

**Multi–annual oscillations in animal population size:
internal and external factors**

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Abstract

We find multi-annual oscillations in the population size of seven Canadian species, based on century-long time-series of fur harvests. Our statistical analysis aims to ascertain the factors that influence the dynamics of the populations hunted. To do so, we use the advanced spectral methods of singular spectrum analysis and multi-tapering. The dynamics of the seven populations have several common features. First, they share periodic components with periods of 2.5, 3 and 10 years. Second, all of them exhibit small-amplitude oscillations during the first decades of the century of record (1752–1849), and a much larger amplitude in the following decades. We determine the dominant frequency of each time-series at a given epoch, and the shifts between these dominant frequencies from epoch to epoch. A simple predator-prey model helps us interpret of these results. The two integer-valued periods, of 3 and 10 years, are likely to arise from the food-web interactions between the four species most involved in the predation. The 2.5-year period is attributed to the remote climatic effects of the tropical Pacific's quasi-biennial oscillation.

Keywords: population dynamics, spectral analysis, predator-prey models, environmental factors

Short title: Multi-annual population oscillations

1. INTRODUCTION

Ecologists have long used fur harvesting data as proxy records of animal population size (Odum 1953). Fairly long time-series of such data exist, even though their accuracy and representativeness of total population numbers is not entirely satisfactory. This length allows ecologists to test several assumptions about population dynamics and food-web organisation. From a very simple Lotka-Volterra model (Leigh 1968) to models based on both food supply and predation (Krebs *et al.* 1995), a variety of theoretical studies tried to explain the dynamics of fur-yielding mammal populations.

Considerable concern has arisen recently about the effects of global and regional environmental changes on animal populations. Several authors have documented the effects of environmental changes on the different species of an ecosystem. The purpose of our work is to help clarify the impact of external pressures on ecosystem dynamics.

Section 2 outlines the data selection procedure and the techniques we use for the spectral analysis of the time-series. In Section 3, the seven time-series are analysed with the help of the SSA-MTM Toolkit (Dettinger *et al.* 1995; Ghil *et al.* 2001).

To help interpret the results of this analysis we introduce in Section 4 a simple predator-prey model. The results of this model are compared with those of the spectral analysis to understand the main factors, external and internal, that influence the population dynamics. In Section 5, we discuss the distinction between the role of internal factors, mainly the interactions between the animals species, and the role of external factors, such as environmental variations.

2. DATA AND METHODS

Biological as well as physical effects act on population size over many years. Both types of effects may also involve delayed feedbacks. Therefore, the evaluation of their relative influence requires the use of long, continuous records. These are provided by fur-harvesting data. To deduce the corresponding animal population from the number of its furs harvested, one has to assume that the two are proportional. This hypothesis has been customary in the ecological literature so far, although more sophisticated sampling methods have been applied to recent fisheries data. These methods cannot be extended to the limited records from the past that span a full century.

The seven data sets analysed here are fur-harvesting records from the Hudson Bay Company (Jones 1914). Each time-series is almost one century long (98 years for most of them). The exact date for the beginning and end of each time-series are given in Table 1. The length of these series allows us to study interannual (*i.e.*, year-to-year) and interdecadal (*i.e.*, decade-to-decade) variations in species abundance, whether due to internal population dynamics or to environmental effects. Some of the species interact by predation, other by competition.

[Table 1 near here, please.]

All seven time-series have a non-linear trend whose apparent period is about twice the series' length. This trend couldn't be studied therefore with the records available. The elimination of this trend and the extraction of the signals' oscillatory components were done with the help of the SSA-MTM Toolkit.

The SSA–MTM Toolkit (Ghil *et al.* 2001; <http://www.atmos.ucla.edu/tcd>) supports four different spectral methodologies: classical Fourier analysis, singular spectrum analysis (SSA), multi–taper methods (MTM), and maximum entropy methods (MEM). The toolkit provides a battery of statistical significance tests for each method, as well as visualisation tools that help compare results between the methods. For the time–series under examination, we found SSA and MTM to be the most useful. More complete descriptions of the two, as well as of the entire toolkit, can be found in Dettinger *et al.* (1995), Ghil *et al.* (2001), the toolkit’s User Guide (<http://www.atmos.ucla.edu/tcd>), and references therein.

