Ann. Zool. Fennici 39: 161–171 ISSN 0003-455X
Helsinki 14 June 2002

Travelling waves in spatial population dynamics

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Received 28 February 2001, accepted 22 May 2001

Kaitala, V. 2002: Travelling waves in spatial population dynamics. — *Ann. Zool. Fennici* 39: 161–171.

The modern theoretical ecology has identified travelling waves as one of the appealing features suggesting that spatially structured populations may be self-organized. Using a set of population renewal models in one-dimensional space, generating regular periodic fluctuations, we seek possibilities to identify travelling waves superimposed on the local dynamics. The waves move at a known speed to one direction. The speed of the waves and the local population dynamics may be modulated by noise. Our study suggests that the indicators of travelling waves are, first, the overall level of synchrony among the populations is low, second, the frequency distribution of the synchrony measure is bimodal (i.e., it has low central tendency); and third, there is either no or a weakly decreasing trend between the level of synchrony and distance between the populations compared. These features are most easily recovered by cyclic or quasi-periodic dynamics. Data has recently started to accumulate to indicate that the theory-anticipated travelling waves are also found in dynamics of natural populations.

Introduction

Theoretical ecology dealing with population dynamics is becoming increasingly interested in studying spatio-temporal patterns of spatially distributed sub-populations (Bascompte & Solé 1995, 1997, Tilman & Kareiva 1997). The central issue in this approach is that the local populations are coupled together with dispersing individuals. This research has identified travelling waves as one of the intriguing determinants showing that spatially structured populations tend to be self-organized (Hassel *et al*. 1991, 1994, Bascompte & Solé 1995, Perry 1995). Spatial interactions in population dynamics — through dispersal and/or external forcing —

have been shown to create a rich variety of spatial patterns changing in time in cellular automata and coupled map lattice-structured population models (Hassell *et al*. 1991, 1994, Comins *et al*. 1992, Solé *et al*. 1992, Boerlijst *et al*. 1993, Rohani & Miramontes 1995, Murray 1993, Solé & Valls 1991, just to mention a few pioneering examples).

The eye-catching patterns generated by spatially linked dynamics comprise a suite of spatial and temporal patterns including, e.g., travelling waves, spiral waves, standing waves, spiral chaos, rings, patches and crystal lattices. However, these patterns have rarely been reported in real data. Hence, predictions of the population dynamic models are an important challenge for empirical work on spatial scale of population renewal (Rohani & Miramontes 1995, Bascompte & Solé 1995).

Let us emphasize here that we do not intend to focus on the topic of ecological invasions (e.g., Shigesada & Kawasagi 1997), where the term "travelling wave" is used to refer to species expanding their distribution to new, previously unoccupied areas. Here good examples are the expansion of the distribution area of muskrat and American mink in Europe in the early 1900s (Shigesada & Kawasagi 1997). Such a wave could be rather referred to as "tsunami" for its potentially devastating effect on the environment. For many authors cited above, travelling wave or rather travelling waves, indicate temporal and spatial fluctuations of high and low population density areas in an organized way. One rarely observes population waves passing by, even though they may be due to dispersing individuals. Rather, population waves are generated as a consequence of common density-dependent processes being locally in differing phase. This may as well be due to spatial linkage between the local units, biotic interactions, or global and local noise affecting the sub-units differently. It is very likely that all the components mentioned are involved. Often it is assumed in this context that the waves are moving from one place to another. That is, they posses certain features, such as speed and direction.

Not until very recently, have data become to substantiate that travelling waves are not only a privilege of theoreticians but are also found in dynamical structures of natural populations. The few first examples include vole dynamics in Finland and France (Ranta & Kaitala 1997, Kaitala & Ranta 1998) and in Scotland (Lambin *et al*. 1998, Mackinnon *et al*. 2001). These data and their analyses are the only research which have explicitly addressed the presence of travelling waves in data on real animal population dynamics. However, there are good reasons to propose that the classical Hudson Bay Company's fur return data on Canadian lynx and snowshoe hare indicate features that strongly suggest the presence of travelling waves (Ranta *et al*. 1997a, 1997b, 1997c, 1998, 1999, Stenseth *et al*. 1999) as is perhaps also the case with some grouse populations (Moss *et al*. 2000).

