} \rightarrow \bullet \text{DP}$ $\text{GR} \rightarrow \text{DMS}$ $\text{DMS} \rightarrow \text{PR}$ $\text{DMS} \rightarrow \bullet \text{DMS}$
Model 5	48%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$	42%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$ $\text{GR} \rightarrow \bullet \text{DP}$
Model 5n	42%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$	35%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$
Model 7	50%	$\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{DMS} \rightarrow \bullet \text{DP}$	43%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$
Model 7n	55%	$\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{DMS} \rightarrow \bullet \text{DP}$	50%	$\text{DP} \rightarrow \bullet \text{DP}$ $\text{DP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{OP}$ $\text{OP} \rightarrow \bullet \text{DP}$ $\text{GR} \rightarrow \bullet \text{DP}$ $\text{PR} \rightarrow \bullet \text{PR}$

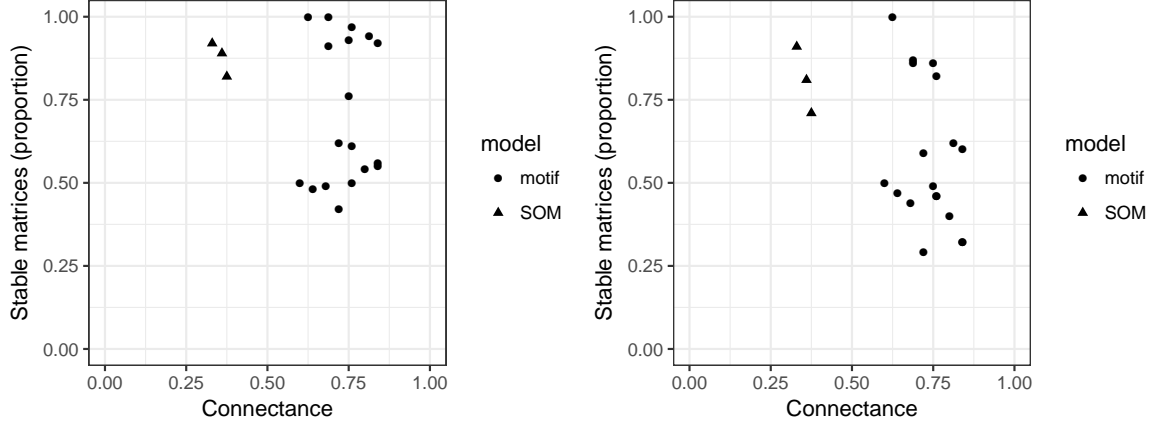


Figure B.1: Connectance versus the proportion of matrices (from QPress) that are stable for each model. The smaller motif models are indicated with points and the larger Southern Ocean models with triangles. Left = stability results from models as described in main text, with some validators and/or constraints applied; Right = stability results of the same models without any validators or constraints applied in QPress.

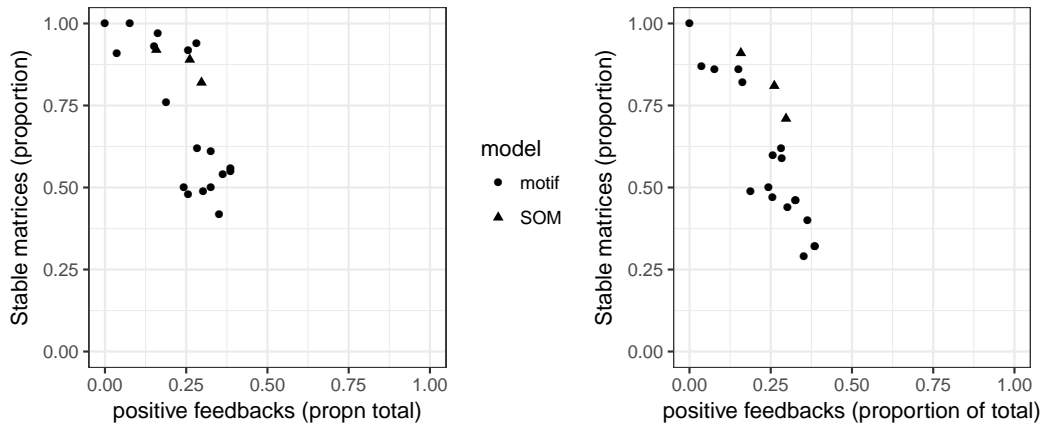


Figure B.2: Proportion of the total feedbacks that are positive versus the proportion of matrices (from QPress) that are stable for each model. The smaller motif models are indicated with points and the larger Southern Ocean models with triangles. Left = stability results from models as described in main text, with some validators and/or constraints applied; Right = stability results of the same models without any validators or constraints applied in QPress.

Table B.2: Symbolic loop analysis results for models including nutrient feedbacks. Reported for each model is the connectance (C), class (based on Hurwitz criteria for Lyapunov stability; weighted feedback at highest level wF_n , weighted determinant wD_n , and ratio of the weighted determinant to a control model C, as per Dambacher et al. 2003), net sign (at highest level) of feedbacks, total number of feedbacks and the total number of positive feedbacks in parentheses. The positive feedback sequences at each level of feedback are listed, with the total number of times each sequence appears in different positive feedback cycles in the model stated in parentheses.

Model	C	Class	Sign at highest level	Feedbacks, total and (positive)	Positive feedback sequences			
					Length 2	Length 3	Length 4	Length 5
M1n	0.688	Class I, $wF_4=-0.50$, $wD_3=0.33$, ratio to model C=3.6	negative	26 (2)	none	DP→Gr→Pr→DP (2)	none	NA
M2n	0.75	Class I, $wF_4=0$, $wD_3=0.29$, ratio to model C=3.2	neutral	32 (6)	none	DDP→GR→PR→DP (2) DP→DMS→PR→DP (2)	DP→DMS→PR→GR→DP (1) DP→GR→DMS→PR→DP (1)	NA
M3n	0.813	Class I, $wF_4=0.091$, $wD_3=0.17$, ratio to model C=1.9	positive	39 (11)	GR→DMS→GR (4)	DP→GR→PR→DP (2) DP→DMS→PR→DP (2)	DP→DMS→PR→GR→DP (1) DP→GR→DMS→PR→DP (1) DP→DMS→GR→PR→DP (1)	NA
M4n	0.68	Class I, $wF_5=0$, $wD_4=0.017$, ratio to model C=1.9	neutral	86 (26)	DP→OP→DP (10)	DP→GR→OP→DP (4) DP→OP→GR→DP (4) DP→GR→PR→DP (4) OP→GR→PR→OP (4)	none	none
M5n	0.72	Class II, $wF_5=0$, $wD_4=0.0061$, ratio to model C=0.65	neutral	108 (36)	DP→OP→DP (11)	DP→GR→OP→DP (4) DP→OP→GR→DP (4) DP→GR→PR→DP (4) DP→DMS→PR→DP (5) OP→GR→PR→OP (4)	DP→DMS→PR→GR→DP (2) DP→GR→DMS→PR→DP (2) OP→GR→DMS→PR→OP (2)	none
M6n	0.8	Class II, $wF_5=-0.056$, $wD_4=0.0053$, ratio to model C=0.57	negative	156 (53)	DP→OP→DP (11) GR→DMS→GR (8)	DP→GR→OP→DP (4) DP→OP→GR→DP (4) DP→GR→PR→DP (4) DP→DMS→PR→DP (5) OP→GR→PR→OP (5)	DP→DMS→GR→OP→DP (2) DP→DMS→PR→GR→DP (2) DP→GR→DMS→PR→DP (2) DP→DMS→GR→PR→DP (2) DP→OP→GR→DMS→DP (2) OP→GR→DMS→PR→OP (2)	none
M7/8n	0.84	Class II, $wF_5=0$, $wD_4=0.0048$, ratio to model C=0.57	neutral	160 (62)	DP→OP→DP (11) GR→DMS→GR (8)	DP→GR→OP→DP (4) DP→DMS→OP→DP (5) DP→OP→GR→DP (4) DP→GR→PR→DP (4) DP→DMS→PR→DP (5) OP→GR→PR→OP (5)	DP→DMS→GR→OP→DP (2) DP→GR→DMS→OP→DP (2) DP→DMS→OP→GR→DP (2) DP→DMS→PR→GR→DP (2) DP→GR→DMS→PR→DP (2) DP→DMS→GR→PR→DP (2) DP→OP→GR→DMS→DP (2) OP→GR→DMS→PR→OP (2)	none
M9n	0.84	Class II, $wF_5=-0.095$, $wD_4=0.022$, ratio to model C=2.4	negative	160 (41)	GR→DMS→GR (10)	DP→OP→GR→DP (4) DP→GR→PR→DP (4) DP→DMS→PR→DP (5) OP→GR→PR→OP (5)	DP→GR→PR→OP→DP (2) DP→DMS→PR→OP→DP (2) DP→DMS→OP→GR→DP (2) DP→DMS→PR→GR→DP (2) DP→GR→DMS→PR→DP (2) DP→DMS→GR→PR→DP (2) DP→OP→GR→DMS→DP (2) OP→GR→DMS→PR→OP (2)	DP→DMS→PR→GR→OP→DP (1) DP→GR→DMS→PR→OP→DP (1) DP→DMS→GR→PR→OP→DP (1)

