Ecological paradigms, change detection and prediction

G. Harris

CSIRO, Hobart, Tasmania

Abstract: In an environment of massive environmental degradation it is very important that we get our basic assumptions and tools correct. Whether or not we are able to perceive the environmental problems being created, and whether we are able to respond effectively will depend on what evidence we can muster for environmental degradation, how we explain the phenomena we observe and how we plan, predict the outcomes of our actions and set policy. Hitherto we have tended to let theory drive observation rather than the reverse. There has been much emphasis on Gaussian statistics, sampling power, analysis of variance and various forms of dynamical simulation models. Effort has been placed on controlling "noise" in data rather than trying to understand and model it.

Recent analyses of water quality data have revealed that what was hitherto thought to be noise in the data is actually small-scale information. The data reveal multi-fractal behaviour, and provide evidence for self-organised criticality and strong non-linear coupling at small scales. Different nutrient pools and biological components exhibit differing turnover times and contingent histories. Ignoring this small scale information means that many (if not most) ecological data are probably collected at inappropriate scales and are seriously aliased. Small scale interactions can have far reaching consequences in non equilibrium systems.

The realisation that all water bodies contain much contingent small-scale information raises a serious question of indeterminism and questions the ability of widely accepted models to predict the outcomes of land use change on receiving waters. Models and predictions have been based around the properties of means and central tendencies only at scales in the region from hours to weeks – these are now seen to be an insecure basis for prediction and management.

Techniques of data based modelling use the data itself to allow for the inclusion of prior experience and to define more parsimonious predictive models. Use of such models recognises the partial nature of our knowledge and requires adequate monitoring and adaptive management programs. Agile institutions and adequate data collection programs are the only solution to environmental management in this environment.

Keywords: modeling, statistics, non-equilibrium systems, self organized criticality, complex adaptive systems

1. INTRODUCTION

Just as in other areas of human endeavour the basic arguments and philosophical underpinnings of ecology (the fundamental science of environmental management) are changing. The basis of ecology lies in theories of the dynamics of populations and communities of organisms, based largely on nineteenth century ideas of plenitude and equilibrium (Kingsland 1985, McIntosh 1985). Much of ecological theory has been based around the role of competition in equilibrium communities (e.g. May 1973). More recently the sheer complexity of ecosystems and landscapes is being addressed with a range of "neutral" models which, rather than competition, stress the role of dispersal, chance and regional evolutionary histories (e.g. Hubbell 2001).

Ecosystems are complex entities which show dynamic behaviour and spatial and temporal heterogeneity (Wu and Loucks 1995), discontinuities and multiple equilibria at a range of scales (O'Neill 1999). They display many of the properties attributed to Complex Adaptive Systems (CAS, Harris 1998) and show self-organised criticality (Sprott et al. 2002). Many properties of landscapes show fractal-like variability across a wide range of temporal and spatial scales (Lohle and Li 1996, Sole et al. 1999, Li 2000, Brown et al. 2002). With variability showing self similar properties across many scales, prediction, particularly for things like community composition and dynamics, is a matter of some difficulty (Lawton 1999).

Fox Keller (2002) has recently noted that there is a strong distinction between the philosophy and practice – between the status of evidence and explanation – in physics and biology. In physics, theory has precedence; evidence is collected to confirm or refute the fundamental theoretical basis of the science. In biology on the other hand, the evidence has precedence over theory – so that biological explanations are contingent and may take the form of "just so stories", contingent explanations or descriptions of natural history

(Gould 1991). Ecological theories are provisional; but we are beginning to shift away from theory laden "physics envy" to a more sensitive reliance on what the data actually tells us.

Catchments, land use and water quality
Introduction

Catchments are the natural biophysical units in which we have made massive changes in land use for agriculture and urban development, altered the hydrology through the building of dams and weirs, extracted water for irrigation and urban use, fragmented habitats and reduced biodiversity. All this has had major effects on water quality and riverine ecosystems. Throughout the world rivers are degraded, species are being lost, flows are reduced and water quality is degraded. There are few pristine rivers left around the world – in addition to conservation and preservation of what is left, one of the major challenges is now restoration of our degraded catchments and rivers.

If restoration is to be attempted there is an urgent need to better understand and explain the linkages and pathways between land use, soil nutrient status and water quality. There is already some strong evidence for control of water quality through small scale interactions with the pore structure and microbial processes in soils which are poorly understood (e.g. Harris 1999, 2001, 2002a, b). Soils and their condition are closely linked to water quality (e.g. Engstrom et al. 2000, Markewitz et al. 2001, Foy and O'Connor 2002).