Self-organized structures in dynamics of spatially coupled populations are usually determined on the basis of visual inspection, although the need for new analytical and statistical approaches for distinguishing spatial order from randomness has been recognized already some time ago (Hassell *et al*. 1994). Thus, if the spatial population dynamics show wave patterns, identifiable to the human eye, then the patterns are considered to be a product of self-structuring process in action in the spatially set population. Quantitative measures of identifying travelling waves are still scanty (Ranta & Kaitala 1997, Kaitala & Ranta 1998, Lambin *et al*. 1998, Mackinnon *et al*. 2001).

This all prompts us to develop means to uncover the conditions under which travelling waves will be generated and especially when they will become visible by using objective analytical tools. Also, the questions of relevance are how sophisticated tools should be used and what kind of data one has to have in order to be able to infer the impact of travelling waves affecting dynamics of local populations. Admitting the complexity of the problem, we have made some simplifications. We shall delimit ourselves to study the problem in three dimensions: continuous *population size* at any given discrete point of *time* in discrete *one-dimensional space*. That is, our sub-populations, obeying known temporal dynamics, are all arranged on a line. Of course, a spatial arrangement of population sub-units like this is rather arbitrary and may not find a perfect match in nature. However, seeking for statistics capable of detecting the presence of travelling waves calls for simplifying the setting where the population dynamics and the travelling waves superimposed on the local populations are known. One can conclude that progress is made only if the tools used are capable of objectively pointing out that the observed spatial pattern calls for the presence of travelling waves.

Population data and measures of synchrony

Tools for detecting and identifying travelling waves in population dynamics are badly needed. In fact, this holds true for being objectively able to identify any kind of moving regular pattern that occur in space. From the onset it is obvious that the population data needed to prove the existence of the waves have features that are rare for time series collected from nature. The key features include that there is information for a focal species on fluctuations of population densities in geographically replicated locations over a long enough time-span. This requirement is rarely met in the tradition of ecological research. Ecological time series when covering long periods of time often originate from a single site, or they are from several locations but cover short time periods (Powell & Steele 1995). In addition, ecological time series are not only short but they are swamped with noise. With long time series the sampling method will often be changed over the time, not to belittle the effect that the environment itself is likely to vary over a long time-span.

To stress that we are on shaky ground when looking after the signs of travelling waves, we shall also point out in the very beginning of our exploration the problem of scale. There is little information of what is the correct geographical scale for data on dynamics of populations to be used in the hunt for travelling waves. It is obvious that if the scale is too small, the wave may remain undetected because all the local time series are samples of the same stage of the wave passing by. The other extreme is that the sampling localities are so widely spaced out that they miss most of the peaks of the waves. This binds curiously together all the relevant components involved in studying travelling waves: length, speed and direction of the wave, and the features of the underlying population dynamics. We shall make here a clarification due to cyclic population dynamics. The length of a wave (measured from top to top in space) may be regarded as a function of travelling speed and period length (measured from top to top in time) of the underlying dynamics.

In a most idealized case, data on noiseless fluctuations of the focal species are long-term observations from a dense enough geographical grid. Unfortunately, such data do not exist! Therefore, as a starting point, we limit ourselves to simulated time series that will fulfil our three criteria. For these data, we will compute simple statistical measures, which we think are of relevance when seeking for indications of presence of travelling waves modulating local dynamics.

The first measure is cross correlation (e.g., Chatfield 1984), with time lag 0. This is a standard tool to assess the level of synchrony in dynamics between any pair of populations. Large positive correlation coefficients indicate that the populations are fluctuating in synchrony. Large negative values indicate fluctuations of the two populations to be out of phase. And cross correlation close to zero suggests that the populations do not have much in common in their temporal variation.

As a measure of general level of synchrony, cross correlation is somewhat problematic for two reasons. Once the number of populations compared exceeds two, the correlation coefficients calculated in pairs between all n subpopulations are not statistically independent. This is, however, a minor issue if the cross correlation coefficients are used as descriptive means only, and no interference of statistical significance is made. The problem of non-independence of data points can be overcome by resampling techniques (Ranta *et al*. 1995b) or by other special methods (Koenig 1999).