Table B.3: Comparison of results of selected model simulations in QPress when excluding constraints and validators (see also Fig. B.3). Note that use of constraints varies in the models due to differences in mediated interactions, and that Model 1n did not contain constraints because DMS did not mediate any interactions in that model.

Model	Stable matrices (%)		Influential edges	
	Including validator (and constraints where relevant)	No validator or constraints included	When validator and constraints included	No validator or constraints included
M2	91%	87%	DP→DP DMS→DMS DP→DMS GR→DP DMS→PR	DP→DP DMS→DMS DP→DMS
M2n	76%	50%	DP→DP DMS→DMS DP→DMS DMS→PR	DP→DP PR→DP DMS→DMS DMS→PR PR→PR DP→DMS
M3	93%	87%	DP→DP GR→DMS GR→GR DMS→DMS	DP→DP GR→GR GR→DMS DMS→DMS PR→PR DMS→GR
M3n	94%	62%	DP→DP DMS→DP DMS→DMS	PR→DP PR→PR DMS→DP DMS→PR DP→DP
M7	50%	46%	DP→DP DP→OP OP→OP OP→DP	OP→OP OP→DP DP→DP DP→OP DMS→DP DMS→OP
M7n	55%	32%	OP→OP OP→DP DP→DP DP→OP DMS→DP	OP→OP OP→DP DP→DP DMS→DP DP→OP PR→PR PR→DP

Detailed comparison of results from the two different qualitative approaches for Model 2 and Model 7

Model 2 contains a single positive feedback through which DMS-producing phytoplankton could promote their own population growth: by releasing DMS, which attracts predators, which reduce grazers and thus reduces grazing mortality of the DMS-producing phytoplankton (Fig. 3.1, Table 3.1). Three of the edges identified as being most influential in determining stability (through QPress and random forests) are contained in this positive feedback: DMS release by phytoplankton, attraction of predators to DMS (this edge is not present in any negative feedbacks) and grazing on phytoplankton. Each of these interactions tend to be strong in unstable matrices but weak in stable matrices. This is because if these interactions are strong, then the positive feedback could overwhelm the stabilising negative feedbacks. On the other hand, the remaining two interactions identified as being influential in determining stability, are the self-limitation of DMS-producing phytoplankton and of DMS of itself. These negative self-effects can only be in negative feedbacks because the only positive feedback in the model contains all 5 nodes. Hence, strong negative self-effects increase the strength of stabilising negative feedbacks in comparison to the positive feedback.

Model 7 contains 42 positive, and 87 negative feedbacks and so is slightly more complicated than the previous example (Fig. 3.1, Table 3.1). The 42 positive feedbacks come from 10 base positive sequences, all of which are then amplified at higher levels when combined with complementary adjunct loops. For example, the positive feedback sequence consisting of the competition between the two phytoplankton groups includes just two negative interactions (which multiply to produce a positive feedback). The sequence is repeated multiple times at level three (containing three interactions) where it is separately reinforced by the self-limitation of each of grazers, DMS and predators. In total, this competition positive feedback sequence appears in 11 different positive feedbacks at different levels. Additionally, competitive phytoplankton interactions are contained in 27 of the 31 other positive feedbacks. For this and other the competition models, strong competition strengthens the positive feedbacks, making the network unstable. Conversely, strong self-limitation of phytoplankton stabilises this and the other competition models by reducing the ability of either phytoplankton group to exclude the other. In comparison to Models 4 - 6, Model 7 contains 3 positive feedback sequences not contained in those models: $DP \rightarrow DMS \text{---} \bullet OP \text{---} \bullet DP$, $DP \rightarrow GR \rightarrow DMS \text{---} \bullet OP \text{---} \bullet DP$ and $DP \rightarrow DMS \text{---} \bullet OP \rightarrow GR \text{---} \bullet DP$. Together these sequences are present in 9 positive feedbacks in Model 7, and the $DMS \text{---} \bullet OP$ edge (which arose as influential in the random forests for this model, but not for Models 4-6) is present in all 9 of those positive feedbacks. The $DMS \text{---} \bullet DP$ edge on the other hand, which tends to be weak in unstable matrices, is only present in two positive feedbacks but acts as another control on DMS-producing phytoplankton.

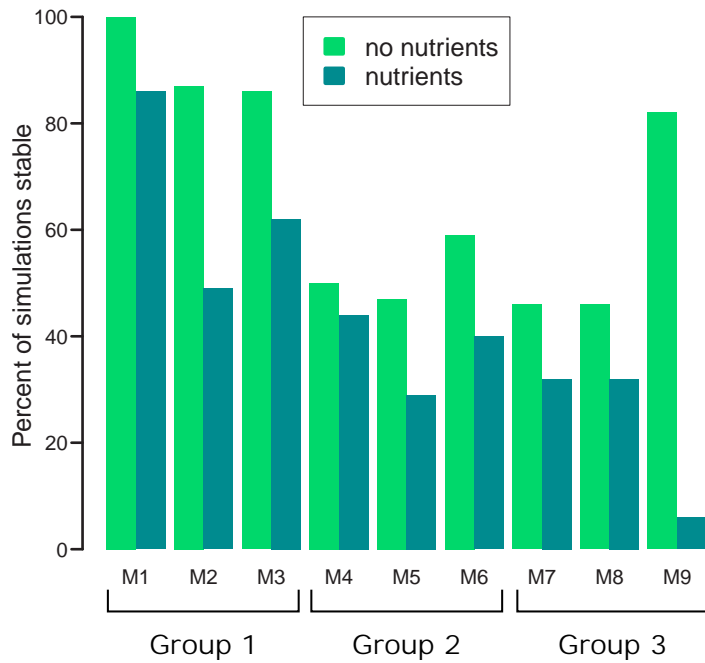


Figure B.3: Percentage of simulated community matrices (of 10,000) that were stable for each model, in the absence of any validators or constraints. Dark blue-green bars correspond to models including predator contribution to a nutrient pool (via faeces), realised as a positive effect from predators to phytoplankton (grey edges in Fig. 3.1); light green bars correspond to models without this edge.