Non-equilibrium systems – variability at a range of scales

Aquatic ecosystems are particularly useful as model ecological systems because of the wide range of spatial and temporal scales encountered – scales range from the large and slow (kilometres to decades) in catchments to the small and fast (micrometres to seconds) in the water. Catchments appear to have fractal properties, with the concentrations of elements in stream flow showing fractal scaling properties and memories of events at all scales (Kirchner et al. 2000). Ecosystems show variability at a wide range of scales – from microns and millimetres to decades and thousands of kilometres (e.g. Harris 1980, Steele 1995) so that the choice of scales of observation is usually arbitrary and chosen on the basis of either human convenience or the availability of funding. Ecological data are notoriously noisy and flout the standard statistical assumptions of Gaussian distributions and constant means and variances. This has caused problems with interpretation.

The little we know about catchments and their receiving waters shows that there are significant periodicities in climatological drivers of these systems at inter-annual, seasonal, 40-50 days, 5-10 day, 1-2 days and diurnal scales (see Harris 1980, 1987, Harris et al 1988, Harris and Baxter 1996). Much of the higher frequency end of the spectrum is very poorly understood because much of the data we collect is collected weekly at best, and often more infrequently than that.

So the first preconception that we need to change is the idea that ecosystems, particularly catchments, rivers and estuaries are equilibrium systems. Disequilibrium occurs over a range of scales, but hitherto we have never appreciated the importance of small scale disequilibrium on our world view.

What is the evidence for small scale self-organised criticality and non-equilibrium?

Richard Vollenweider (as yet unpublished) has developed a technique of moving correlations to display the small scale correlations within water quality data sets. The technique is identical in concept to the moving average technique in time series analysis but uses moving correlations instead of moving averages. Vollenweider's motive (personal communication) was to attempt to find correlations within daily time series of water quality data from the Adriatic Sea where he could find no statistically significant correlations between the entire time series, but might have reasonably expected to do so on mechanistic grounds. He was, for example, puzzled that he could find no correlation between chlorophyll and dissolved oxygen.

Vollenweider discovered that there were strong correlations between the data sets during short epochs but that the sign of the correlation changed along the length of the series. Therefore, overall there was no significant relationship because the epochs of reversed sign cancelled out. Harris and Trimbee (1986) also noted this phenomenon but did not realise the significance of the observation at the time. We have now examined numerous time series of water quality data and they all show this phenomenon. Figure 1 displays the results of the analysis of water quality data from the Avon River in WA.

Analysis of numerous data sets (Harris, Haygarth and Heathwaite in preparation) shows a number of consistent phenomena:

- All water quality data sets show strong and changing internal correlations over short time and space scales

- These correlation patterns occur at all scales examined – from data collected at scales of minutes to weeks

- These correlations do not arise from random data sets – the data are consistently non random as long as the sampling interval is short enough to resolve the true dynamics

- The water quality data sets show evidence of multi-fractal variability and power law statistics

- Aliasing is a severe problem in weekly water quality data sets

These data most probably arise from small scale reaction-diffusion interactions between catchments, throughflow and runoff, between biological and chemical processes at small scales. Others (Hatje et al 2001, Seuront et al 2002) have recently noted the prevalent and importance of small scale variability in water quality data and have offered similar explanations. Seuront et al. (2002) suggested that "the observed small-scale nutrient patches could be the result of complex interactions between hydrodynamic conditions, biological processes related to phytoplankton populations, and the productive efficiency of bacterial populations". The importance of small scales variability has previously been under estimated. Together these new results may be taken as evidence of self-organised criticality in the interaction of physical, chemical and biological processes in catchments and runoff. There is an emerging literature that studies SOC phenomena and the emergence of large scale patterns from small scale interactions in ecosystems (Wootton 2001, Bjornstad et al 2002).
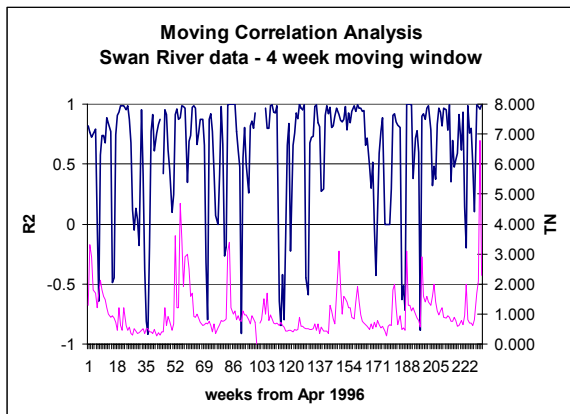