Our second measure is the central tendency of the frequency distribution of synchrony measures (Ranta *et al*. 1999). To measure the central tendency we aggregate the cross correlation coefficients into 0.1 bins ranging from –1 to 1. The bin containing the average of the frequency distribution of the synchrony measures is discovered and the number of observations falling into this bin and one bin on both sides is then counted. The larger the proportion of all observations fall into these three bins, the higher the central tendency is. A frequently neglected feature in synchronous dynamics of populations is that the time-series may consist of two (or more) sets composed of groups of populations being internally in synchrony but the different sets fluctuating out of phase. This would yield to a bimodal frequency distribution of cross correlation coefficients, one mode close to high positive values and the other one close to high negative values, the average level of synchrony falling close to zero. The central tendency would then also be a low value indicating the bimodality. Of course, a uniform distribution of correlation coefficients from –1 to 1 will have a mean close to zero and a low central tendency. We are aware of this, and have taken care to report bimodal frequency distributions only.

The third measure we use here is the relationship between the level of synchrony and distance among the population sites compared. An empirical finding in many data sets on population dynamics, but not in all, is that the overall level of synchrony levels off with increasing distance among the populations compared (Ranta *et al*. 1995a, 1995b, 1997a–d, 1999). As these three measures, average synchrony, central tendency of synchrony and distance-dependency of synchrony, are often used to characterize synchronous dynamics of populations, we expect them to serve as tools in identifying travelling waves superimposed on local population dynamics.

Dynamics of populations with travelling waves

To begin with, we assume that a total of *n* local populations are located on a one-dimensional vector. The spacing-out between the adjacent cells in the string is one distance unit. Our exploration of detecting the presence of travelling wave superimposed on dynamics of local populations goes in three steps with increasing complexity. The first one is the most naïve and the reason for it being included is that we would like to be assured of the capacity of simple tools in being able to identify the presence of travelling waves. To this end, we shall generate population dynamics based on the sine function as follows:

$$X_{t+1}^{i} = \sin\left[\frac{2\pi\left(t+\bar{\mu}i\right)}{P}\right] + \varepsilon_{t+1}^{i}. \tag{1}$$

Here X_{t+1}^{i} refers to the size of the i^{th} population at time $t + 1$, while P is the period length of the transformed sine function. The term μ is the speed of the travelling wave, always with the speed $0 < \mu$. The notation $\bar{\mu}$ indicates that the speed of the wave can also be from a stochastic distribution with known characteristics. Thus, the sine function generates cyclic dynamics with precise periodicity against time, and the speed of the travelling wave displaces the periodic dynamics between the adjacent populations. Note that μ allows fractional, non-integer wave speeds (*see below*). Finally, the error term ε can be used to introduce noise into the local dynamics. Here the noise is drawn from normally distributed random numbers with zero mean and 0.2 as variance, unless otherwise stated. Let us emphasize that the population dynamics generated by Eq. 1 is not based on any biological assumptions. It only attempts to mimic cyclic dynamics with precisely known characteristics when not disturbed too much with noise. The usage of such naïve dynamics will find justification below.

Next, we shall present a more realistic model for the dynamics of local populations by making use of the Ricker dynamics (Ricker 1954). The Ricker dynamics has the following expression

$$X_{t+1} = X_t\exp[r(1 - X_t/K)] + e_{t,G} \tag{2}$$

where parameter r (here $1 \leq r \leq 4$) is the growth rate and K is the carrying capacity. If not otherwise stated $K = 100$ for all sub-units. The range of r used generates dynamics from stable to chaotic fluctuations (May 1976). The additive global noise $\varepsilon_{t,G}$ is drawn from random numbers with normal distribution with 0 and 0.2 as mean and variance.

To get travelling waves with Eq. 2, we first generated 1000 time steps of data for each parameter value, from these we selected a ran-

