

PROJECTIONS FROM POPULATION AND COMMUNITY MODELS OF ROCKY SHORES

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ABSTRACT

Environmental concerns motivated by issues such as climate change, harvesting or the loss of biodiversity often focus on the rates of change or ecological stability. These issues of population and community dynamics can be analysed in a number of ways. A modelling approach complements time series and experimental studies and can be applied to a wider range of contexts. Complex models can be difficult to parameterise, hence a simpler approach often provides more useful insights about population and community dynamics. One such approach is to use transition (Markov) matrix models specified from repeated observations. Projections from transition matrix models are used to describe rates of change, composition and stability. Examples from rocky shores demonstrate the importance of recruitment variability in population dynamics and may predict community responses to loss of biodiversity. A particular advantage of the transition matrix approach is that the models are relatively easy to formulate from field surveys.

INTRODUCTION

Populations and communities are generally in a state of flux. Change may be driven by the internal dynamics of a system or may reflect responses to external factors. The patterns and causes of change become particularly relevant in areas such as conservation and sustainable resource exploitation. This paper introduces a set of modelling tools that may be particularly useful in analysing the population and community dynamics of rocky intertidal systems.

There are a number of approaches that can be used to understand and predict environmental change. In the rare cases where long-term data sets exist, time series analysis

can be used to characterise the system. This characterisation can include estimates of long-term trends (Southward 1991; Allen *et al.* 1998), return times of extreme events such as large waves (Gaines and Denny 1993) and the presence of cyclic fluctuations (Jassby and Powell 1990; Kendall *et al.* 1998). Commonly applied techniques include spectral analysis and autocorrelation (Chatfield 1996). More recent advances include phase plots and other techniques for identifying patterns in population time series (Sugihara and May 1990). Such techniques relate the current state of a system to a historical context and indicate the patterns that are likely to reoccur. As time series techniques characterise pattern, they cannot unambiguously identify the processes associated with the pattern (Jassby and Powell 1990). It is difficult to predict how a system will respond to novel situations such as the loss or introduction of a species. More formally, time series analysis cannot generally be used to discriminate between alternative hypotheses concerning the mechanisms of ecosystem function. In contrast, experimental manipulations are an unambiguous method of characterising ecosystem process (Underwood 1997). Unfortunately, due to restrictions on the timescale of grants and PhDs, experiments may only run for a relatively short period. Hence experimental studies have tended to provide a snapshot of slow-moving or abundant species and may underestimate important population and community processes occurring at longer timescales (Underwood 2000).

In an ideal situation, time series and experimental approaches would be combined into a single investigation of population and community dynamics. However, the availability of resources and the pressing nature of many environmental problems often mean that combined investigations are rare. In such circumstances a modelling approach can bridge the gap between time series and experimental studies and can be applied to a wider range of contexts. Numerical models can aid in hypothesis construction, focus on what is actually known or testable (Speirs *et al.* 2000) and allow a fuller description of possible system behaviour. Of course mathematical models have their own limitations. Some of these problems, such as hidden or unwarranted assumptions, are also found in verbal models of ecological communities. It is, however, difficult for mathematical models to deal with the complexity of natural systems while remaining mathematically tractable. Hence models often simplify ecological interactions. This is not necessarily a problem, as tests of predictions examine whether a limited set of processes in the model is sufficient to describe the natural world (Kareiva 1990). However, models may be reduced to generic descriptions of phenomena such that they can make only the broadest predictions for particular systems (Tilman and Kareiva 1997). When constructing tractable mathematical models, a further issue arises over choice of parameter values. Parameter values (e.g., population intrinsic growth rate) affect model behaviour, but they are often estimated or imported from separate studies. The errors associated with different parameters may be unknown, limiting the use of complex or realistic models (Johnson 1998).

A potential solution to some of the problems of model construction is to use a framework where parameters are estimated in a single field study. By basing a model directly on observations, the parameters are estimated from the same source and predictions can be made for a specific system. Markov transition matrix models are a class of models suited to this observation-based approach. The techniques can be applied

to communities or populations. Wootton (2001) emphasised that Markov models are probably the easiest community models to parameterise from field data. A comprehensive review of transition matrix models for populations is given by Caswell (2001). This paper will describe the application of a Markov transition matrix approach to rocky intertidal communities. For more detailed examples of intertidal population modelling see Åberg (1992a,b), Engel *et al.* (2001) and Hyder *et al.* (2001). Developments and limitations of the models are discussed under the heading of 'projection or prediction in the intertidal?' and in the concluding remarks.

