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Nonlinear time series modelling of highly fluctuating biological population over space - main results

Research report

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Nonlinear Time Series Modelling of Highly Fluctuating Biological Population Over Space — main results

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Common dynamic structure of Canada lynx populations within three climatic regions

Across the boreal forest of Canada, Lynx populations undergo regular density cycles. Analysis of 21 time series from 1821 onward reported in Stenseth, Chan, Tong, Boonstra, Boutin, Krebs, Post, ODonoghue, Yoccoz, Forchhammer and Hurrell (1999) demonstrated structural similarity in these cycles within large regions of Canada. The observed population dynamics are consistent with a regional structure caused by climatic features, resulting in a grouping of Lynx population dynamics into three types (corresponding to three climatic-based geographic regions): Pacific-maritime, Continental, and Atlantic-maritime. A possible Link with the North Atlantic Oscillation is suggested.

Common structure in panels of short ecological time series

Following Elton's pioneering work 1924, one of the key issues in ecology has been to understand the mechanisms underlying the periodic population fluctuations of northern regions. For terrestrial vertebrates such as microtine rodents and the Canadian snowshoe hare, attention has recently been focused on the food chain interaction (e.g. plant-herbivore and predator-prey interactions) as a possible explanatory mechanism. Unfortunately, there is a general lack of data on both predator and prey from the same area and over the same time period. The recent availability of Canadian annual muskrats and minks data over 81 trapping regions over a period of 25 years offers a unique opportunity to carry out systematic statistical analyses aiming at a deeper understanding of the ecological interaction from a quantitative point of view. Statistically speaking, we deal with a nonlinear stochastic system with two inputs and two outputs here. To overcome the difficulties of only 25 data points in each series, a bootstrap test for common structure in panels of time series has been developed (Yao, Tong, Finkenstädt and Stenseth 2000). Applying the test to the muskrat-mink data, the finding is exciting. Ecologically interpretable groupings are obtained: one may divide the trapping regions into three groups in terms of their geographical locations.

Varying-coefficient linear modelling for population dynamics

Varying-coefficient linear models for time series can be viewed as an extension of threshold autoregressive models. The approach is a kind of semiparametric local fitting with appreciable flexibility to analyze complex and multivariate nonlinear structures without suffering from the "curse of dimensionality". Cai, Fan and Yao (2000) illustrated the varying-coefficient linear model through Canadian lynx data for which threshold model has been tremendously successful. While retaining the capacity of modelling phase-dependence and density-dependence, the new model replaces piecewise constant coefficients in threshold models by continuous and gradual changing coefficient functions, which represent one step closer to reality.

A further development of varying-coefficient linear modelling techniques has been exploited in Fan, Yao and Cai (2002) in which the generic index which controls nonlinearity is selected by the data. This adaptive model facilitates the data analysis of the biological food chain interaction model by portraying the nonlinearity through varying-coefficient functions. The selection of smoothing variable in our algorithm is equivalent in this context to the selection of the regime effect indicator, which in itself is of biological interest. The application to Canadian muskrat-mink data indicates that there is a strong evidence of predator-prey interaction between mink and muskrat in the central and western areas. However, no evidence for such an interaction exists in the eastern area. In the light of what is known in the eastern area, this is not surprising. There is a larger array of prey-species for the mink to feed on, making it less dependent on muskrat.

Phase coupling and synchrony in the spatiotemporal dynamics of muskrat and mink populations across Canada

Population ecologists have traditionally focused on the patterns and causes of population variation in the temporal domain for which a substantial body of practical analytic techniques have been developed. More recently, numerous studies have documented how populations may fluctuate synchronously over large spatial areas; analyses of such spatially extended time-series have started to provide additional clues regarding the causes of these population fluctuations and explanations for their synchronous occurrence. Haydon, Stenseth, Boyce and Greenwood (2001) report on the development of a phase-based method for identifying coupling between temporally coincident but spatially distributed cyclic time-series, which we apply to the numbers of muskrat and mink recorded at 81 locations across Canada. The analysis reveals remarkable parallel clines in the strength of coupling between proximate populations of both species-declining from west to east-together with a corresponding increase in observed synchrony between these populations the further east they are located.

Bürmann expansion and test for additivity

Chan, Kristoffersen and Stenseth (2002) have proposed a Lagrange Multiplier test for additivity based on the Bürmann expansion of a conditional mean function. The asymptotic null distribution of the test is shown to be χ^2, under some regularity conditions. In contrast, the Lagrange Multiplier test proposed by Chen *et al.* (1995) is based on the Volterra expansion of the conditional mean function. We have discussed some desirable properties of the Bürmann expansion over the Volterra expansion for nonlinear time series modeling. We have also carried out an empirical study which shows that in terms of empirical power, the Lagrange Multiplier test motivated by the Bürmann expansion outperforms Chen *et al.* (1995)'s test for the cases for which the Lagrange Multiplier test is designed. For other cases for which none of the tests are specifically designed, the empirical power of the two tests are comparable. Finally, we illustrated the use of the Lagrange Multiplier test with a blowfly experimental system.