APPENDIX C

Supplementary material to Chapter 4

Sensitivity to maximum window size

In initial testing, there was some sensitivity of CLS estimates to the maximum window size considered. For a transect of a given length, the number of samples of the maximum window size decreases as this maximum window size increases (because fewer windows fit along the length of the transect). The sample size for each window size is then constrained to this. This tends to result in a ‘bumpy’ appearance of the spectra, a degree of which can be seen in some of the coral reef examples presented here, but which becomes more extreme with longer window lengths. This ‘bumpiness’ in the spectra can affect the interpretation of the CLS. It is therefore recommended that when using the 1D CLS methods, the length of transects and maximum window size considered be consistent between time-steps and regions of comparison. For the coral reefs we considered, our results suggest that the optimal transect length is the same or larger than the 60 m transects used here (to provide unambiguous estimates of the CLS). Because collecting line-intercept transect data is intensive work, using videos to collect transect data may be a more appropriate means for collecting longer transect data to use with this method.

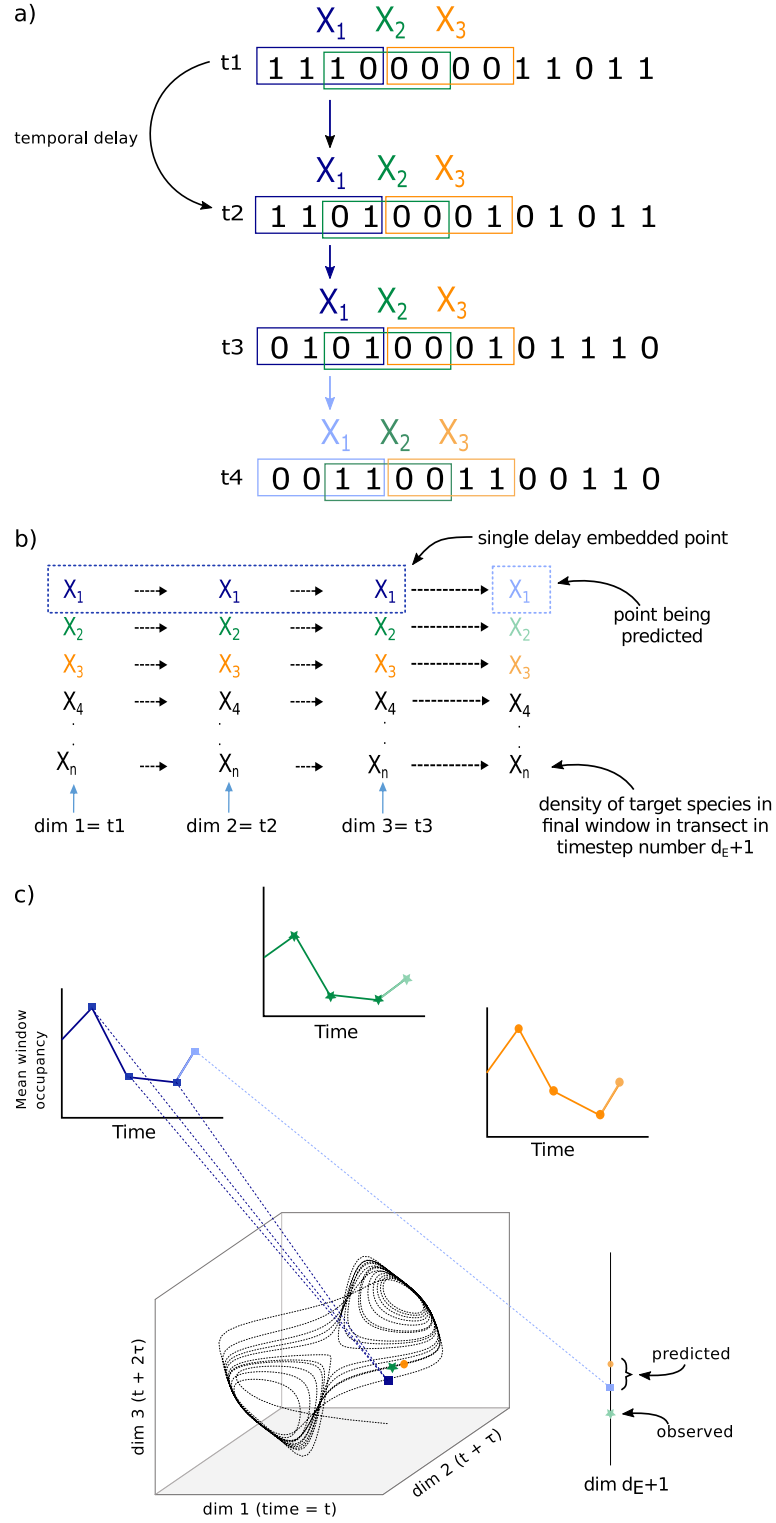


Figure C.1: Short time series approach to delay embedding and prediction. a) Transects are collected at four points in time (for $d_E=3$) and the mean species occupancy in each window position (X_P) is tracked through time. b) Each time step represents different dimension in the delay embedding, and the mean occupancy in the final time step is what we want to predict. c) The nearest neighbours in the reconstructed attractor have similar trajectories (of mean species occupancy) through time. Refer to Fig. 4.2 in the main text for the equivalent images for the sliding window method and further description of the method.

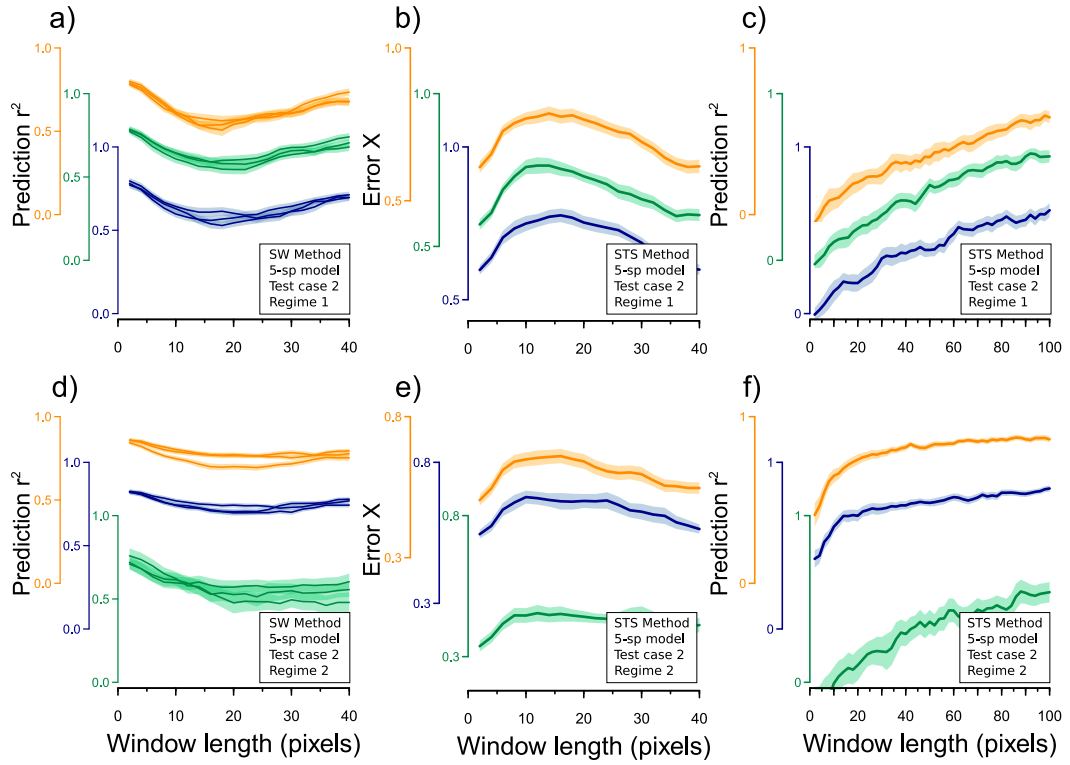


Figure C.2: Test case 2 sliding window Prediction r^2 spectra (a,d); short time-series Error X spectra (b,e) and Prediction r^2 spectra (c,f) for regime 1 (a,b,c) and regime 2 (d,e,f).