CONSTRUCTION AND ANALYSIS OF MARKOV MODELS

Markov models are based on estimating the probability of transition between different states. For a community these states are different species, aggregated groups of species or functional groups. A population model describes transitions between age or size classes. Transition probabilities are derived from repeated observations of marked individuals or areas. Hence p_{jk} , the probability of transition from state k to state j , is defined by the number of transitions from k to j over the defined time period divided by the number of cases of state k at the start of the time period. A set of field observations are summarised in a transition matrix (**A**) of the form:

$$\mathbf{A} = \begin{pmatrix} p_{11} & p_{12} & p_{13} & \cdots & p_{1n} \\ p_{21} & p_{22} & p_{23} & \cdots & p_{2n} \\ p_{31} & p_{32} & p_{33} & \cdots & p_{3n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ p_{n1} & p_{n2} & p_{n3} & \cdots & p_{nn} \end{pmatrix} \quad (1)$$

Transition probabilities can be zero. For example there can be no transitions to younger age classes, so an age-structured model contains zeros in the top right corner. A restriction on community models is that columns in the matrix sum to one, as sites are usually not destroyed or created. The matrix is a summary of transitions occurring between two dates. The gap between the two dates (the time step) gives the model an explicit timescale. A null hypothesis can be proposed: all the transitions are random. If this is the case a Markov model is not applicable. The null hypothesis is tested using a likelihood ratio test (Usher 1979) where the quantity $-2\ln\lambda$ is calculated as:

$$-2 \ln \lambda = 2 \sum_{j=1}^m \sum_{k=1}^m \frac{n_{jk}}{n_j} \ln \left(\frac{p_{jk}}{p_j} \right) \quad (2)$$

where

$$p_j = \frac{\sum_{k=1}^m n_{jk}}{\sum_{j=1}^m \sum_{k=1}^m n_{jk}} \quad (3)$$

and n_{jk} is the number of transitions from state k to j in the original data matrix, p_j is the sum of transition probabilities to state j and m is the order of the transition matrix (number of rows). The test statistic $(-2\ln\lambda)$ is compared to χ^2 with $(m-1)^2$ degrees of freedom. Rejection of the null hypothesis suggests that a Markov approach can be followed.

Accepting a Markov model implies that the state of a system can be predicted from the state of the system one time step previously. In mathematical notation:

$$\mathbf{x}_{(t+1)} = \mathbf{A}\mathbf{x}_{(t)} \quad (4)$$

where $\mathbf{x}_{(t)}$ is a vector describing the frequencies of separate states in the population or community at time t (e.g., four size classes of barnacle, Hyder *et al.* 2001). It is therefore possible to simulate the dynamics of a system through several time steps by repeatedly multiplying a column vector. Simulations of this type are straightforward to lay out using a spreadsheet programme on a personal computer. Most transition matrices will reach a stable steady state, defined by the right hand eigenvector of the transition matrix (Tanner *et al.* 1994). Other mathematical properties can be used to summarise elements of the system described by a transition matrix. For example, the rate of convergence to a steady state is given by the 'damping ratio' (Tanner *et al.* 1994; Caswell 2001):

$$\rho = \lambda_1 / |\lambda_2| \quad (5)$$

where ρ is the damping ratio and λ_n is an eigenvalue of the transition matrix. λ_1 is the largest eigenvalue. Convergence to a steady state will generally be smooth unless the larger eigenvalues are complex numbers, in which case damped oscillations are possible. The damping ratio can be referenced to the time step in the Markov model using a convergence ratio, t_x (Caswell 2001):

$$t_x = \ln(x) / \ln(\rho) \quad (6)$$

Typically x equals ten, giving the time taken for influence of the first eigenvalue on matrix dynamics to be ten times larger than the contributions from the second eigenvalue (Caswell 2001).