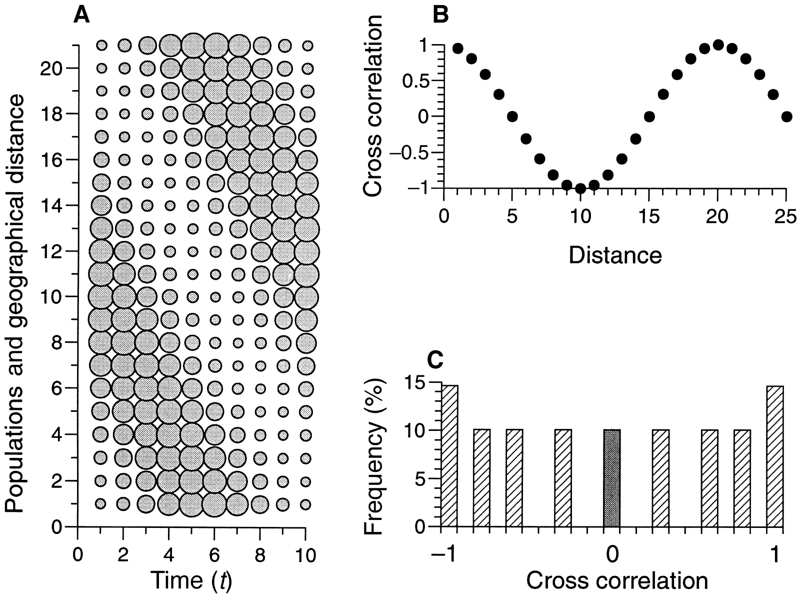

Fig. 1. Travelling wave and dynamics of cyclic populations. Equation 1 with $P = 10$, $\mu = 0.5$ is used to generate the data. Panel **A** shows how the wave is expressed both in time (x-axis direction) and in space (y-axis direction). The size of the dots indicates relative population size. Based on the selected parameter values it takes 10 time units to accomplish a full cycle in time, while with the speed $\mu = 0.5$ it takes 20 spatial units for the wave to repeat itself (the bottom row and the top row are matching; note that the wave is coming from top to bottom). Panel **B** gives the level of synchrony in population fluctuations against distance between the population pairs compared (the slight wobbling is due to the noise). The frequency distributions of all pair-wise synchrony measures is given in panel **C**. Note that ca. 10% of observations are in the bin including the average of the frequency distribution of the cross correlation coefficients. Thus the central tendency is low and the bimodality is obvious.

dom starting point τ so that $200 < \tau < 900$. From this point onwards we build up local population dynamics for $k = 100$ time units so that we have for the running index i as follows: $\tau + i$, $\tau + k + i$, with ranging from 1 to n. Note that by doing so with the Ricker dynamics we generate a wave speed $\mu = 1$. On top of the dynamics generated by Eq. 2, we added sub-population specific local noise, $\varepsilon_{t,L}$ which was drawn from random numbers with the same parameters as $\varepsilon_{t,G}$.

As the third step of our exploration we, for obvious reasons (*see* Results), restricted ourselves to the dynamics generated with Eq. 1. We focused on uncovering the significance of noise in wave speed and in the temporal dynamics to the performance of the wave-detection tools. We are also interested to see how the size of the data set (number and length of the available time series) may influence the detection of the travelling wave.

Results

We first examine how the three measures of synchronous dynamics behave when selecting the parameters of Eqs. 1 and 2. To our mind, there should be no doubt that a wave in population dynamics travels throughout the n populations with a known speed and with limited noise (Figs. 1 and 2). The speed of the wave in Eq. 1 is $\mu = 0.5$, while the period of the generated population dynamics was set to $P = 10$. This makes a single wave take 20 distance units to repeat itself in space. The speed of the wave in the Ricker equation is $\mu = 1.0$, and with a two-point periodicity ($r = 2$) the populations in the spatial dimension are out of phase every second distance unit. The progress of the wave in space is clearly visible in the spatio-temporal graphs (Fig. 1A and Fig. 2A). For both dynamics, showing a clear pattern of a travelling wave, the