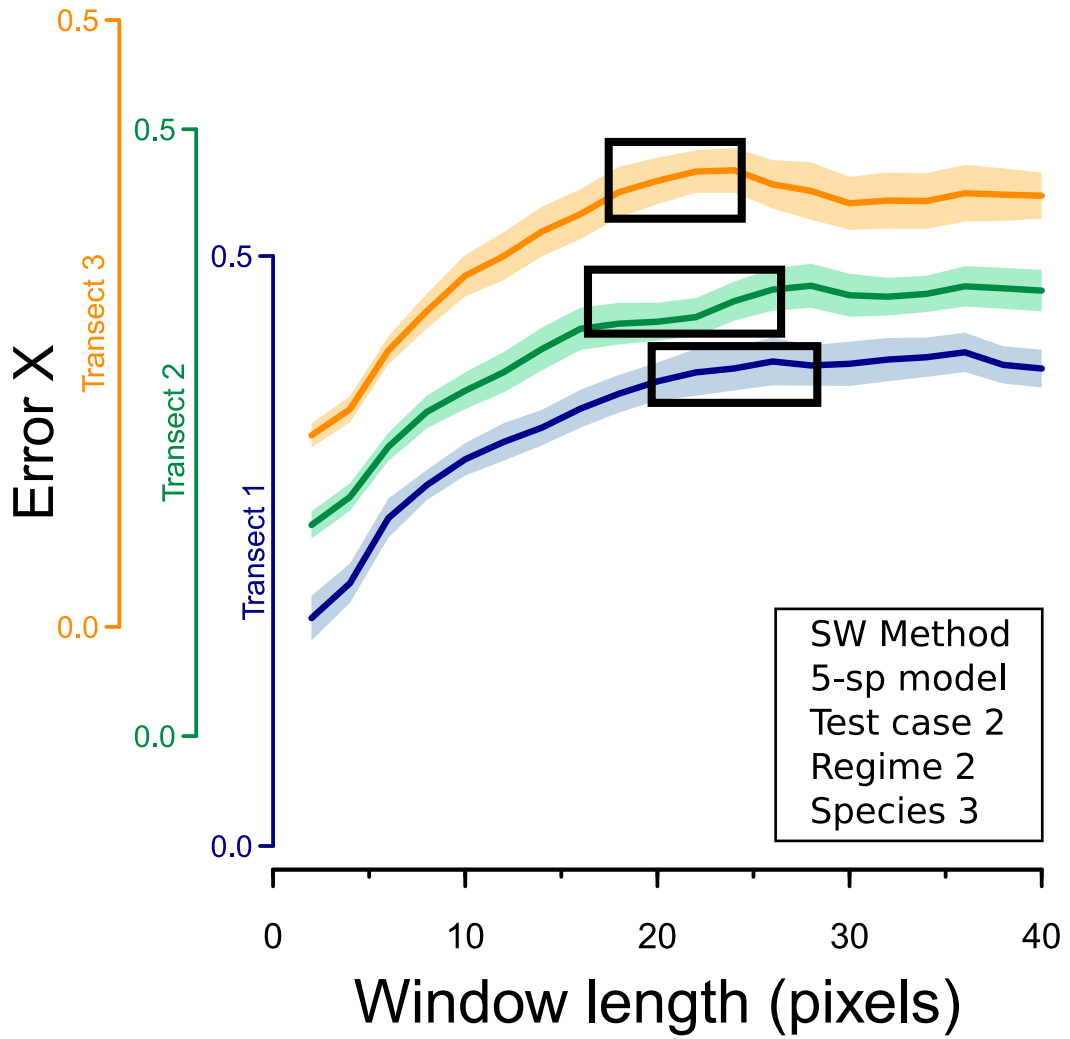


Figure C.3: Test case 2, Sliding window Error X spectra for Species 3 from three different transects in regime 2. These are the same spectra as those presented in Fig 5c of the main text, except that they are presented over a smaller y-range. This makes it clear that the CLS for Species 3 in regime 2 is 20-25 pixels – similar to that of the other species - and highlights the variability between transects for this species.

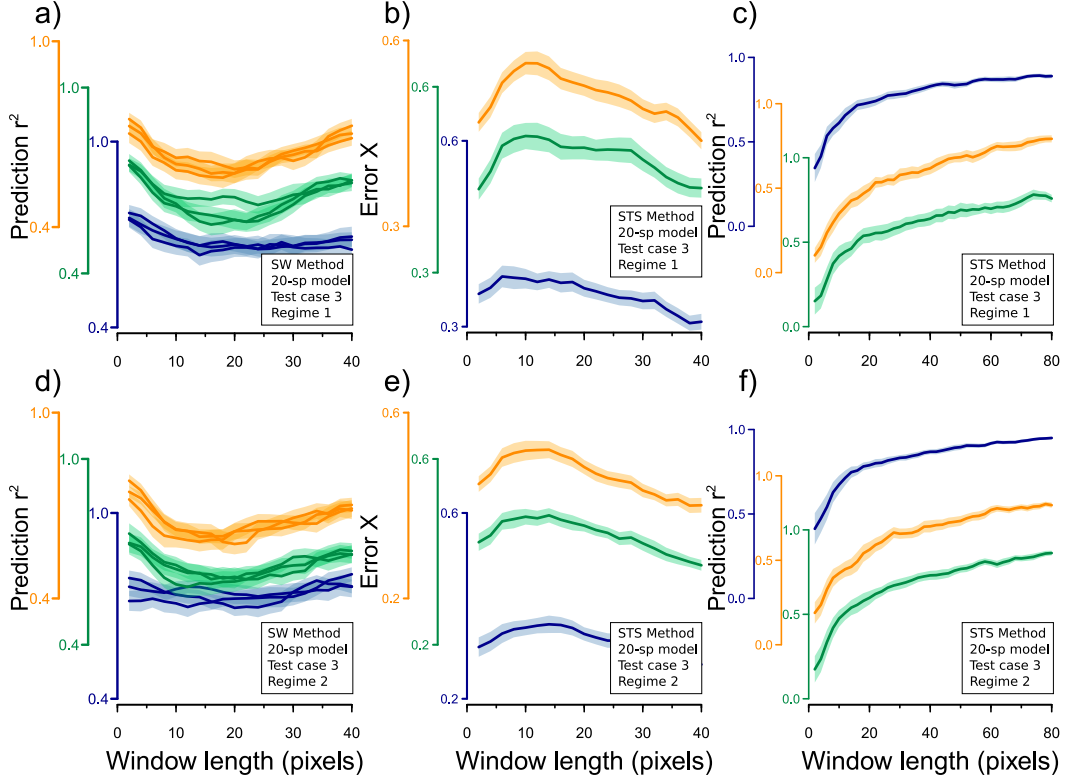


Figure C.4: Test case 3 Prediction r^2 spectra from sliding window (a,d) and short time series Error X spectra (b,e) and prediction r^2 spectra (c,f) from short time-series for regime 1 (a,b,c) and regime 2 (d,e,f).