ROCKY SHORE COMMUNITY TRANSITION MATRICES

Field data are not generally collected in a form that can be used for transition matrices. Often the locations of quadrats or measurements are not recorded as investigators are generally not interested in going back to exactly the same location. The justification for this is that measurements need to be independent in order to meet the assumptions of many statistical tests (e.g. ANOVA). In contrast, a matrix model summarises the dependence between measurements at the same location on different occasions. Repeated measurements are, however, relatively easy to incorporate into most field studies. Rocky shores are particularly tractable as many of the organisms are sessile and it is easy to mark locations with paint or screws put in holes drilled into the rock.

Repeated measurements at the same location are available for three of the maps used in a study on the spatial structure of intertidal communities in the Isle of Man (Johnson *et al.* 1997). This study involved surveys of 5×5 m quadrats, with the corners of each quadrat marked using screws in the rock. A 0.25 m^2 quadrat, divided into 0.01 m^2 squares ('cells'), was moved methodically across the larger quadrat to produce a map of the community. The community in each cell was recorded as dominated by mature fucoid algae (over 0.1 m long), containing juvenile *Fucus* algae only, dominated by barnacles, dominated by coralline red algae or dominated by bare rock. Cells were also classified as empty or containing limpets, the most important grazers in the community (Hawkins *et al.* 1992). The mapping was repeated after one year for three of the 5×5 m quadrat locations (Port St. Mary a, Port St. Mary b and Gansey). This allowed matrix models to be derived from a total of 2500 observed transitions for each location. An example transition matrix is shown in Table 1.

Observed transitions relate to some of the community dynamics proposed for moderately exposed shores by Hartnoll and Hawkins (1985). For example, juvenile *Fucus* are more likely to appear in areas of coralline algae, bare rock or barnacles when limpets are locally absent. The derived matrices represented non-random transitions at all three locations (likelihood ratio test, $p < 0.001$ in each case). The equilibrium communities at each location differed. Mature algae dominated at Port St. Mary a (79% of the predicted community as m+ or m-). The most common community state at Gansey was also mature algae, but community composition was more even (39% of the predicted community was m+ or m-). The pattern was quite different at Port St. Mary b. The most common states at equilibrium for this location were bare rock, juvenile algae and barnacles, all in the absence of limpets (Figure 1). This may reflect that Port St. Mary b was higher on the

Table 1. Example transition matrix for an intertidal site surveyed at Gansey in the Isle of Man. Cell states are classified as barnacle dominated (b), juvenile *Fucus* present with no larger algae (j), mature *Fucus* dominant (m), coralline red algae dominant (cr) and bare rock (r). The presence (or absence) of limpets is indicated by + or - modifiers to the states based on the presence of sessile organisms. Column headings represent the original state with rows as the state after one time step

	b+	b-	j+	j-	m+	m-	cr+	cr-	r+	r-
b+	0.038	0.015	0.000	0.014	0.072	0.034	0.000	0.037	0.086	0.022
b-	0.423	0.351	0.600	0.359	0.299	0.332	0.000	0.279	0.241	0.324
j+	0.000	0.010	0.000	0.007	0.021	0.006	0.000	0.000	0.000	0.002
j-	0.269	0.309	0.400	0.310	0.134	0.100	0.000	0.167	0.121	0.233
m+	0.000	0.002	0.000	0.007	0.031	0.037	0.000	0.005	0.034	0.002
m-	0.038	0.015	0.000	0.049	0.041	0.057	0.000	0.028	0.034	0.016
cr+	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000
cr-	0.000	0.010	0.000	0.014	0.000	0.011	0.000	0.219	0.069	0.014
r+	0.038	0.015	0.000	0.000	0.021	0.037	0.500	0.019	0.052	0.017
r-	0.192	0.274	0.000	0.239	0.381	0.384	0.500	0.237	0.362	0.370