(a) Singular spectrum analysis (SSA)

SSA is based on the Karhunen–Loève theorem in the time domain. Colebrook (1978) pioneered the application of the key ideas involved in SSA to ecological time–series. SSA is a non–parametric method, like the Blackman–Tukey method of Fourier analysis and unlike MEM. This means that it does not try to fit the series according to an assumed model, but uses a data–adaptive set of basis functions. This is done in three basic steps:

–The time–series $\{X(t): t=1, 2, \dots, N\}$ is embedded in a vector space of dimension M by considering M lagged copies $\{X(t-j): j=1, 2, \dots, M\}$. The choice of M involves a trade–off between the number of spectral features detected and their reliability (Vautard *et al.* 1992). In the case of the present study, the factors potentially influencing the system can have long–term effects. Consequently, we took $M=30$ ($\sim N/3$).

–The $M \times M$ lag–covariance matrix \mathbf{C}_D of the time–series (Broomhead & King

(1986) is defined by

$$\mathbf{C}_D = N^{-1} \cdot \mathbf{D} \cdot \mathbf{D}^T. \quad [1]$$

For a true covariance matrix, the eigenvalues are necessarily non-negative and any small negative eigenvalue indicates problems of under-sampling due to the shortness or non-stationarity of the time-series analysed.

The \mathbf{C}_D matrix is diagonalised and its eigenvalues λ_k are ranked in decreasing order. Each λ_k gives the variance of the time-series along the associated eigenvector \mathbf{E}_k ; these eigenvectors are called empirical orthogonal functions (EOFs) in the climate dynamics literature.

Potential noise sources are either intrinsic, *i.e.*, arising from the ecological and environmental processes manifest in the time-series, or extrinsic, *i.e.*, arising from the measurement process. The signal is normally associated with the leading eigenvalues and exhibits a negative λ_k -vs.- k slope, while the noise is associated with the flat "tail" of the spectral plot (Vautard & Ghil 1989). The SSA-MTM Toolkit contains a number of more sophisticated tests for distinguishing signal from noise (Allen & Smith 1994, Ghil *et al.* 2001)

For each EOF \mathbf{E}_k with components $\{E_{kj} : j=1, \dots, M\}$ in the lag-domain, one has the corresponding k -th principal component :

$$A_k(t) = \sum_{j=1}^M x(t+j) E_{kj} \quad t = 0, \dots, N-M. \quad [2]$$

With SSA, one can study separately the contributions of the different components to the time-series. Thus one can study separately the signal portion or certain oscillatory components (see below).

Choosing a subset of K eigenelements associated with the components of

interest, the corresponding principal components can be used to reconstruct the components R_k in question,

$$R_K(t) = \frac{1}{M} \sum_{k \in K} \sum_{j=1}^M A_k(t-j) E_{k,j}, \quad t = 0, \dots, N. \quad [3]$$

One can use this formula with the components of the signal only – as determined by their dominant rank in the spectral plot, or by other more sophisticated criteria – as explained above. A diverse and powerful battery of tests is provided by the SSA–MTM toolkit for their reliable identification. In our fur–harvest records it was possible to detect dramatic changes in amplitude of the oscillations and rapid shifts in dominant frequency by restricting attention to the statistically significant components of the time–series.

(b) Multi–taper method (MTM)

MTM is based on the use of a set of optimal filters that prevent leakage from a narrow spectral band (Thompson 1982). Like SSA, it presents the advantage of being a non–parametric method. The optimal tapers are the eigenfunctions of a Rayleigh–Ritz problem for the minimisation of spectral leakage outside of a frequency band of half bandwidth pf_R , where f_R is the Rayleigh frequency $f_R = 1/(N \Delta t)$ (Slepian 1978). The eigenvalues associated with the successive tapers have a sharp roll–off and the number K of useful tapers is always inferior to $2p-1$. The choice of this number K of tapers and of the bandwidth parameter p determines a trade–off between the frequency resolution and the stability of the spectrum (Ghil *et al.* 2001). Here, we take $K=3$ and $p=2$.