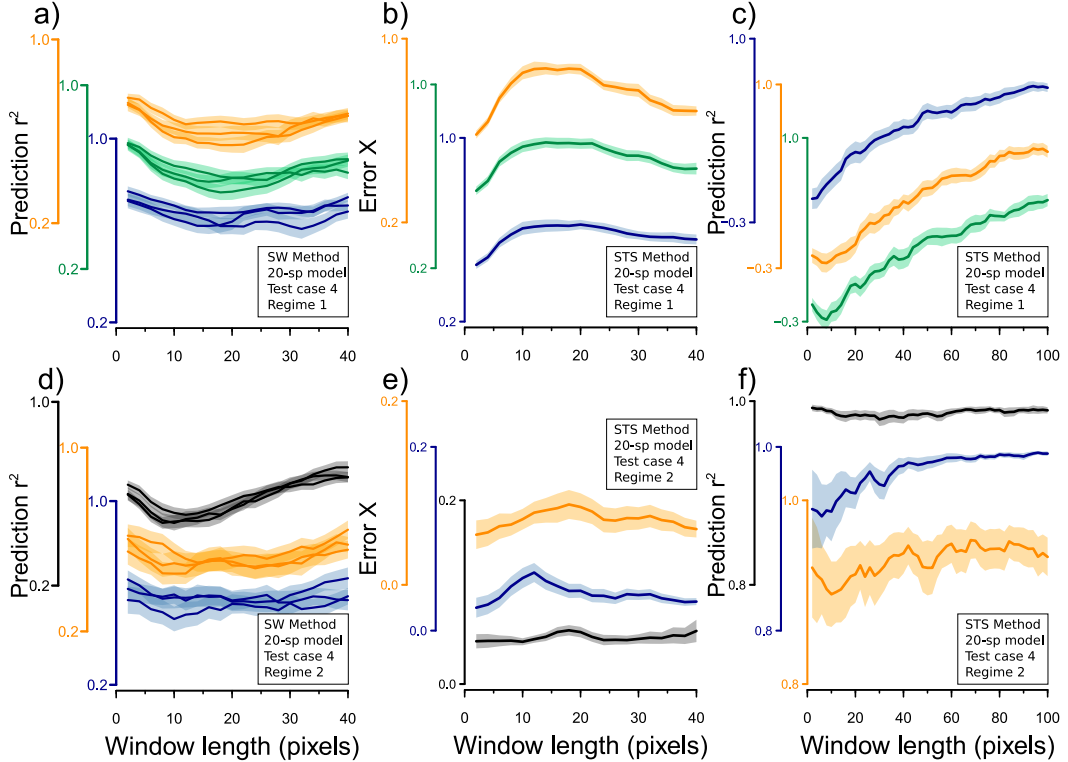


Figure C.5: Test case 4 Prediction r^2 spectra from sliding window (a,d) and short time series Error X spectra (b,e) and prediction r^2 spectra (c,f) from short time-series for regime 1 (a,b,c) and regime 2 (d,e,f). Note the varying y-ranges.

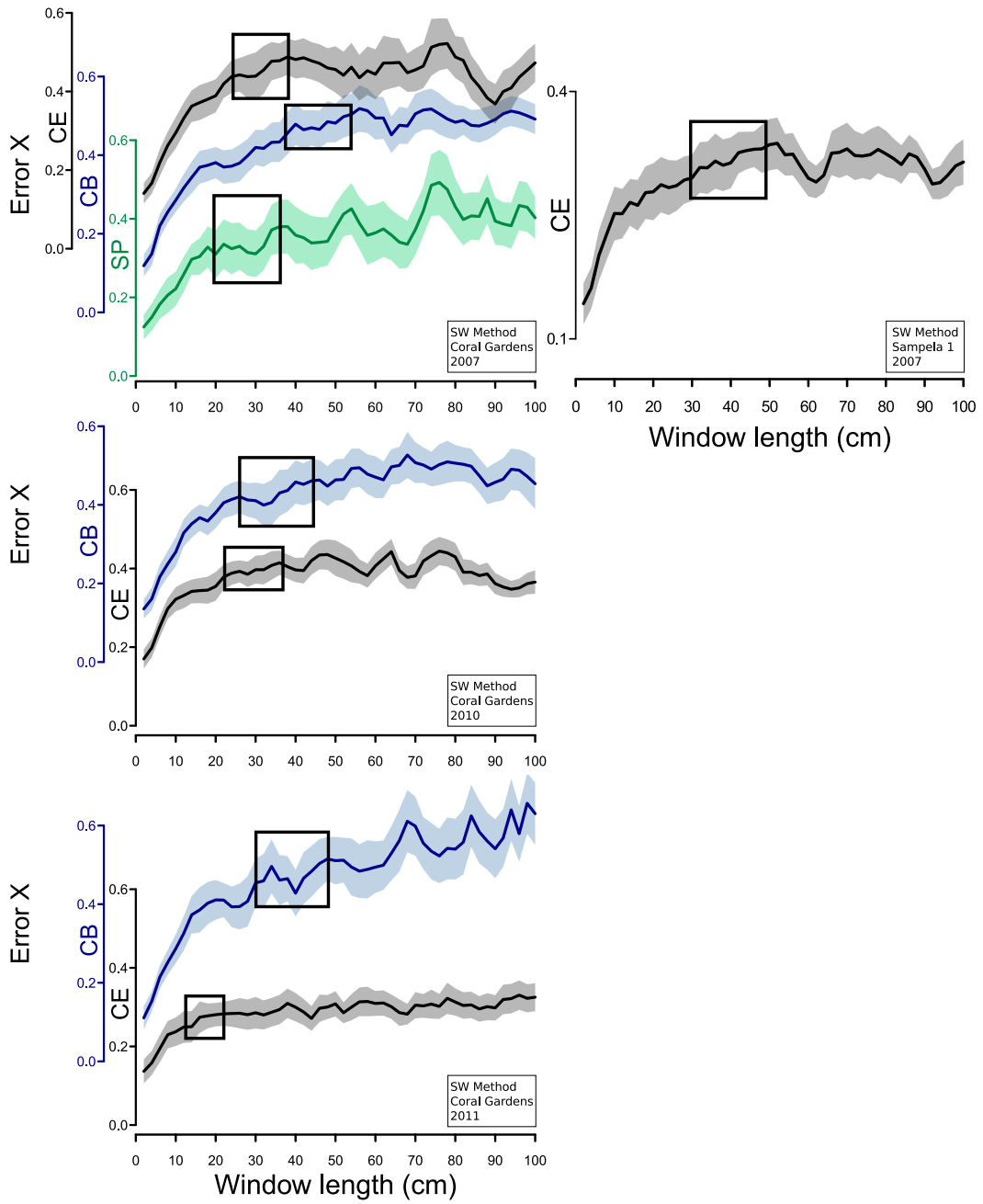


Figure C.6: Coral Gardens and Sampela Error X spectra as estimated from select morphotypes presented on a smaller y-scale than they appear in Figure 4.9 of the paper.