Figure 1. The results of Vollenweider's moving correlation analysis on total N and total P data from the Swan River (thick line). Whilst the correlation is mostly positive there are significant periods when the correlation is strongly negative. The thin line is the time series of total nitrogen (mg.l^{-1}). Positive correlations between TN and TP

mostly occur during periods of high TN (and high flows). These data were kindly supplied by Malcolm Robb of the (then) Water and Rivers Commission. (With this moving correlation kernel, statistically significance ($p < 0.05$) occurs with $R^2 > +$ or $- 0.84$)
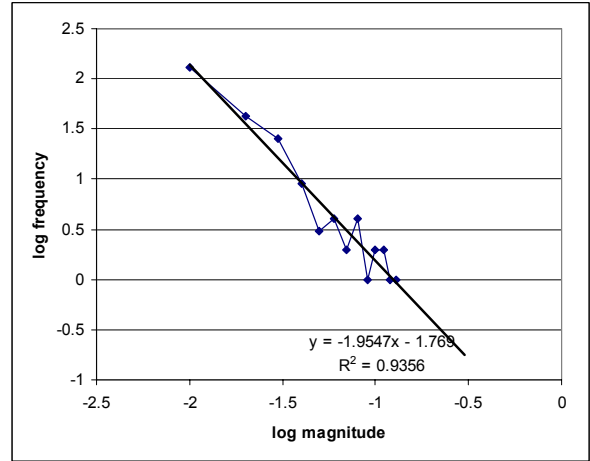

Figure 2. Total phosphorus data from the Swan River. Power law plot of the frequency and magnitude of changes in the weekly time series data from Walyunga station (first differences).

From microns to continental scales, there is contingency and indeterminism brought about by the vagaries of dispersal and environmental heterogeneity. Different processes come to predominate at different levels in the hierarchy and "more is different" Anderson (1972). While biogeochemistry sums processes across spatial and temporal scales by looking at entities watersheds, at very small scales microbial processes are patchy and contingent. Riverine nutrient inputs come from small scale interactions between the landscape and the river (Alexander et al 2000).

Why do disequilibrium, non-linear coupling and indeterminacy over a wide range of scales shake the foundations of ecological data analysis, variance analyses and dynamical simulation modelling? Analysis of much water quality data has, hitherto, been based on the use of mean values because it has been assumed that the observed variability was merely noise and the parameters were uncorrelated.

Frequentist approaches to ecological data have focussed more on controlling and modelling statistical variability – believing the variability to be random noise. Richard Vollenweider's analyses have suggested that the probability density functions and higher moments are not Gaussian *and* that the small scale cross-correlations and co-variances are highly

significant. Small scale indeterminacy, fractal variability and emergence have major implications for modelling and prediction because the antecedent conditions for each patch of water at small scales are unknowable but may, nonetheless, have large scale emergent repercussions.

Systems which show multi-fractal variability and evidence of self-organised criticality – including small scale indeterminacy - mean the death of "phenomenological" models based on means and central tendencies. In such systems it is extremely difficult to define a model for any particular phenomenon because of emergence and a lack of data. A hierarchy of models may be constructed – but any model at any level is not only scale dependent but also an averaging of lower level processes. The question must be well posed and the relevant data must be available at the correct scale – even then small scale contingency; multi-fractal scaling and non-linear coupling render predictions based on averages inherently unsafe.

Ecological explanation and prediction

Dynamical simulation models are large sets of differential equations describing ecological processes, major functional groups and their interactions. Dynamical simulation models of aquatic ecosystems are, in fact, little changed since the work of Riley et al. (1949). The approach has been widely used; e.g. the Great Lakes models of Scavia, Thomann and Di Toro (Thomann et al 1975, 1976) were the basis of the phosphorus reduction programs in the Great Lakes, and the Port Phillip Bay model of Murray and Parslow (Harris et al. 1996, Murray and Parslow 1999a, b) was the basis of the recommendations about nutrient loading reductions in that coastal lagoon. Other examples could be quoted.

The selection of the processes modelled is based on experience and the "state of the art" at the time. These models can either be used heuristically to synthesize knowledge and to guide further data collection or they can be used to predict the outcomes of management action and other forms of human intervention. Either way they form the basis of explanations of ecological pattern and process. Distributions, processes and interactions which vary in space and time are averaged and simplified. Deterministic equations replace probabilistic and contingent distributions. The models are strongly scale dependent. The models represent noisy, non-equilibrium systems with variability at a wide range of temporal and spatial sales. No attempt is made to represent all the species or interactions, relying instead on a "lumped" representation of the ecosystem and its constituent species.

The data used in attempts to calibrate and validate such models is also partial and noisy. Any set of ecological data is a sample from the normal spatial and temporal variability encountered in natural systems. Most ecological data are therefore aliased – they are, in effect, sparse samples which are unrepresentative of the full spectrum of natural variability (Clark et al. 2001). Thus we have the problem of evidence based on partial information and of explanations based on unrepresentative, deterministic dynamical models.