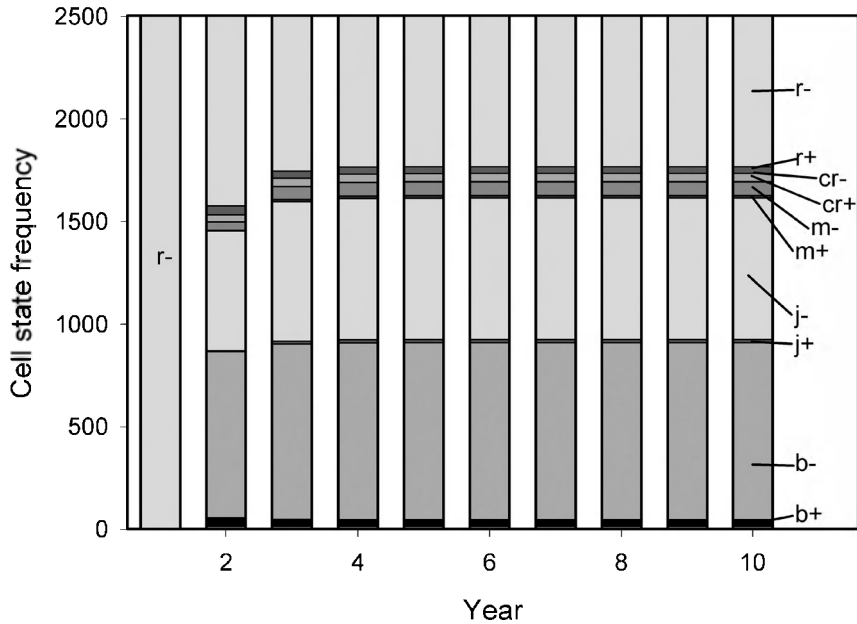


Figure 1. Projected cell state frequencies for a Markov transition matrix model of Port St. Mary location b. States are classified as barnacle occupied (b), juvenile *Fucus* (j), mature *Fucus* (m) coralline red algae (cr) and bare rock (r). The presence or absence of limpets in the cells is indicated by \pm modifiers. Community composition is simulated from an initial condition of 2500 cells containing bare rock without limpets.

shore than the other two locations. Simulated community dynamics also indicate how a shore might recover from a disturbance. For example Port St. Mary b is predicted to recover to a steady state within a few years of a perturbation that reduces the shore to bare rock (e.g. an oil spill and clean up, Southward and Southward 1978).

Recovery rates from a perturbation vary between locations, with t_{10} values of 4.17, 1.51 and 1.23 years for Port St. Mary a, Port St. Mary b and Gansey respectively. These convergence times are illustrated by the relative speeds of approach to equilibrium in frequencies of mature algae and limpets at the different locations (Figure 2). It is not yet clear why Port St. Mary a appears to be the least resilient location. One possibility under investigation is that community stability can be related to the complexity of the rock surface.

PROJECTION OR PREDICTION IN THE INTERTIDAL?

Although the Markov matrix approach makes a minimum of assumptions in deriving a model from observations, there are three important conditions (Caswell 2001):

- 1) The classification of individuals into ages and sizes or of communities into states is appropriate.
- 2) Dynamics within and age/size/state classification are not important
- 3) The system is linear and transition rate processes do not vary over time.

The first condition is not overly restrictive, but it does emphasise that the most appropriate stage classifications will vary between models. Age may not always be a good predictor of the growth and mortality of individuals (Caswell 2001). For example, predation of sessile organisms may be size-dependent (Hughes and Burrows 1993). The classification of communities into states is a novel area of research. The division of states in the quadrats on the Isle of Man was based on the most conspicuous species. More sophisticated algorithms could include multivariate definitions of states. The second condition affects the temporal and spatial scales of the transition matrix. Dynamics should be homogeneous in the area where the transitions are defined. Hence a transition matrix that combines data from the high and low intertidal may be meaningless. A more robust approach is to construct matrices for different areas and compare predictions and transition probabilities (Usher 1979; Tanner *et al.* 1994) before combining data. Dynamics should also be homogeneous for all individuals or patches within a particular state. This issue is reflected in the development of algorithms to choose category widths in population models (Vandermeer 1978). Åberg (1990) applied the category selection method to size class selection in a model for *Ascophyllum nodosum* (L.) However, these category selection methods may not always work (Hyder *et al.* 2001). An analysis by Tanner *et al.* (1996) found that community states in their model of coral reefs should include subdivision of states by age, although the dynamics of more complex second order models were not greatly different from their original age-averaged models.