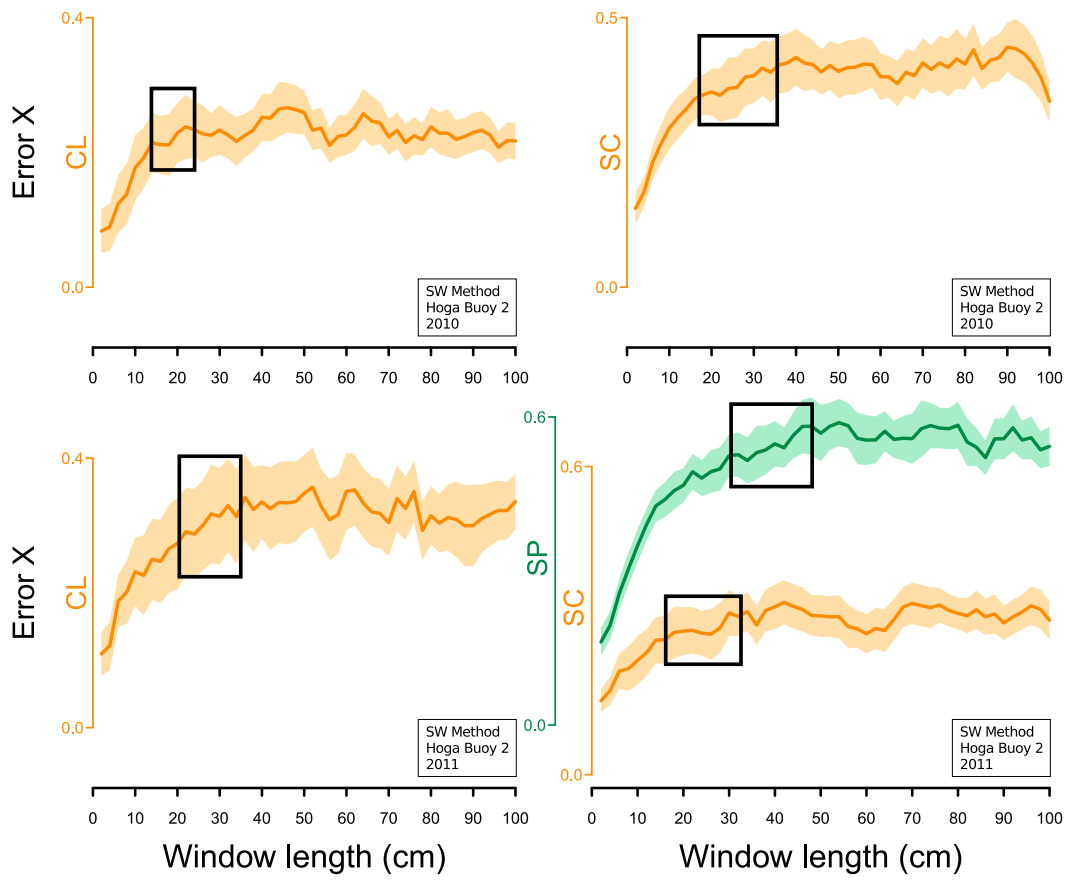


Figure C.7: Hoga Buoy Error X spectra as estimated from select morphotypes presented on a smaller y-scale than they appear in Figure 4.10 of the paper.

APPENDIX D

‘CLS1D’ *R* package documentation

Package ‘CLS1D’

October 24, 2017

Title Characteristic Length Scales from 1D Spatial Data

Version 0.0.0.9000

Description Provides facilities for computing the characteristic length scale of ecological systems from one dimensional spatial data.

Depends R (>= 3.4.1)

Imports RANN, zoo

License GPL-3

Encoding UTF-8

LazyData true

RoxygenNote 6.0.1

Suggests knitr, rmarkdown

VignetteBuilder knitr

Author Delphi Ward [aut, cre],
Simon Wotherspoon [aut]

Maintainer Delphi Ward <Delphi.Ward@utas.edu.au>

R topics documented:

CLS1D-package	2
bb2007	2
bb2010	3
CLS1D	3
CLS1Dsts	5
embed50	6
knn	7
plotCLS	8
regime1_sw	8
regime2_sw	9
Sp2R1_sts	9
Sp2R2_sts	10
window50	10
window50sts	11
Index	12

CLS1D-package

Characteristic Length Scales from 1D Spatial Data.

Description

Provides facilities for computing the characteristic length scale of ecological systems from one dimensional spatial data.

Author(s)

Delphi Ward, Simon Wotherspoon

bb2007

Coral reef benthic line-intercept transect data from 2007

Description

Coral reef benthic community transect data from Blue Bowl Reef, Wakatobi Marine National Park, Sulawesi Indonesia.

Usage

bb2007

Source

<https://doi.org/10.4226/77/587E953EBFDB3>

References

Haapkyla J, Melbourne-Thomas J, Flavell M, Ward D (2016). Hoga coral reef benthic community transect data. Centre for Tropical Waters and Aquatic Research, James Cook University. DOI: 10.4226/77/587e953ebfdb3

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

bb2010

*Coral reef benthic line-intercept transect data from 2010***Description**

Coral reef benthic community transect data from Blue Bowl Reef, Wakatobi Marine National Park, Sulawesi Indonesia.

Usage

bb2010

Source

<https://doi.org/10.4226/77/587E953EBFDB3>

References

Haapkyla J, Melbourne-Thomas J, Flavell M, Ward D (2016). Hoga coral reef benthic community transect data. Centre for Tropical Waters and Aquatic Research, James Cook University. DOI: 10.4226/77/587e953ebfdb3

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

CLS1D

*Sliding window prediction error computation***Description**

Compute the prediction error spectra for a range of window sizes using the sliding window approach, for Characteristic Length Scale (CLS) estimation.

Usage

```
CLS1D(x, Lhalf, d, metric = c("PRSq", "errX"), n.samples = 10, k = 7,
      replace = TRUE)
```

Arguments

x	One-dimensional transect data.
Lhalf	The maximum half window size.
d	The embedding dimension.
metric	Metric to calculate. Options are "errX" (Error X) or "PRSq" (prediction r-squared). Error X is the preferred option for this sliding window approach.
n.samples	The number of resamples to draw from the embedding. Default is 10.
k	The number of neighbours to use in prediction. Default is 7.
replace	Sample from the embedding with replacement. Default is TRUE.

Details

The transect x must be numeric with each element corresponding to the presence 1 (or concentration > 0) and absence 0 of the target species at one point along the transect. The spatial resolution must be constant along the length of the transect and optimally at as fine a resolution as practical. The density of the target species in windows of size 2 to $2 \times L_{half}$ is computed with the [window50](#) function. Using the [embed50](#) function an embedding is created for each window size into d dimensions. Using the [knn](#) function the k nearest neighbours of each d dimensional point in the embedding are weighted according to their inverse distance, and the trajectory to the $d+1$ dimension predicted. Difference between the predicted and observed trajectory is calculated either as Error X "errX" or Prediction r-squared "PRsq".

$$ErrorX = \sqrt{l \times E_t \times \left[\left(X_l^t - \hat{X}_l^t \right)^2 \right]}$$

Where l is the window size, X_l^t is the observed and \hat{X}_l^t is the predicted density of species X , and E_t is the expectation of their difference (mean difference).

$$Predictionr^2 = 1 - \frac{E_t \times \left[\left(X_l^t - \hat{X}_l^t \right)^2 \right]}{Var(X_l^t)}$$

Note that Error X is the preferred metric for this sliding window approach. Choice of L_{half} will be constrained by the length of the transect. For example, if $d=3$, L_{half} should be 0.49% of the transect length to have 200 replicates or 0.96% to obtain 100 replicates of the largest window size.

The CLS is defined as the window length at which the spectra reaches a plateau (when plotted).

Value

A matrix of Prediction r-squared or Error X estimates in which each row is a different window size and each column is a different subsample of the delay embedding.

References

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkylä J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

See Also

[window50](#), [embed50](#), [knn](#)

Examples

```
#Calculate Error X from Blue Bowl reef in 2007
set.seed(2)
x <- CLS1D(ifelse(bb2007 == "CF", 1, 0), Lhalf=50, d=3, metric="errX", n.samples=20)
plotCLS(x, metric="errX")
#The CLS is 60-70 cm

#Compare that to the Error X spectra from the same reef in 2010
set.seed(2)
x <- CLS1D(ifelse(bb2010 == "CF", 1, 0), Lhalf=50, d=3, metric="errX", n.samples=20)
plotCLS(x, metric="errX")
```

```
#The CLS has declined from 60-70cm to around 30-40 cm.

#Now check the Prediction r-squared spectra
x <- CLS1D(ifelse(bb2007 == "CF", 1, 0), Lhalf=50, d=3, metric="PRsq", n.samples=20)
plotCLS(x, metric="PRsq")
```

CLS1Dsts

Short time-series prediction error computation

Description

Compute the prediction error spectra for a range of window sizes using the short time-series approach, for Characteristic Length Scale (CLS) estimation.

Usage

```
CLS1Dsts(x, Lhalf, metric = c("PRsq", "errX"), n.samples = 10, k = 7,
  replace = TRUE)
```

Arguments

x	One-dimensional transect data.
Lhalf	The maximum half window size.
metric	Metric to calculate. Options are "errX" (Error X) or "PRsq" (prediction r-squared). Error X is the preferred option for this sliding window approach.
n.samples	The number of resamples to draw from the embedding. Default is 10.
k	The number of neighbours to use in prediction. Default is 7.
replace	Sample from the embedding with replacement. Default is TRUE.