Since the early days there have been worries over the philosophical basis of dynamical simulation modelling (Berlinksi 1976) and the ability to calibrate and validate such models (Oreskes et al. 1994). There is always much hand waving and lack of rigour in comparisons between water quality data and model outputs (usually in the form of visual comparison of time series plots of data and model predictions). There is insufficient objective statistical analysis of model bias and the fit to the data. Of course, an ability to fit the data does not, in itself, make any definitive statement about the adequacy of the model structure or its parameterisation (Klemes 1986, Rykiel 1996). There "may be more than one set of parameterisations and more than one set of parameter values that can give equally acceptable predictions of the observational data available" (Beven 2000) This is not a new debate and further references may be found in (Beven 2000).

One thing that has become clear in recent years is that the predictive properties of simulation models are related to their structure (in terms of the network of links). This insight has emerged from graph and network theory (Buchanan 2002). Thus the ability of dynamical simulation models to predict ecological outcomes is a function of the level of abstraction and the supposed network of key interactions – all of which are abstractions from a much more complex natural entity. Dynamical models rarely have the kind of network structure seen in real world networks – which are usually hierarchical and scale-free (Buchanan 2002, Ravasz et al. 2002). Differing models, with differing structures may well give quite different dynamical behaviour – but is the data sufficient to distinguish between the various models?

Raupach et al. (2002) have recently described a method for evaluating the bias in such models. The reliability of the aggregated model depends critically on the accurate estimation of the means, variances and co-variances of model variables and parameters. Raupach et al. (2002) presented a Taylor expansion model for critical functions which shows that considerable bias may be introduced if the third, and higher order terms, are large. i.e. if there are significant non Gaussian

distributions in the probability density functions of the values and the co-variances are significant. As Raupach et al. (2002) note, if estimates of the means, variances and co-variances are not available "attempts to improve the performance of an aggregated model by further measurement of only the mean variables and parameters are futile, because measurements of mean quantities cannot eliminate bias arising from the interaction between model nonlinearity and small-scale variability".

Simulation models are only capable of modelling the central tendencies in the data – not the actual small scale variability (Harris 1999b). What Vollenweider's work has revealed is that there is much meaningful small scale variability – it is not mere noise. While dynamical simulation models of estuaries and lakes can show large scale hysteresis effects (Harris et al. 1996, Murray and Parslow 1999a, b) which are quite realistic (Scheffer et al. 2001) the worrying thing about Vollenweider's result is the proof of the widespread existence of small scale non-linearity and cross-correlations between parameters which make Raupach's concerns highly valid ones.

What the small scale dynamics also shows is that fractal variability and non-linearity at small scales may be sufficient to render the predictions of simulation models unsafe at larger scales or higher levels. Clearly there are fundamental limitations to our ability to measure and predict the contingent variability in catchments, rivers and estuaries. We know that stochastic events can lead to hysteresis effects and state shifts in natural ecosystems (Scheffer et al. 2001). Any predictions had therefore better be probabilistic and hedged about with uncertainty.

Furthermore, small scale events - including the time history of particular bodies of water and the occurrence of individual species; things that we would like to know – will be inherently unpredictable (Harris 1994). Observations bear out this assertion. Magnusson et al. (1990) showed that the temporal unfolding of a suite of properties from a group of "similar" lakes was unpredictable and Reynolds (1986) had the same problems with attempts at ecosystem scale "controls" in large enclosures.

Parameterisation and data availability

The debate about parameterisation and data availability has been the subject of much discussion the hydrological literature (Loague and Freeze 1985, Beven 1989, 1993). In fact, Beven (1993) preferred the term prophecy to prediction! The problems of scale, missing data and the lack of inclusion of key processes were discussed by Haus (1990). Clark et al. (2001) raised the issue

of partial and incomplete data and this, together with the problems of climate prediction means that there are some fundamental problems with calibration, validation and prediction (Oreskes et al. 1994).

Spatial and temporal emergence

Algorithmic process models logically underlie the dynamical simulation models. These algorithmic models of individual survival and growth must account for the outcomes of numerous processes – disturbance, dispersal, birth, growth and death for different species and functional groups in the ecosystem – and the process base for both model types must be basically the same. Much can be predicted from a basic understanding of some basic physics, physiology and the design of the organisms (Harris and Griffiths 1987, Harris 1999a, b, 2001) but the fundamental difference between the two types of models is the lack of spatial pattern and temporal and spatial emergence in the dynamical models.