The third condition seems to be the most restrictive. One would surely expect rates to change as one state or another becomes more common. For example, dominance by a state could lead to increases the local reproductive output or some density-dependent response such as higher levels of predation. 'Supply side' ecology emphasises variation

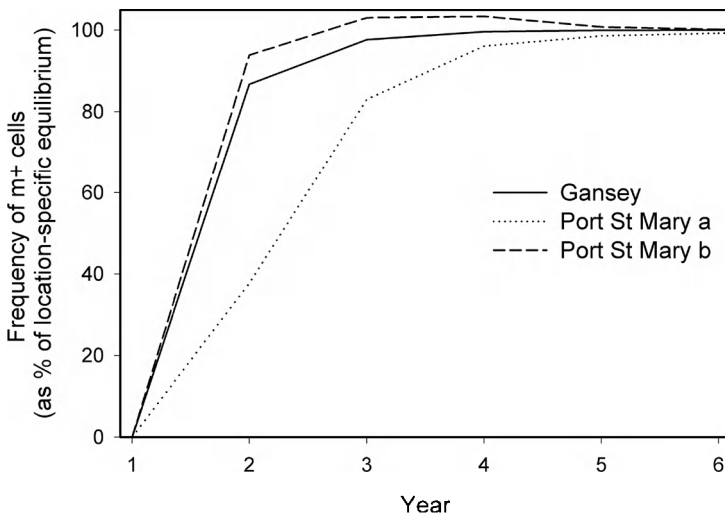


Figure 2. Comparison of rate of return to equilibrium between Markov models for Port St. Mary a, Port St. Mary b and Gansey. Simulations start with all sites as cr- (comparisons could not be made on the basis of bare rock as this state was not recorded at Port St. Mary a).

in recruitment to marine populations and communities, so variation in transition rates between years can be expected. Caswell (2001) and other demographers have addressed this problem by emphasising the difference between projection and prediction. Variable rates would be needed to make a prediction of what will happen to a particular population or community. In contrast a projection emphasises ‘what would happen if the present state of the community were to be maintained indefinitely?’ Caswell (2001) uses the analogy that a speedometer reading of 60 miles per hour is a poor prediction of where the car will be in one hour. Additional information on traffic and road layout is the minimum that would be needed to predict where the car will be. The information on speed is, however, a projection giving relevant information on the current state of the car and how it might respond to external events (such as an emergency stop). Hence projection is used to emphasise that useful information is still possible in the absence of exact predictions.

Despite the conditions associated with matrix modelling, comparisons with field data are often favourable. Steady state projections for the three locations in the Isle of Man explained between 45% and 95% (r^2) of the variation in observed frequencies (e.g. Figure 3).

Projections were always closer to observations than randomly assembled communities (G tests, p fit better than random < 0.05). However, significant G tests between observed

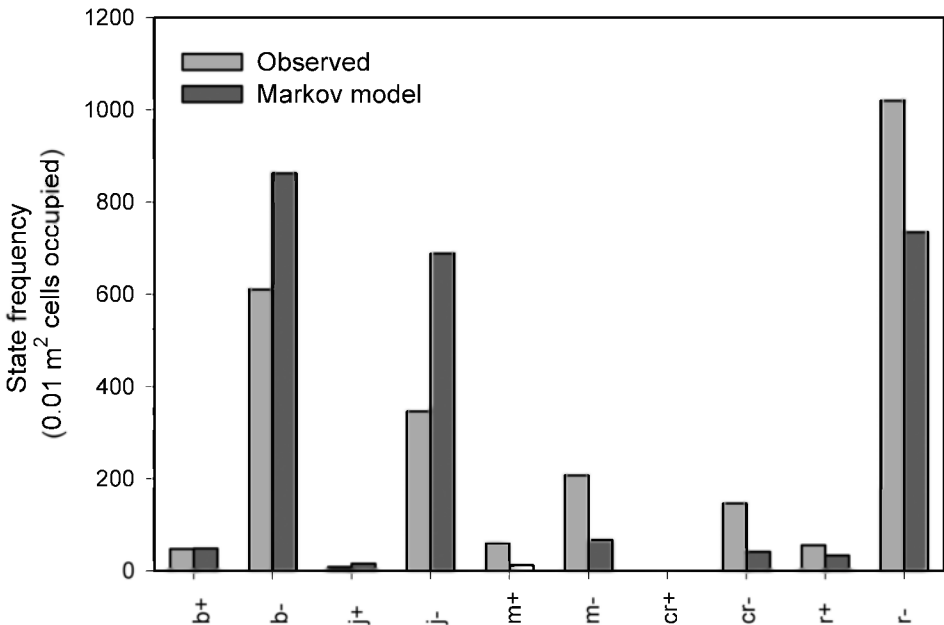


Figure 3. Comparison of observed and projected Markov model state frequencies for Port St. Mary b. States are classified by the same codes as in Figure 1. The projected cell state frequencies are equilibrium values from a transition matrix model. Model predictions are significantly better than random (G tests, $p < 0.05$) and explain a majority of the variance in observed frequencies ($r^2 = 75\%$).