The global spectrum is given by the weighted sum of the K different

eigenspectra:

$$S(f) = \frac{\sum_{k=1}^K \lambda_k |Y_k^2(f)|}{\sum_{k=1}^K \lambda_k}. \quad [4]$$

Here $Y_k(f)$ is the discrete Fourier transform of $X w_k$, $X(t)$ being the time-series and $w_k(t)$ being the k -th taper. To better understand this, let us assume that the time-series can be split into two parts, one being a purely periodic signal and the other being the noise:

$$X(t) = \mu e^{ift} + \xi(t). \quad [5]$$

The Slepian (1978)–Thompson (1982) spectrum in eq. [4], above, as well as the associated, amplitude-independent F -test for the peaks, is truly optimal for pure oscillations embedded in white noise. The amplitude μ of the signal is estimated using a least-square fit in the frequency domain:

$$\tilde{\mu}(\tilde{f}) = \frac{\sum_{k=1}^K U_k(0) y_k(\tilde{f})}{\sum_{k=1}^K |U_k(0)|^2}, \quad [6]$$

where $U_k(f)$ is the discrete Fourier transform of the eigentaper w_k .

Using the combination of MTM methods and statistical significance tests available in the SSA–MTM Toolkit, one can find the periods, amplitudes and phases of a signal's periodic or quasi-periodic components. The advantage of the method is that it is able to find low-amplitude signals in relatively short time-series, with a high degree of statistical significance. For a sampling rate Δt , the maximum frequency that can be found is the Nyquist frequency $f_N = 2 / \Delta t$.

Following the SSA–MTM toolkit's philosophy of method inter–

comparison, the MTM results are used here to confirm the frequencies given by the SSA method and to evaluate their contribution to the time-series under investigation. We determine the main frequencies of our signals, using first Monte-Carlo SSA (Allen & Smith 1994) and then MTM. The reconstruction of the doubly-validated oscillatory components by using the SSA method allows us determine the span of time where either frequency is dominant and the position of the shifts from one frequency to another.

3. RESULTS OF THE TIME-SERIES ANALYSIS

Because of the space constraints, only a subset of selected results can be presented here. Figure 1 displays the time-series of the bear population. During the first half-century, the amplitude of variations is very low. This amplitude becomes significantly larger during the final half-century. This large and fairly sudden increase in the amplitude of the population cycles occurs for all seven animal species (not shown). For every species, the sudden change occurs almost simultaneously, in the first years of the nineteenth century.

[Figure 1 near here, please.]

Figure 2a shows the scree diagram λ_k -vs- k for the lynx population. In this case, an obvious gap exists between the four leading eigenvalues, which capture the lion's share of the variance (notice the logarithmic scale on the ordinate), and the remaining ones. This suggests that the former contain most of the signal, while the latter represent the fairly flat noise background (Vautard & Ghil 1989).

[Figure 2 near here, please.]

The four leading eigenvalues fall into two well-separated pairs of nearly

equal eigenvalues. A number of additional statistical tests (not shown) confirm that each pair is associated with a periodic oscillation. For the other six time-series, the scree diagrams (not shown) also indicate a clear decomposition between the signal and the noise. In every case, the signal part contains two or three pairs of nearly equal eigenvalues, each of which captures an oscillatory mode.

The SSA-MTM Toolkit contains a number of methods to capture the frequency or frequencies associated with an oscillation and estimate its statistical significance. One of these methods is Monte-Carlo SSA (Allen & Smith 1994). In this method, a single main frequency f_k is associated with each eigenvector \mathbf{E}_k , by least-square fitting a sinusoid to it. The eigenvalues are then displayed *vs.* the associated main frequency (λ_k -*vs.*- f_k plot, figure 2*b*), rather than the order (as in figure 2*a*).

The associated error bars are computed by a Monte-Carlo procedure with respect to a red-noise background that has the same variance and lag-one autocorrelation as the time-series being analysed. If the eigenvalue for a given frequency is above these error bars, it is statistically significant. In the example of the mink population (figure 2*b*), the two frequencies that are significant at the 95% level are 0.11 and 0.33 year⁻¹; the corresponding periods are 9 and 3 years (see also Table 1).

We cross-check the spectral peaks obtained by Monte-Carlo SSA with the MTM version of Mann & Lees (1996; not shown). The two sets of results agree overall very well for all seven species. Occasionally, slight differences arise for minor peaks that are significant at the 90% level in one analysis but not the other .

For every one of the seven species we computed the SSA scree diagram as well as the Monte–Carlo SSA and MTM spectra, which are shown in figures 2*a* and 2*b* for only one selected species each. The frequencies retained in the subsequent discussion for each animal population are significant at the 90% level or higher in both the Monte–Carlo SSA and MTM spectra. The results of the computations are summarised in Table 1.