Spatially explicit models of individual dispersal, growth and death show the emergence of large-scale patterns (Wootton 2001). Patch dynamics are critical in terrestrial habitats (Wu and Loucks 1995) whereas temporal dynamics, (rainfall, flood, drought, ENSO) are dominant in fluid environments. Catchments are combinations of both but the spatial patterning and emergence is critical in terrestrial systems (Wootton 2001). Dynamical simulation models do not adequately represent the spatial and temporal emergence and the temporal unfolding that is so critical for the function of catchments and receiving waters. Even simple estuarine models (Webster and Harris 2003) respond in unexpected ways to the higher statistical moments of pulsed nutrient inputs. Catchment exports do follow a central tendency of Redfield ratios (Harris 1999, 2001, 2002a, b) but these ratios must now be seen as emergent properties of much small scale pattern and process.

Changes to land use in catchments not only changes the annual averaged nutrient loads to rivers and estuaries but also changes flood frequencies and the frequency and magnitude of events. Raupach et al.'s (2002) problem arises once again. The function of the entire entity is an emergent property and therefore prediction is limited except in terms of central tendencies and statistical properties at a fairly high level (Harris 1998). Throughout this process of building models it is necessary to remind ourselves that ecosystems are in many ways irreducibly complex (O'Neill 1999), that knowledge of key parameters will be lacking and that the necessary data will not always be available at the correct scales. Omniscience is rare and hubris is to be avoided at

all costs. Berlinski (1976) published a wonderfully pungent critique of ecosystem modelling and all its faults.

A further complication arises from the fact that the underlying stochastic drivers of ecosystems as well as the chaotic internal dynamics lead to the biodiversity that we observe (Gragnani et al. 1999, Huisman and Weissing 1999, Huppert et al 2001, Lima et al 2001), and we know that the biodiversity controls the overall function, often in idiosyncratic ways (Emmerson et al. 2001). While there are some overall patterns of response, dynamical simulation models do not predict the dynamics, emergence, contingency and biodiversity of real world systems.

The fundamental question that now needs to be answered is "how often do the small scale contingency, indeterminacy, non-linearity and the cross-correlations that Vollenweider has revealed, engender surprises at higher levels so as to render predictions of central tendencies unsafe?" We simply do not know.

Alternatives to standard simulation modelling techniques

The time is ripe for new approaches to observation and statistical analysis of ecological data. There are alternatives to the usual dynamical simulation modelling techniques. Instead of building large, over parameterised, models of catchments and ecosystems (models which are almost impossible to validate) it is possible to use the data to objectively determine the most parsimonious models. These data based modelling (DBM) techniques have been shown to produce much simpler, but more robust models, of these complex systems (see e.g. Young et al. 1996, Young 1998). New techniques of time varying parameter (TVP) analysis have begun to reveal much new information in water quality data and form the basis of new explanations (Young 1999, 2000). There are objective techniques, derived from the econometric literature, which can replace Vollenweider's methodology.

These new statistical and modelling techniques directly address the issues of "lumping" processes and parameters, of missing parameters, of lack of data and indeterminacy discussed above. In essence the data defines the most parsimonious model. In addition the new objective TVP techniques directly address the non-stationarity and other problems in ecological data. These techniques also go the heart of the "theory" versus "data" problem of Fox Keller (2002) and lead to new approaches to biological systems which rely more on reality than some predetermined theoretical framework, with all its epistemological shortcomings.

Surprises occur when these models are used. For example, a recent analysis of global atmospheric carbon dioxide data (Jarvis and Young 2002) has revealed new and hitherto unrecognised feedbacks which make the present forecasts of future atmospheric concentrations unsafe. If the new DBM models are confirmed then the future path of the greenhouse effect may be quite different from that of the present predictions.

The time is ripe for new observations and models – new evidence of the coupling of land use change to water quality will be produced, new explanations will become possible and this will have impact on "evidence based" policy development and management techniques.

Ecological evidence

As noted above ecosystems show variability at a range of scales. They are open systems in which the spatial and temporal variability is part and parcel of the maintenance of biodiversity and function. Quite clearly small scale microbial processes dominate many large scale patterns (Harris 1999b, 2001, 2002a, b). Much of what we see in catchments and water quality seems to emerge from much small scale pattern and process – microbiology rules. This problem urgently needs some new science. This is no time to reduce effort on water quality monitoring. We need better evidence upon which to base our policies. What we thought was mere noise isn't!

Human intervention in landscapes changes the spatial and temporal scales of variability (through things like land use change, habitat fragmentation and flow regulation in rivers) and thereby changes biodiversity. Biodiversity controls ecosystem and landscape function, so that habitat fragmentation reduces biodiversity and leads to changes in hydrology and the cycling of energy and nutrients in catchments (Harris 2002a, b).

New technologies are now available, particularly in the area of hydrology and water quality, which make it possible to collect much more complete and representative data sets. Automatic sampling equipment, internet connections and computer data storage make it possible to collect high frequency data from catchments and rivers which are more representative of the full range of spatial and temporal scales of variability. In particular it is now possible to move away from arbitrarily chosen sampling schemes to a more complete analysis of the most significant time and space scales – and then to optimise the sampling accordingly. This, in itself, will produce more concrete evidence of the links between land use and river degradation and provide a firmer base for "evidence based" policy development and management interventions.