and projected frequencies suggested that the models could be improved (G tests, p projected and observed frequencies equal < 0.05). There is a danger of circularity in that these comparisons are between observed data and models derived from the same data. Wootton (2001), however, reported good fits to data collected independently from that used to derive transition matrices.

CONCLUSIONS AND FUTURE DIRECTIONS

Applications of matrix modelling to intertidal populations include studies of barnacles and macroalgae. Model analyses suggested that *Chthamalus montagui* populations in the mid to upper shore were intrinsically stable with a high adult survivorship (Hyder *et al.* 2001). These results were consistent across a number of European shores, with some differences in timing of events between the Mediterranean and Atlantic. The stability of populations means that population fluctuations can be interpreted in terms of environmental influences on recruitment or mortality (Hyder *et al.* 2001). Models of *Ascophyllum nodosum* also emphasise high adult survivorship (Åberg 1992a). The models applied to rocky shores have included competition for space (Hyder *et al.* 2001) and stochastic variation in environmental conditions (Åberg 1992b). More generally, the methodology of population models has been expanded to address density dependence in transition rates and stochastic variability in transitions (Nakaoka 1997; Tuljapurkar 1997; Caswell 2001). Such modifications may improve models to the extent that they are considered robust enough to make predictions about population persistence (Fieberg and Ellner 2001).

Markov models of rocky shore communities are less common than population models. Wootton (2001) has modelled mussel assemblages on the Pacific coast of North America. Comparison of model output and field data suggested that the transition matrix approach could have predictive power: Wootton's (2001) model described the changes in community composition between horizontal and vertical surfaces associated with changes in mussel recruitment and predation by birds. The quadrat maps from the Isle of Man could be used to make similar predictions about phenomena such as loss of species from the community. Limpets have a clumped spatial distribution (Johnson *et al.* 1997), so it is possible to derive a 'no limpets' matrix of transitions from areas where limpets were locally absent. Transitions were recorded in cells where there were no limpets in any of the adjacent cells (square neighbourhood consisting of 9 cells). Applying the 'no limpets' condition left 943 transitions to derive a matrix model from (for Port St. Mary a: results from other locations were similar). In this instance, the projected dynamics can be referred to as a prediction for the shore community in the absence of limpets. The predicted dynamics for a limpet-free shore, starting from all sites occupied by barnacles, are shown in Figure 4. Predictions of community dynamics qualitatively match those seen in experiments where limpets are excluded from areas of the shore (Hawkins *et al.* 1992). Juvenile algal abundance peaks and then falls away as the community becomes dominated by mature fucoid algae. Barnacle abundance declines under the canopy of fucoids (Lewis 1964). The predicted abundance of coralline algae is three times higher than the level observed