Details

Takes a matrix or dataframe x where each column contains transect data from a different time step, and each row contains numeric data on the presence 1 (or concentration > 0) and absence 0 of the target species at one point along the transect. The spatial resolution must be constant along the length of the transect and optimally at as fine a resolution as practical. The density of the target species in each window is computed with the [window50sts](#) function. Then, using the [knn](#) function the k nearest neighbours of each point in the embedding are weighted according to their inverse distance, and the trajectory to the final dimension (column) predicted. Difference between the predicted and observed trajectory is calculated either as Error X "errX" or Prediction r-squared "PRsq".

$$ErrorX = \sqrt{l \times E_t \times \left[\left(X_l^t - \hat{X}_l^t \right)^2 \right]}$$

Where l is the window size, X_l^t is the observed and \hat{X}_l^t is the predicted density of species X , and E_t is the expectation of their difference (mean difference).

$$Predictionr^2 = 1 - \frac{E_t \times \left[\left(X_l^t - \hat{X}_l^t \right)^2 \right]}{Var(X_l^t)}$$

Value

A matrix of Prediction r-squared or Error X estimates in which each row is a different window size and each column is a different subsample of the delay embedding.

References

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

See Also

[window50sts](#), [knn](#)

Examples

```
x <- CLS1Dsts(Sp2R1_sts, Lhalf=20, metric="errX", n.samples=20)
plotCLS(x, metric="errX")

x <- CLS1Dsts(Sp2R2_sts, Lhalf=20, metric="errX", n.samples=20)
plotCLS(x, metric="errX")

x <- CLS1Dsts(Sp2R1_sts, Lhalf=20, metric="PRSq", n.samples=20)
plotCLS(x, metric="PRSq")

x <- CLS1Dsts(Sp2R2_sts, Lhalf=20, metric="PRSq", n.samples=20)
plotCLS(x, metric="PRSq")
```

embed50

Create a Delay Embedding

Description

Form all embeddings of dimension d for window size $2 \times l_{half}$ where each window along the transect overlaps the previous by l_{half} .

Usage

```
embed50(x, lhalf, dim)
```

Arguments

<code>x</code>	The spatial transect data.
<code>lhalf</code>	The window size increment.
<code>dim</code>	The embedding dimension + 1.

Details

Takes one-dimensional spatial (transect) presence-absence or concentration data and creates a delay embedding of density along the transect. The transect `x` must be formatted so that each element in the vector `x` represents the occupancy of one species, morphotype or habitat in one position along the transect. Returns a matrix where each row is the trajectory of species density along $d+1$ windows.

Value

An embedding as a matrix.

See Also

[window50](#)

Examples

```
x <- seq(1, 100, by=1)
embed50(x, 5, 4)
```

knn	<i>K-Nearest Neighbour Prediction</i>
-----	---------------------------------------

Description

Compute k-nearest neighbour predictions for the last dimension of an embedding.

Usage

```
knn(emb, k = 7)
```

Arguments

emb	An embedding constructed with window50 .
k	The number of neighbours.

Details

This function is based on the [nn2](#) function from **RANN**. Given an array representing an embedding, it constructs inverse distance weighted k-nearest neighbour predictions for the last column of the embedded array.

Value

Returns a list with two components

obs	the observed responses.
pred	the predicted responses.

See Also

[window50](#), [embed50](#), [nn2](#)

plotCLS	<i>Plot prediction error spectra</i>
---------	--------------------------------------

Description

Plot the prediction error spectra for a range of window sizes, for estimation of the Characteristic Length Scale (CLS).

Usage

```
plotCLS(X1, Lhalf = nrow(X1), metric, ylim, xlab, xticks = 10)
```

Arguments

X1	Matrix of prediction error estimates returned by CLS1D or CLS1Dsts
Lhalf	The maximum half window size for which prediction error was estimated. Should be equal to nrow(X1).
metric	Optional. Specify metric for y-axis label. Options are "errX" (Error X) or "PRSq" (prediction r-squared).
ylim	Optional. Specify y-axis range. Default is range(X1).
xlab	Optional. Specify x-axis label. Default is "Window length".
xticks	Optional. Specify spacing of ticks on x-axis. Default is by 10.

Details

Takes matrix of Error X or Prediction r-squared estimates from [CLS1D](#) or [CLS1Dsts](#). Uses [rollapply](#) from package **zoo** to estimate the rolling mean (rolling window width = 3) of the estimates for each window size, and plots with pointwise 95 percent confidence intervals.

Value

Returns a plot of the prediction error spectra.

Examples

```
x <- CLS1D(ifelse(bb2007 == "CF", 1, 0), Lhalf=50, d=3, metric="errX", n.samples=20)
plotCLS(x, metric="errX")
```

regime1_sw	<i>Simulated spatial model output transect data</i>
------------	---

Description

Transect data from the first regime of Test Case 2 in Ward et al (submitted)

Usage

```
regime1_sw
```

References

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

regime2_sw

Simulated spatial model output transect data

Description

Transect data from the second regime of Test Case 2 in Ward et al (submitted)

Usage

regime2_sw

References

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

Sp2R1_sts

Simulated model short time-series transect data

Description

Transect data from three time steps (separated by 10 time steps) of the first regime of Test Case 2 in Ward et al (submitted). This example contains only Species 2 presence-absence data.

Usage

Sp2R1_sts

References

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

Sp2R2_sts

Simulated model short time-series transect data

Description

Transect data from three time steps (separated by 10 time steps) of the second regime of Test Case 2 in Ward et al (submitted). This example contains only Species 2 presence-absence data.

Usage

Sp2R2_sts

References

Ward D, Wotherspoon S, Melbourne-Thomas J, Haapkyla J, Johnson CR (submitted). Detecting ecological regime shifts from transect data.

window50

Compute averages in sliding window

Description

Compute averages in windows of length $2 \times \text{lhalf}$ along a transect, where each window overlaps the previous window by lhalf .

Usage

window50(x, lhalf)

Arguments

x	One-dimensional spatial presence absence data.
lhalf	The window size increment.

Details

Computes averages in sliding windows along transect by taking differences of cumulative sums.

Value

A numeric vector containing mean density in each window of size $2 \times \text{lhalf}$.

window50sts	<i>Compute averages for short time-series</i>
-------------	---

Description

Compute averages in windows of length $2 \times \text{lhalf}$ along each transect in a set of time-delayed transects. Each window overlaps the previous window by lhalf within the same transect. Between transects the windows are in the same position spatially.

Usage

```
window50sts(x, lhalf)
```

Arguments

x	Data frame or matrix of 1-dimensional spatial transects
lhalf	the window size increment.

Details

Computes averages in windows along transects by taking differences of cumulative sums.

Value

a matrix or dataframe containing mean density in each window of size $2 \times \text{lhalf}$

Index

*Topic **datasets**

bb2007, [2](#)

bb2010, [3](#)

regime1_sw, [8](#)

regime2_sw, [9](#)

Sp2R1_sts, [9](#)

Sp2R2_sts, [10](#)

bb2007, [2](#)

bb2010, [3](#)

CLS1D, [3](#), [8](#)

CLS1D-package, [2](#)

CLS1Dsts, [5](#), [8](#)

embed50, [4](#), [6](#), [7](#)

knn, [4–6](#), [7](#)

nn2, [7](#)

plotCLS, [8](#)

regime1_sw, [8](#)

regime2_sw, [9](#)

rollapply, [8](#)

Sp2R1_sts, [9](#)

Sp2R2_sts, [10](#)

window50, [4](#), [7](#), [10](#)

window50sts, [5](#), [6](#), [11](#)

APPENDIX E

Application of the 1D-CLS method to a Southern Ocean dataset

The original intent with the 1-dimensional Characteristic Length Scale (1D-CLS) estimation method developed in Chapter 4, was to apply it to a dataset of zooplankton occurrence data - the Southern Ocean Continuous Plankton Recorder (SO-CPR) dataset. The CPR is a device towed by ships that contains a long silk membrane that continuously spools along the voyage. Seawater enters the device through a small opening (1 cm²) and passes through an exposed section of the silk membrane. As the water passes through the silk, any plankton contained in the seawater become trapped on the silk, essentially creating a transect of zooplankton occurrence data along the ships track. After the voyage, the long silk is cut into segments representing 5 nautical miles, and all the zooplankton contained on the silk are identified under a microscope.