Three main periodicities appear for all the populations. The longest of these is of 9–10 years and is found for five species out of seven. The 3–year period is found for all the populations, except the lynx. The 2.5–year period is found for all the species except the muskrat.

The 10–year period is well–known in animal population dynamics. Keith (1963) outlined the possible reasons for such a period and additional results were provided recently by Krebs *et al.* (1995), among others. The 3–year period has been reported in a number of works about rodents and their predators (Seldal *et al.* 1994; Turchin *et al.* 2000). The 2.5–year period appears to be new and we shall return to it in Sections 4 and 5.

SSA reconstruction [3] of the signals’ oscillatory components provides complementary information about these periodicities’ relative importance in time. It allows us to know which periodicities dominate in the dynamics of the population under study at a given moment of the record.

Let us for example consider the mink population. The signal corresponding to this time–series can be split into three periodic components (see Table 1), two of them (0.1 and 0.33 years^{-1}) being much more significant than the third one (0.4 years^{-1}). The reconstruction based on the first two eigenelements gives the 3–year oscillatory mode present in the time–series. The reconstruction

using the third and fourth eigenelements captures the variation in amplitude and phase of the 10–year mode along the record.

Figure 3*a* shows the superposition of these two reconstructions. Both modes grow in amplitude with time. Still, the 10–year mode dominates the first half of the record, while the 3–year mode dominates the second half.

[Figure 3 near here, please.]

For each of the six other populations we plotted the counterpart of figure 3*a* (not shown) and assessed from it the relative contributions of the periodicities involved. In figure 3*b*, each animal species is shown as a vertical time bar and several horizontal date marks are drawn. The dominant cycles are designated by different types of hatchings and time intervals where neither cycle dominates are left blank.

Our results so far exhibit three major points that require an explanation:

- (i) The amplitude of the population variations changes dramatically between the latter half of the 18th century and the early half of the 19th.
- (ii) All seven population records contain the same periodicities; two of these are known and appear to be well approximated by an integer number of years (3 and 10 years), the third one (2.5 years) is neither.
- (iii) The repeated shifts from one periodicity being dominant to another one in each time–series.

We seek an explanation of these three major observations by constructing and analysing a simple dynamic model of interactions between species and with external stresses.

4. DYNAMIC INTERPRETATION OF THE RESULTS

(a) Variation in the oscillations' amplitude

We propose here to link the striking change in amplitude of the observed oscillations to a slight variation of environmental conditions. To do so, consider the very simple model:

$$\begin{aligned}\frac{dx}{dt} &= x \left[r \left(1 - \frac{x}{\alpha} \right) - \frac{y k}{\beta + x} \right] + C, \\ \frac{dy}{dt} &= y s \left(1 - \frac{h y}{x} \right),\end{aligned}\tag{7}$$

of the interaction between a prey population x and its predator population y . The parameters r and s represent the birth rate of prey and predator respectively, while α stands for the carrying capacity. The predation function is of Holling type, h is the rate of mortality of the predator, and k is the rate of predation exerted on the prey.

All parameters are strictly positive, except C , which stands for the effects, whether negative or positive, of external pressures on the prey population; C is zero if $x=0$ but is otherwise assumed to be independent of x . Our model [7] is close to harvesting models used in fisheries management; see for example Bassan & Fogarty (1997), Bhattacharya & Begum (1996), and Cooke & Nusse (1987). Our C , however does not depend here on the prey density, as it typically does in the fisheries–management models. This is so mainly because the pressures exerted on the prey population x considered here are not exclusively of the "catching" type. We are interested in much more general stresses that include food supply and variations of climate, as well as hunting.

Non-dimensionalizing the model [7] gives:

$$\begin{aligned}\frac{du}{d\tau} &= u \left[(1-u) - \frac{av}{d+u} \right] + e, \\ \frac{dv}{d\tau} &= b v \left(1 - \frac{v}{u} \right),\end{aligned}\tag{8}$$

where

$$a = \frac{k}{hr}, \quad b = \frac{s}{r}, \quad d = \frac{\beta}{\alpha}, \quad e = \frac{C}{r\alpha}, \quad u = \frac{x}{\alpha}, \quad v = \frac{ky}{\alpha}, \quad \tau = rt.\tag{9}$$

The equilibria associated with the system [8,9] were studied using the CONTENT software (Kuznetsov & Levitin 1997). We are most interested in the effects of the environmental–pressure parameter e on the model solutions. An oscillatory instability occurs at $e=e_H$; if $e>e_H$ the equilibrium is stable. For $e\leq e_H$, the unstable equilibrium gives rise to a limit cycle. The larger the difference e_H-e , the larger the amplitude of the oscillations (see figure 4a). The amplitude is roughly proportional to the square root of the difference e_H-e , as expected for a Hopf bifurcation (Guckenheimer & Holmes 1983).