These data may now be used to define parsimonious models upon which to base management action and policy development. Models may be developed which use as much information as the data provide – recognising that all knowledge is partial at best. In a world of climate change and climate variability, even with new technologies, it is usually difficult to design and complete adequate performance monitoring after management interventions. Evidence for environmental change is therefore noisy and incomplete at best. It is therefore difficult to develop unequivocal arguments with which to support "evidence based policy" development. A more rigorous definition of the required scales of measurement is usually required. i.e. what is changing over what time scales and what evidence of change is required?

All of the above places more and more emphasis on the need for adaptive management (see e.g. Walters and Holling 1990). Once we recognise that our knowledge is partial and they our predictive powers are limited then there is a real need for institutional agility and rapid feedback from knowledge to response (Lessard 1998). How quickly can we respond to changing information and new concepts? Why do we cancel hydrological and water quality data collection programs when we need to data for adaptive management?

2. ACKNOWLEDGEMENTS

3. REFERENCES

Alexander, R.B., Smith, R.A. and Schwarz, G.E., Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature*, (403), 758-761, 2000.

Anderson, P.W., More is different. *Science*, (177), 393-396, 1972.

Berlinski, D., On systems analysis: an essay concerning the limitations of some mathematical models in the social, political and biological sciences. MIT press, Boston, 1976.

Beven, K., Changing ideas in hydrology – the case of physically-based models. *Journal of Hydrology*, (105), 157-172, 1989.

Beven, K., Prophecy, reality and uncertainty in distributed hydrological modelling. *Advances in Water Resources*, (16), 41-51, 1993.

Beven, K., On model uncertainty, risk and decision making. *Hydrological Processes*, (14), 2605-2606, 2000.

Bjornstad, O.N., Peltonen, M., Liebhold, A.M. and Baltensweiler, W., Waves of Larch Budmoth outbreaks in the European Alps, *Science*, (298), 1020-1023, 2002.

Brown, J.H., Gupta, V.K., Li, B-L., Milne, B.T., Restrepo, C. and West, G.B., The fractal nature of nature: power laws, ecological complexity and biodiversity. *Philosophical Transactions of the Royal Society of London*, *Serie B*, (357), 619-626, 2002.

Buchanan, M., Nexus, small worlds and the groundbreaking science of networks. Norton, New York, 235p, 2002

Clark, J.S., Carpenter, S.R., Barber, M. and 14 others., Ecological forecasts: an emerging imperative. *Science*, (293), 657-660, 2001.

Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M. and Rafaelli, D., Consistent patterns and idiosyncratic effects of biodiversity in marine systems. *Nature*, (411), 73-77, 2001.

Engstrom, D.R. Fritz, S.C., Almendinger, J.E. and Juggins, S., Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature*, (408), 161-166, 2000.

Fox Keller, E., Making sense of life: explaining biological development with models, metaphors and machines. Harvard University Press, 2002

Foy, R.H. and O'Connor, W.C.K. Managing the effects of agriculture on water quality in Northern Ireland. p 417-440 in Haygarth, P.M. and Jarvis, S.C. (Eds) "*Agriculture, hydrology and water quality*", CABI publishing, London, 2002.

Gould, S.J., Wonderful life: the Burgess shale and the nature of history. Penguin, London, 347p, 1991.

Gragnani, A., Scheffer, M. and Rinaldi, S., Top-down control of cyanobacteria, a theoretical analysis. *The American Naturalist*, (153), 59-72, 1999.

Harris, G.P., Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models and management. Can. J. Fish. *Aq. Sci.* (37), 877-900, 1980.

Harris, G.P., Time series analysis of water quality data from Lake Ontario: implications for the measurement of water quality in large and small lakes, *Freshwater Biol.* (18), 389-403, 1987.

Harris, G.P., Pattern, process and prediction in aquatic ecology - a limnological view of some general ecological problems, *Freshwater Biology*, (32): 143-60, 1994.

Harris, G.P., Algal biomass and biogeochemistry in catchments and aquatic ecosystems: scaling of processes, models and empirical tests, *Hydrobiologia*, (349), 19-26, 1997.

Harris, G.P., Predictive models in spatially and temporally variable freshwater systems, Australian Journal of Ecology, (23), 80-94, 1998.

Harris, G.P., This is not the end of limnology (or of science): the world may well be a lot simpler than we think, Freshwater Biology, (42), 689-706, 1999 [a].

Harris, G.P., Comparison of the biogeochemistry of lakes and estuaries: ecosystem processes, functional groups, hysteresis effects and interactions between macro- and microbiology, *Marine and Freshwater Research*, (50), 791-811, 1999[b].