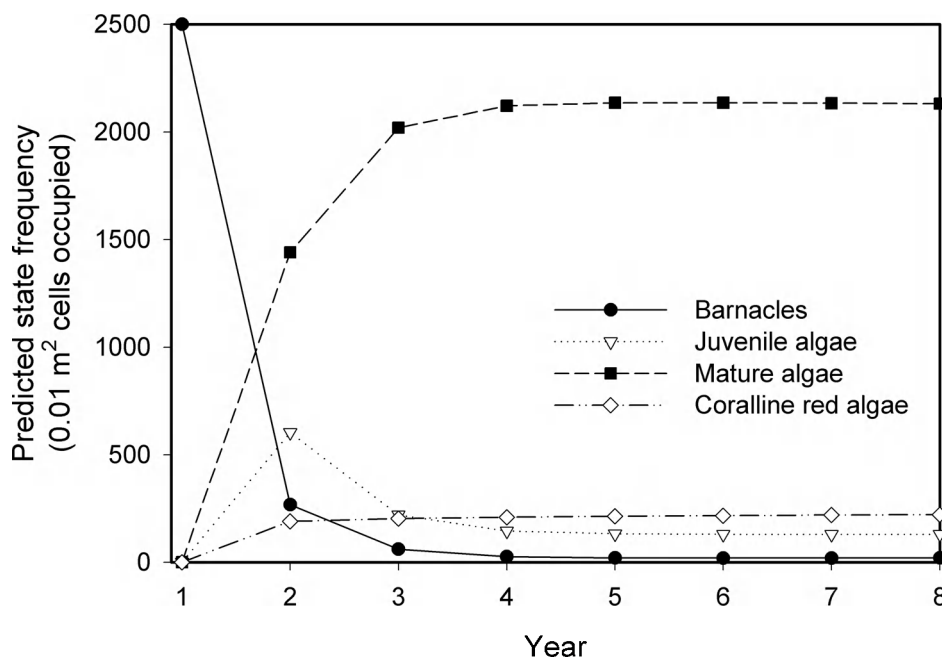


Figure 4. Predicted dynamics in the absence of limpets for Port St. Mary a. The transition matrix model used was derived from areas of the shore where limpets were absent. All cells were initially specified as barnacle occupied.

in the presence of limpets. This may reflect the processes that lead to facilitation of 'red algal turfs' by fucoid canopies (Jenkins *et al.* 1999). Although the simulated community patterns following limpet removal qualitatively resemble those seen in grazer exclusion experiments, the predictions could be confounded by other factors that may have been different in areas where limpet densities were low (for example these may also have been slightly drier or wetter areas). Experimental tests of transition matrix predictions are needed to define the limits of where predictions can be made.

As mentioned previously, rocky shores may be an ideal system in which to apply Markov transition matrix models. Many individuals are sessile and locations can be fixed. The utility of Markov models may be enhanced where populations and communities are 'open'. When new recruits to the community arrive from external sources, parameters such as transition or recruitment rates are unaffected by local densities (e.g. Hyder *et al.* 2001). Hence the assumption that rates do not change with state frequencies may not be too inaccurate. The projected community dynamics have real timescales and provide reasonable approximations to patterns seen in the field. Convergence ratios could potentially be used to classify the sensitivities of different communities to disturbances. Further work is needed on the choice of states, appropriate spatial scales and cell sizes in community models. Tests to identify 'keystone' species have been developed (Tanner *et al.* 1994; Wootton 2001), but these tests need refining due to problems in dealing with covariance of different transition rates. Applied developments of the models could be to

study sustainable harvesting of intertidal species (c.f. Frisk *et al.* 2002). A key advantage of Markov models is that they can be parameterised from repeated field surveys. Observed transitions are easy to define in comparison to more traditional model parameters such as carrying capacities. As Markov models can complement survey and experimental work for little extra effort, future studies are likely to benefit from integrating such observation-based models into the research framework.

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REFERENCES

- Åberg, P. 1990. Measuring and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. *Marine Ecology Progress Series* **63**, 281–287.
- Åberg, P. 1992a. A demographic-study of 2 populations of the seaweed *Ascophyllum nodosum*. *Ecology* **73**, 1473–1487.
- Åberg, P. 1992b. Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology* **73**, 1488–14501.
- Allen, J.R., Slinn, D.J., Shammon, T.M., Hartnoll, R.G. and Hawkins, S.J. 1998. Evidence for eutrophication of the Irish Sea over four decades. *Limnology and Oceanography* **43**, 1970–1974.
- Caswell, H. 2001. *Matrix population models*. Sunderland, Maine. Sinauer Associates.
- Chatfield, C. 1996. *The analysis of time series: an introduction*. 5th ed. London. Chapman and Hall.
- Engel, C., Åberg, P., Gaggiotti, O.E., Destombe, C. and Valero, M. 2001. Population dynamics and stage structure in a haploid-diploid red seaweed, *Gracilaria gracilis*. *Journal of Ecology* **89**, 436–450.
- Fieberg, J. and Ellner, S.P. 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters* **4**, 244–266.
- Frisk, M.G., Miller, T.J. and Fogarty, M.J. 2002. The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses. *ICES Journal of Marine Science* **59**, 576–586.
- Gaines, S.D. and Denny, M.W. 1993. The largest, smallest, highest, lowest, longest, and shortest – extremes in ecology. *Ecology* **74**, 1677–1692.
- Hartnoll, R.G. and Hawkins, S.J. 1985. Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia* **24**, 53–63.
- Hawkins, S.J., Hartnoll, R.G., Kain (Jones), J.M. and Norton, T.A. 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In D.M. John, S.J. Hawkins