[Figure 4 near here, please.]

For comparison, let us take two animal populations linked by predation in our Canadian data set: the mink (predator) and the parchment beaver (prey). If we plot the reconstruction of their common dominant mode, which is the 3–year mode (see Table 1), along the axes of figure 4b, we obtain an outward–circling spiral. This corresponds to a limit cycle of approximately constant period, whose amplitude is increasing in time.

The very simple model [8] shows that, as the external conditions deteriorate even slightly, the amplitude of both the predator and the prey’s

population cycles increases. The large change in the oscillations' amplitude for all the population records studied here could therefore be linked to a deterioration in Canada's environmental conditions in the early 1800s. This deterioration might include increased hunting pressures, as well as the indirect effects of the Tambora eruption (Briffa *et al.* 1998; Stothers 1984).

Our simple model suggests that this combination of environmental factors could explain the observed increase in the oscillations' amplitude.

(b) Multiple cycles and their shifting dominance

The seven animal species under study differ in a number of aspects, especially in their way of life. Based on food–web interactions, we can divide these seven species into two groups.

The first group contains three species that are relatively extraneous to the predation interaction: bears, wolverines and, to some extent, beavers. Wolverines are mostly scavengers. The bears hunted on behalf of the Hudson Bay Company are mostly omnivorous. Beavers are relatively isolated from the predation interaction as well. They are occasionally hunted by mink, lynx and wolves, but usually their habits and habitats protect them from their enemies.

The four other species —lynx, mink, muskrat and wolf— have strong predation links with the other animals in the ecosystem. Wolves and lynx are both super–predators, eating minks, muskrats and beavers. The mink is both a predator, for beavers, muskrats and even itself, and a prey, for wolves, lynx and itself. Finally, the muskrat has many predators, including minks, lynx and wolves.

In figure 3b, we have separated the two groups, with those that are only

weakly involved in food–web interactions to the left and those that have strong predator–prey interactions to the right. The ordering of the seven species is the same as in table 1, since the information in the latter complements that in the former.

Both groups contain time intervals during which the 3–year period (solid) is dominant. The only exception is the lynx, while for the muskrat the entire record exhibits shared dominance of the 3–year and 10–year periods (compare table 1). The 3–year period becomes dominant, in particular, during the last 30 or 40 years of the record (except for the lynx and the wolf). Thus, the 3–year cycle seems to arise internally, even when predator–prey dynamics are weak (see also figure 4*b*).

The 10–year cycle (slanted hatching in figure 3*b*) seems to be strong only for the populations in the group on the right (lynx, mink and muskrat). It may thus be due exclusively to a more intense form of predation than the 3–year cycle.

The 2.5–year cycle is the most surprising of the three. It seems to be in contradiction with the fact that all these mammal species produce offspring once a year. This non–integer period clearly points, therefore, to an extrinsic, possibly climatic cause. The evidence in figure 3*b* supports such an inference, as the 2.5–year period is only dominant in the species on the panel’s left–hand side. The only exception is its dominance in the wolf population, very early and very late in the record.

The El Niño Southern Oscillation (ENSO) phenomenon has a quasi–biennial period of about 2.5 years, as well as a longer period of four–to–five years (Ramusson *et al.* 1991; Ghil & Jiang 1998). The climatic impact of ENSO on parts of Canada has been fairly well documented (e.g., Ropelewski & Halpert

1989). Stenseth *et al.* (1999) have suggested a similar role for the North Atlantic Oscillation (NAO), but the periodicities associated with the latter seem closer to 7–8 years and 13–14 years (Moron *et al.* 1998; Ghil *et al.* 2001)

5. DISCUSSION

Our data set comprised seven records of near-century length (roughly 1750–1850) from Canadian mammal populations. Applying the advanced SSA and MTM spectral methods to these time series, we found a wealth of interesting behaviour shared by all the population sizes under study or by subsets thereof.