Harris, G.P., The biogeochemistry of nitrogen and phosphorus in Australian catchments, rivers and estuaries: effects of land use and flow regulation and comparisons with global patterns. Marine and Freshwater Research, (52), 139-149, 2001.

Harris, G.P., A nutrient dynamics model for Australian waterways – Land use, catchment biogeochemistry and water quality in Australian rivers. Technical report for EA SoE group, Canberra, ACT (http://www.ea.gov.au/soe/techpapers/nutrient-dynamics/index.html), 2002a.

Harris, G.P., Simple rules underlie the complex and non-linear dynamics of terrestrial and aquatic ecosystems: implications for catchment biogeochemistry and modeling, CSIRO, *Land and Water Technical report*, #11/02, Canberra, ACT 41p, http://www.clw.csiro.au/publications/technical2002, 2002b.

Harris, G., Batley, G., Fox, D., Hall, D., Jernakoff, P., Molloy, R., Murray, A., * Newell, B., Parslow, J., Skyring, G. AND Walker, S., *Port Phillip Bay Environmental Study*, final report, CSIRO, Dickson, ACT, 239p., 1996.

Harris, G.P. and Baxter, G., Interannual variability in phytoplankton biomass and species composition in a subtropical reservoir, *Freshwat Biol*, (35), 545-560, 1996.

Harris, G.P., Davies, P., Nunez, M. and Meyers, G., Interannual variability in climate and fisheries in Tasmania, *Nature*, (333), 754-757, 1988.

Harris, G.P. and Griffiths, F.B., On means and variances in aquatic food chains and recruitment to the fisheries, Freshwater Biology, (17), 381-386, 1987.

Harris, G.P. and Trimbee, A.M., Phytoplankton population dynamics of a small reservoir: physical/ biological coupling and the time scales of community change, *Journal of Plankton. Research*, (8), 1011-1025, 1986.

Hatje, V., Rae, K. and Birch, G.F., Trace metal and total suspended solids concentrations in freshwater: the importance of small-scale temporal variation, *Journal of Environmental Monitoring*, (3), 251-256, 2001.

Haus, M., Ecosystem modelling: science or technology?, *Journal of Hydrology*, (116) 25-33, 1990.

Hubbell, S.P., The unified neutral theory of biodiversity and biogeography, Monographs in population biology, *Princeton University Press*, 2001.

Huisman, J. and Weissing, F.J., Biodiversity of plankton by species oscillations and chaos. Nature, (402), 407-410, 1999.

Huppert, A., Blasius, B., and Stone, L., A model of phytoplankton blooms, The American Naturalist, (159), 156-171, 2002.

Jarvis, A.J. and Young, P.C., Identification of Temperature Dependency in the

Relationship Between Global Anthropogenic CO_2 Emissions and Atmospheric CO_2, 1856-2000. Submitted to *Nature*, 2002.

Kingsland, S.E., Modelling nature, *University of Chicago Press*, 267p, 1985.

Kirchner, J.W., Feng, X. and Neal, C., Fractal stream chemistry and its implications for contaminant transport in catchments, *Nature*, 403, 524-527.

Klemes, V., Dilettantism in hydrology: transition or destiny, *Water Resources Research*, (22), 177S-188S, 1986.

Lawton, J.H., Are there general laws in ecology?, *Oikos*, (84), 177-192, 1999.

Lessard, G., An adaptive approach to planning and decision making. *Landscape and Urban Planning,* 40, 81-87, 1998

Li, B-L., Fractal geometry applications in description and analysis of patch patterns and patch dynamics, *Ecological Modelling*, (132), 33-50, 2000.

Lima, I.D., Olson, D.B., and Doney, S.C., Intrinsic dynamics and stability properties of size-structured pelagic ecosystem models, *Journal of Plankton Research*, (24), 533-556, 2002.

Lohle, C. and Li, B-L., Statistical properties of ecological and geologic fractals, *Ecological Modelling*, (85), 271-284, 1996.

Loague, K.M. and Freeze, R.A., A comparison of rainfall-runoff modelling techniques on small upland catchments, *Water Resources Research*, (21), 229-248, 1985.

McIntosh, R.P., The background of ecology, concept and theory, *Cambridge University Press*, 383p, 1985.

Magnusson, J.J., Benson, B.J., and Kratz, T.K., temporal changes in the limnology of a suite of lakes in Wisconsin, USA, *Freshwater Biology*, (23), 145-159, 1990.

Markewitz, D., Davidson, E.A., Figueiredo, R. de O., Victoria, R.L. and Krusche, A.V., Control of cation concentrations in stream waters by surface soil processes in an Amazonian watershed, *Nature*, 410, 802-805, 2001.