- and J.H. Price (eds), *Plant-animal interactions in the marine benthos. Systematics Association Special Volume No. 46*, 1–32. Oxford. Clarendon Press.
- Hughes, R.N. and Burrows, M.T. 1993. Predatory behaviour of the intertidal snail, *Nucella lapillus*, and its effect on community structure. In H. Kawanabe, J.E. Cohen and K. Iwasake (eds), *Mutualism and community organisation. Behavioural, theoretical and food-web approaches*, 63–83. Oxford University Press.
- Hyder, K., Åberg, P., Johnson, M.P. and Hawkins, S.J. 2001. Models of open populations with space-limited recruitment: extension of theory and application to the barnacle *Chthamalus montagui*. *Journal of Animal Ecology* **70**, 853–863.
- Jassby, A.D. and Powell, T.M. 1990. Detecting changes in ecological time series. *Ecology* **71**, 2044–2052.
- Jenkins, S.R., Hawkins, S.J. and Norton, T.A. 1999. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series* **188**, 81–92.
- Johnson, M.P. 1998. Data smoothing or data invention: methods and limitations in modelling the predicted impacts of eutrophication. In J.G. Wilson (ed.) *Eutrophication in Irish waters*, 135–45. Dublin. Royal Irish Academy.
- Johnson, M.P., Burrows, M.T., Hartnoll, R.G. and Hawkins, S.J. 1997. Spatial structure on moderately exposed rocky shores: patch scales and the interactions between limpets and algae. *Marine Ecology Progress Series* **160**, 209–215.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London Series B* **330**, 175–190.
- Kendall, B.E., Prendergast, J. and Bjornstad, O.N. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecology Letters* **1**, 160–164.
- Lewis, J.R. 1964. *The ecology of rocky shores*. London. English Universities Press.
- Nakaoka, M. 1997. Demography of the marine bivalve *Yoldia notabilis* in fluctuating environments: An analysis using a stochastic matrix model. *Oikos* **79**, 59–68.
- Southward, A.J. 1991. 40 Years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association UK* **71**, 495–513.
- Southward, A.J. and Southward, E.C. 1978. Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon oil spill. *Journal of the Fisheries Research Board of Canada* **35**, 682–706.
- Speirs, D.C., Gurney, W.S.C., Hildrew, A.G. and Winterbottom, J.H. 2000. Long-term demographic balance in the Broadstone stream insect community. *Journal of Animal Ecology* **69**, 45–58.
- Sugihara, G. and May, R.M. 1990. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time-series. *Nature, London* **344**, 734–741.
- Tanner, J.E., Hughes, T.P. and Connell, J.H. 1994. Species coexistence, keystone species and succession: a sensitivity analysis. *Ecology* **75**, 2204–2219.
- Tanner, J.E., Hughes, T.P. and Connell, J.H. 1996. The role of history in community dynamics: A modelling approach. *Ecology* **77**, 108–117.

- Tilman, D. and Kareiva, P. 1997. *Spatial ecology*. Princeton. Princeton University Press.
- Tuljapurkar, T. 1997. Stochastic matrix models. In S. Tuljapurkar and H. Caswell (eds), *Structured population models in marine terrestrial and freshwater systems*, 59–87. London. Chapman and Hall.
- Underwood, A.J. 1997. *Experiments in ecology*. Cambridge. Cambridge University Press.
- Underwood, A.J. 2000. Experimental ecology of rocky intertidal habitats: what are we learning? *Journal of Experimental Marine Biology and Ecology* **250**, 51–76.
- Usher, M.B. 1979. Markovian approaches to ecological succession. *Journal of Animal Ecology* **48**, 413–426.
- Vandermeer, J. 1978. Choosing category size in a stage projection matrix. *Oecologia* **32**, 79–84.
- Wootton, J.T. 2001. Prediction in complex communities: analysis of empirically defined Markov models. *Ecology* **82**, 580–598.