All the populations-size variations exhibit the well-known 3-year cycle (with the exception of the lynx). The 10-year cycle, also known from previous work, is only prominent in the four species that are strongly involved in predator-prey relationships. It thus seems to arise from their food-web interactions, as opposed to the external factors —such as sunlight flux or food-supply variability— reviewed by Keith (1963).

The fractional periodicity of 2.5 years had not yet been documented in mammal population-size records, as far as we know. It is highly significant in all but two of our seven species, including all of the three (beaver, bear and wolverine) that are not involved in strong predator-prey interactions. It is thus most likely to be caused by external factors. Of these, the remote climatic effects of the quasi-biennial oscillation in the tropical Pacific's coupled ocean-atmosphere system are the prime suspect.

We also analysed two other fur-harvesting records for coyote and mink (Keith 1963). They were only about 40 years long (1914–1953), but still

exhibited the same three periodicities (not shown). Of these, the 10-year period was the most significant, with weaker spectral peaks at 2.5 and 3 years.

Aside from the reliable, cross-validated detection of three separate oscillatory modes, our spectral methods allowed us to follow the variations of these modes in time. Both gradual and sudden shifts in amplitude and in frequency occur in our seven long records. To explore these, we constructed a predator-prey model with an environmental-pressure term built into it. The basic idea is related to some harvesting models used in fisheries management but has greater generality. It is also in tune with the work of Post *et al.* (1999), who studied the effects of temperature variations on a three-level food chain with wolves at the top-level.

In our model, small changes in the environmental-pressure parameter e result in a Hopf bifurcation from a stable steady solution to a stable oscillatory one. The amplitude of this oscillation grows as the distance $|e - e_H|$ in the parameter value e away from the critical value e_H increases. This matches the gradual increase in the amplitude of the 3-year cycle in the beaver and mink populations (see figures 3a and 4a,b) in the second half of the data set. Changes in the frequency of the model oscillations (not shown) also occur as the parameter e changes. The basic idea, as usual, is not new (see for instance Gamarra & Solé 2000) but its fairly detailed documentation with several species adds an unprecedented degree of plausibility to it.

A fairly sudden increase in the oscillation's amplitude —and in total variability as well— occurs for all species in the early 19th century. While we have no complete explanation for this striking phenomenon, external pressures are quite likely to have played a role. These may have included climatic factors as

well as hunting pressures. The ecological system's food–web interactions, though, seem to play a key role in amplifying the effects of environmental pressures.

It is important, therefore, to study the effect of environmental changes not just on a single species but on an ecosystem as a whole.

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Figure Captions

Figure 1: Number of bears' furs harvested between 1752 and 1849, based on digitising the Hudson Bay Company records. The number of furs is supposed to be proportional to the number of bears. The main trend has been subtracted from the original data, using SSA reconstruction (see text for the details).

Figure 2: Singular–spectrum analysis (SSA) results for the lynx and mink populations.

(a) Scree diagram for the lynx population record, displaying the amount of variance λ_k in a given component k . Error bars show an *ad hoc* estimation of the sampling error (see toolkit User Guide for more details). The first four eigenvalues comprise the signal, and are well separated from the noise background of the remaining 26 components.

(b) Monte–Carlo SSA spectrum for the mink population. The error bars are based on a chi–squared test against a red–noise background (see text and references for details). Only the pairs of eigenvalues above the error bars are statistically significant at the 95% level or higher; for this population only the 0.11-year^{-1} (9–year period) and 0.33 year^{-1} (3–year period) frequencies are significant (see also Table 1).

Figure 3: Relative importance of the different oscillatory modes in the seven animal populations

(a) Relative importance of the two main oscillatory modes (3 and 10–year periods) in the mink record, as a function of time: 3–year mode reconstruction

(solid) and 10–year reconstruction (dashed).

(b) Dominance of the different periodicities in time for each record. To simplify the diagram, only the two main periods have been taken into account for each animal population. Solid corresponds to dominance of the 3–year period, slanted hatching to the 10–year period, and horizontal hatching to the 2.5–year period. The blank parts correspond to equal importance of the two dominant modes.

Figure 4: Dynamical model results.

(a) Dependence of the size of the limit cycle on the environmental parameter e . The amplitude of the cycle increases as e decreases away from the Hopf bifurcation point e_H to zero.

(b): Orbit based on the reconstructed time–series for the parchment beaver (abscissa) and mink (ordinate) populations using the three–year mode common to both only. The amplitude of the cycles is increasing in time (see text for details).