The Southern Ocean Continuous Plankton Recorder (SO-CPR) has been towed since 1991 (Hunt and Hosie 2003) and the data now stands at over 21,000 records of 5 nautical mile sections of Southern Ocean transects. The greatest volume of records are from the area of Southern Ocean south of Australia and New Zealand (between 50° and 180°E) (Figure E.1). The dataset is therefore very attractive for assessing change in zooplankton communities over that time period.

Further investigation of this dataset highlighted problems for the application of the 1D-CLS method. The first general challenge is that because relatively few ships travel to Antarctica, the opportunities for sampling an area at the same time of year in multiple years are few. For example, samples may exist in one region for September in one year, and February in another - making it challenging to disentangle the effects of seasonal community progression from longer term community change. There are some transects (e.g. along 110°E) that are repeated in the same month every year, but technical problems can arise with the CPR device resulting in lengthy gaps in the coverage, reducing replication at particular latitudes.

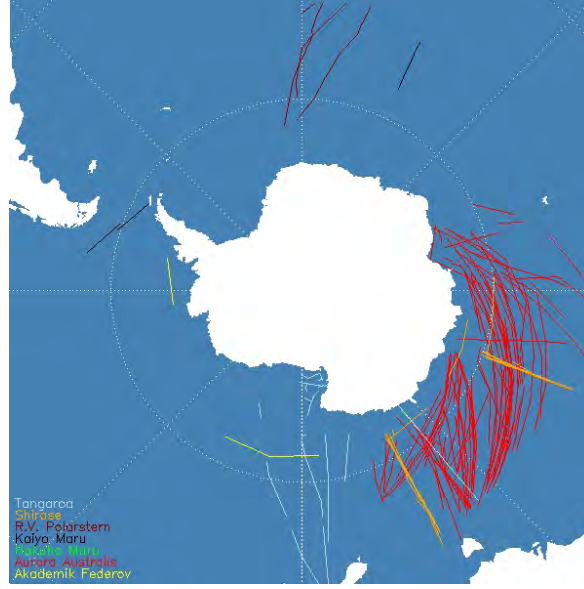


Figure E.1: Map of the Southern Ocean Continuous Plankton Recorder (SO-CPR) data set. The SO-CPR is a device that captures zooplankton from surface waters when towed behind a ship. Different coloured lines represent the SO-CPR transects completed by different ships, as named in the lower left corner. Figure taken from the Australian Antarctic Data Centre.

For application of the 1D-CLS estimation method, the greater and more specific challenge is the spatial resolution of the transects. The silks are cut at 5 nautical mile resolution, which means that along even the longest transects, there will only be a few hundred samples. The maximum window size that can be considered with the 1D-CLS estimation method is limited by the spatial resolution of the data, where coarser resolution means reduced replication of larger window sizes. For example, one of the longest transects is 2365 nautical miles, but this is broken into only 461 silk segments, with each silk segment representing 5.1 nautical miles (Figure E.2). In this case, to be able to obtain 100 replicates of the largest window size, the largest window size considered could only be 8 silk segments (or 41 nautical miles). This is too small to be able to distinguish a CLS, given that the smallest possible window size is 2 silk segments. Nevertheless, I did test the application of the 1-dimensional CLS method to this transect, using a larger maximum window size (40 silk segments, or 204 nautical miles), with reduced replication (10 replicates of each window length). Most species or groups were captured too few times along the transect to produce interpretable results. However, a CLS was interpretable from the Error X spectra of the most abundant species, *Oithona similis*, which is ubiquitously distributed over the Southern Ocean, and also from the Error X spectra calculated from the total abundances of all zooplankton (Figure E.3). While a CLS is interpretable from the Error X spectra of these groups, it is unclear how appropriate it would be to do so given the low replication, and the strong environmental gradients that the transect crosses (e.g. temperature, nutrients, salinity, and others).

Appendix E. Application of the 1D-CLS method to a Southern Ocean dataset

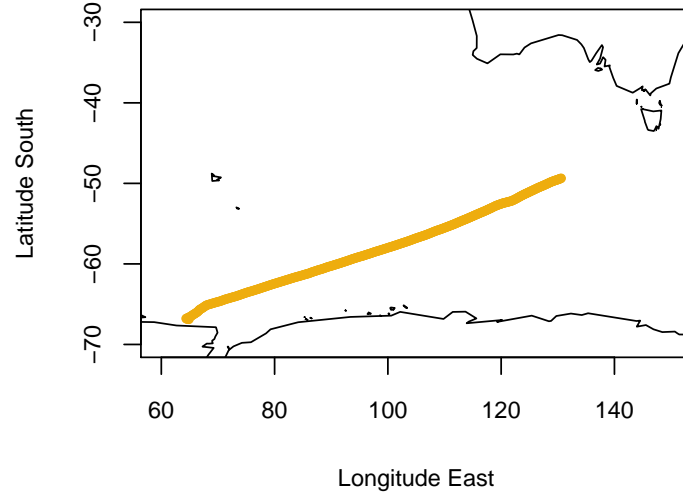


Figure E.2: Transect of zooplankton occurrence collected by the Southern Ocean Continuous Plankton Recorder (SO-CPR) in January 1998.

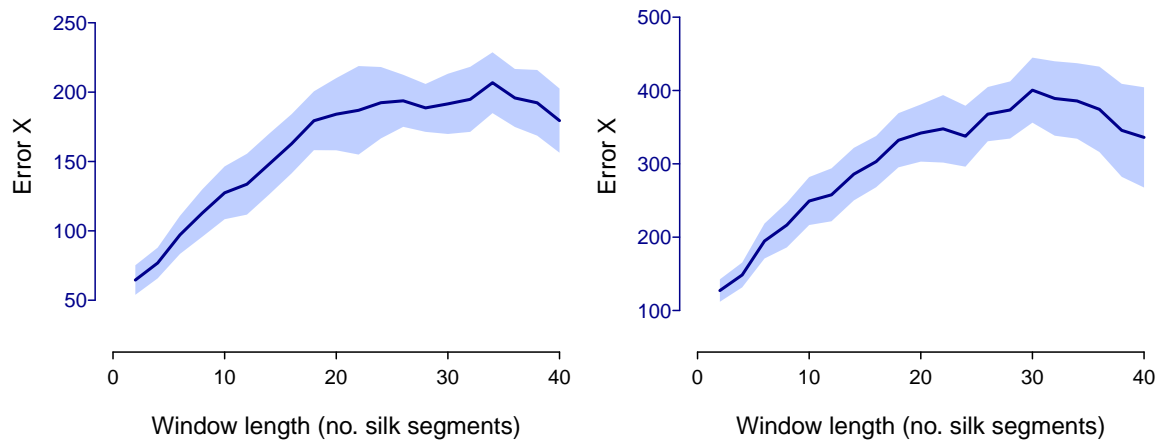


Figure E.3: Error X spectra estimated from occurrence of the ubiquitous copepod *Oithona similis* (left panel) and from the total counts of all zooplankton (right panel) from a Continuous Plankton Recorder trawl during a voyage from Hobart to Mawson Station, Antarctica, in January 1998 (see map E.2). The average distance represented by each silk segment is 5.1 nautical miles, so the maximum window size considered here corresponds to 204 nautical miles.

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