Smoothing estimation for spatio-temporal models

Zhang, Yao, Tong and Stenseth (2002) proposed a spatial smoothing estimation for the parameters which control temporal dynamics in a set of spatially dependent dynamical models. The new approach is particularly relevant for analysing panels of short time series over space. The asymptotic results show that spatio smoothing will improve the estimation in the presence of nugget effect even when the sample size in each location is large. The study was motivated by analysing the annual mink and muskrat data collected in a period of 25 years over 81 locations in Canada. Based on the proposed method, we are able to model the temporal dynamics which reflects the food-chain-interaction of the two species. Further the fitted models also enable us to identify the pattern changes of the food-chain-interaction over space.

Quasi-maximum likelihood estimation for temporal dynamics and spatial correlation

Yao, Tsiotas, Tong and Stenseth (2002) studied a class of of spatio-temporal models for modelling data collected regularly in time and irregularly over space. The aim here is to model temporal dynamics and spatial correlation simultaneously. Following Yao and Brockwell (2002), quasi-maximum likelihood methods based on Gaussian likelihood functions have been employed, and they are numerically implemented instead of an innovation algorithm via prewhitening. Spatial correlation among nearby locations for both Canadian mink-muskrat data and Hokkaido vole data has been identified.

Assessing the effectiveness of releasing cod larvae for stock improvement

Beginning in the 1880s, management of marine fisheries by hatching and releasing yolk-sac stage larvae was advocated in both the US and Norway. Major cod hatchery programs were popular in both countries until the mid-20th century, despite lack of evidence that cod abundance increases with release of hatchery reared fish larvae; the potential value for such management procedures was repeatedly advocated throughout the 20th century. In Norway a still-ongoing beach-seine monitoring program was begun in the early 1900s to collect data on fall abundance of six-month-old demersal fish in 21 fjords along the Norwegian Skagerrak coast. Chan, Stenseth, Kittilsen, Gjøster, Lekve, Smith, Tveite and Danielssen (2002) used these data in conjunction with hatchery data on numbers of yolk-sac larval cod released each spring in several fjords to test for an effect of the releases on the abundance of fjord cod populations. Using both a permutation test and a statistically derived time-series model for the cod's population dynamics, we found a slight, but statistically significant dependence of six-month-old cod abundance on the number of yolk-sac larvae released in four of the 16 fjords (for which we had adequate release and beach-seine data needed for carrying out the testing). However, using the time-series model, we did not find evidence of long-term increases in the abundance of mature cod in any of the fjords. We discuss our findings on the basis of the literature on marine fish population enhancement programs worldwide.

Modeling the population dynamical effects of pulse disturbances

Chan, Stenseth, Lekve and Gj oster (2002) focus on the population-dynamic effects of a pulse disturbance (a toxic algae bloom in the early summer of 1988) to cod (Gadus morhua) populations along the Norwegian Skagerrak coast. For this purpose we apply 'intervention analysis' (sensu Box & Tiao 1975). For the marine system studied, we estimated that the 1988-bloom killed 42% to 81% of the 0-group (6-month old) cods before the fall of the same year (the average effect estimated to be about 60%). The algae bloom is shown to have no detectable direct harmful effect on the 1-group cod (during the same fall), but was found to have a delayed effect (from 58 to 99%) on the survival of the 0-group (in 1988) to the 1-group (in 1989). The bloom is concluded to have no long-term effect on the cods. Our analysis is presented as a case study using intervention analysis within the field of ecology. Assuming a credible ecological model being available and the availability of long-term observational time series (as are the case for our marine system), we suggest that intervention analysis provides a valuable tool for simultaneously studying the unperturbed dynamical structure and the impact of the environmental disturbances.

Seasonality and population cycles: density dependence and density independence in Hokkaido voles

In spite being ecologically fairly similar, voles and lemmings show striking differences in population dynamics across populations and species. This range from the fairly erratic fluctuations in sub-arctic lemmings through the 3-5 year periodic cycles of northern voles to the rather stable populations in many populations at lower latitudes. In an attempt to develop and test a generic hypothesis to explain these differences, Stenseth, Viljugrein, Saitoh, Hansen, Kittilsen, Bolviken and Glöckner (2002) focus on the gray-sided vole (Clethrionomys rufocanus) on Hokkaido, Japan, which exhibits a distinct geographic pattern in population dynamics. A set of consistently sampled survey-data from 84 populations, each covering 30 years, provides an extensive source of comparative data. We use recent modeling approaches such as seasonal decomposition and state-space modeling of sampling error to provide a detailed picture of the population regulation structures in various areas of the island. Consistent with earlier studies, we find that density-dependent regulation is most strongly influenced by winter survival. In contrast to the winter-based density regulation, we find that the summer accounts for more density-independent stochastic processes. Furthermore, we demonstrate that differences in the levels of summer stochasticity accounts for most of the variation in the annual density independent variation across populations. Using the deduced structure of density dependence we demonstrate that changes in season length is sufficient to shift the dynamics from stable to cyclic. Altogether we have thus shown that both density-dependent and density-independent processes as well as seasonality are essential in dissecting geographic variation in population dynamics. In particular we have demonstrated that, given a second order annual process (which may be generated through a variety of underlying processes, about which there has been much controversy), the length of the seasons will be a determining factor for whether the population is fluctuating or not. This shed important new light on how the rodent cycles are generated V one of the classic problems in ecology.