May, R.M., Stability and complexity in model ecosystems, Monographs in population biology, *Princeton University Press*, 235p, 1973.

Murray, A.G. and Parslow, J.S., Modelling of nutrient impacts in Port Phillip Bay – a semi-enclosed marine Australian ecosystem, Marine and Freshwater Research, (50), 597-611, 1999a.

Murray, A.G. and Parslow, J.S., The analysis of alternative formulations in a simple model of a coastal ecosystem, Ecological Modelling, (119), 149-166, 1999b.

O'Neill, R.V., Recovery in complex ecosystems. Journal of Aquatic Ecosystem Stress and Recovery, (6), 181-187, 1999.

Orekes N., Shrader-Frechette K. & Belitz K, Verification, validation and confirmation of numerical models in the earth sciences, *Science* (263), 641-646, 1994.

Raupach, M.R., Barrett, D.J., Briggs, P.R. and Kirby, J.M., Terrestrial Biosphere models and forest-atmosphere interactions. (in press) in Vertessey, R. and Elsenbeer, H (Eds.) Forests and Water, IUFRO press, 2002.

Ravasz, E., Somera, A.L., Mongru, D.A., Oltvai, Z.N. and Barbasi, A-L., Hierarchical organization of modularity in metabolic networks, *Science*, (297), 1551-1555, 2002.

Reynolds, C.S., Experimental manipulations of the phytoplankton periodicity in large limnetic enclosures in Blelham Tarn, English Lake District. Hydrobiologia, (138), 43-64, 1986.

Riley, G.A., Stommel, H. and Bumpus, D.F., Quantitative ecology of the plankton of the western North Atlantic, Bulletin of the Bingham Oceanographic College, (12), 1-169, 1949.

Rykiel, E.J., Testing ecological models: the meaning of validation, *Ecological Modelling*, (90), 229-244, 1996.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and Walker, B., Catastrophic shifts in ecosystems, *Nature*, (413), 591-596, 2001.

Seuront, L., Gentilhomme, V. and Lagadeuc, Y., Small-scale nutrient patches in tidally mixed coastal waters, *Marine Ecology-Progress Series*, (232), 29-44, 2002.

Sole, R.V., Manubria, S.C., Benton, M., Kauffman, S. and Bak, P., Criticality and scaling in evolutionary ecology, *Trends in Ecology and Evolution*, (14), 156-160, 1999.

Sprott, J.C., Bolliger, J. and Mladenhoff, D.J., Self-organised criticality in forest-landscape evolution, Physics Letters A, (297), 267-271, 2002.

Steele, J.H., Can ecological concepts span the land and ocean domains? p. 5-19 in Powell, T.M. and Steele, J.H, (eds) *Ecological time series*, Chapman and Hall, London, 1995.

Thomann, R.V., Di Toro, D.M., Winfield, R.P. and O'Connor, D.J., Mathematical modelling of phytoplankton in Lake Ontario, 1. *Model development and verification,* EPA (660/3-75-005), US Environmental Protection Agency, Corvallis, Oregon, 1975.

Thomann, R.V., Di Toro, D.M., Winfield, R.P. and O'Connor, D.J., Mathematical modelling of phytoplankton in Lake Ontario, 2, *Simulations using lake 1 model,* EPA (660/3-76-065), US Environmental Protection Agency, Corvallis, Oregon, 1976.

Walters, C.J., and Holling, C.S., Large-scale management experiments and learning by doing. *Ecology*, 71, 2060-2068, 1990

Webster, I., and Harris, G.P., Anthropogenic impacts on the ecosystems of coastal lagoons - fundamental processes and management, *Estuaries* (submitted) 2002.

Wiens, J., Riverine landscapes: taking landscape ecology into the water, *Freshwater Biology*, (47), 501-515, 2002.

Wootton, J.T., Local interactions predict large-scale pattern in empirically derived cellular automata, *Nature*, (413), 841-844, 2001.

Wu, J. and Loucks, O.L., From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology, *Quarterly Review of Biology*, (70), 439-466, 1995.

Young, P.C., Data-based mechanistic modelling of environmental, ecological, economic and engineering systems, *Environmental Modelling and Software*, (13), 105-122, 1998.

Young, P.C., Non-stationary time series analysis and forecasting, *Progress in Environmental Science*, (1) 3-48, 1999.

Young, P.C., Stochastic, dynamic modelling and signal processing: time variable and state dependent parameter estimation, p. 74-114 in Fitzgerald, W.J., Walden, A., Smith, R. and Young, P.C. (Eds.), Cambridge University Press, Cambridge, 2000.

Young, P.C., Parkinson, S. and Lees, M.J. () Simplicity out of complexity, Occam's razor revisited, *Journal of Applied Statistics*, 23, 165-210, 1996.