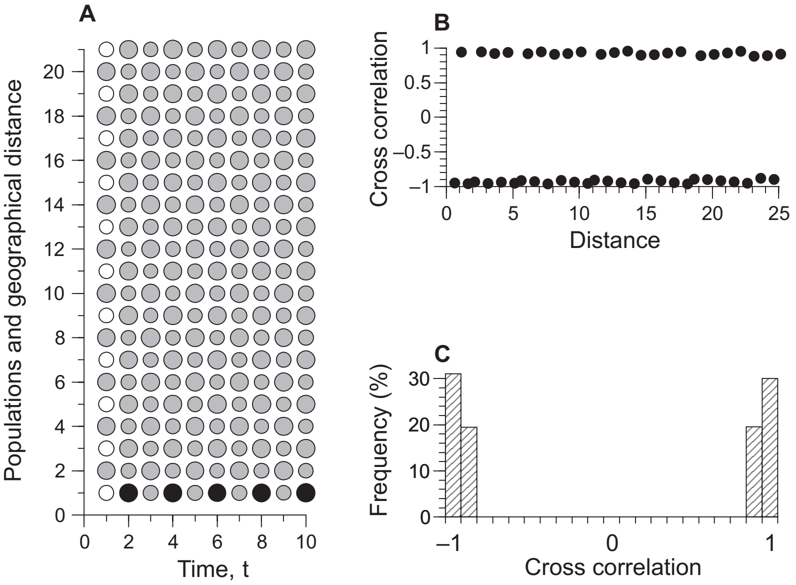

Fig. 2. Travelling wave and dynamics of populations obeying the Ricker model, Eq. 2, with $r = 2$. Panel **A** shows how the wave is expressed both in time (x-axis direction) and in space (y-axis direction). The size of the dots indicates relative population size. The two-point cycle travels with a speed of $\mu = 1$. For clarity the smallest populations in the geographical direction are indicated with white (only the first time step) while in the temporal direction the population highs are indicated with black (only the first population). Panel **B** gives the level of synchrony in population fluctuations against distance between the population pairs compared (the slight wobbling is due to the noise). The frequency distributions of all pair-wise synchrony measures is given in panel **C**. Here the central tendency is extremely low (0% of observations fall into the bin of the average synchrony) and the bimodality is striking.

level of synchrony against distance echoes both the speed of the wave and the period of the dynamics (Fig. 1B and Fig 2B). However, there is no clear correlation between the level of synchrony and distance (Pearson $r = -0.004$, $r = 0.017$, panels B in Fig. 1 and Fig. 2, respectively). Also, in both cases the average level of synchrony is very low (–0.009 and –0.01), as is also the central tendency, which is 10.1% in Fig. 1C and 0% in Fig. 2C.

In these two examples, by parameter choices in Eqs. 1 and 2, the temporal dynamics has a strong periodic component (10 year cycle, and two-point cycle), and there should be no doubts about the presence of the travelling wave in the dynamics. It appears that all the three measures, used when assessing the level of synchrony in real data, have a bearing in finding the signature of travelling wave in dynamics. We shall tentatively suggest that with a travelling wave the average of the cross correlations is close to zero, the central tendency of synchrony is low or even non-existent, and there is no distance-dependency in synchrony.

Our next exploration is in two parts. First, we explored the Ricker dynamics over the full range of the growth rate ($1 \leq r \leq 3.5$, $\mu = 1$). This is to analyze the relationship between the known dynamics (from stable to chaotic) and our potential wave indicators. Second, in Eq. 1 we varied the speed of the travelling wave from 0.01 to 0.5. This was to score how the potential wave indicators behave when the length of the travelling wave varies. The results indicate that with the Ricker dynamics the central tendency of synchrony achieves low values only within the range of r yielding periodic dynamics (Fig. 3). However, with the wave speed $\mu = 1$ the other two measures were invariably low through the entire range of r explored.

On the other hand, with the clearly cyclic dynamics all the three candidate measures for

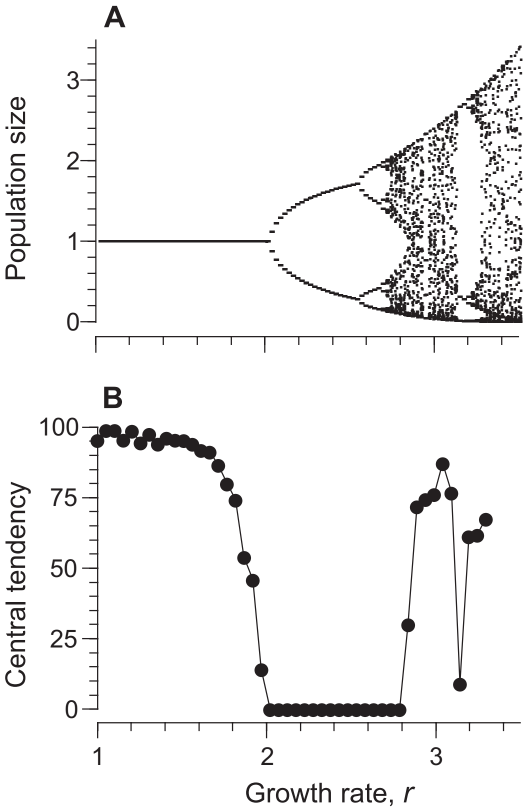

Fig. 3. — **A**: Bifurcation diagram for the Ricker dynamics with r as the bifurcation parameter ($K = 1$). Stable dynamic prevails till $r = 2$, with $2 < r < 2.6924$ the dynamics is periodic, while $r > 2.6924$ yields chaotic dynamic (May, 1976). — **B**: Central tendency (in percentage) of the frequency distribution of the synchrony values calculated between all pairs of populations. High values indicate that most values are associated with the mean of the frequency distribution of the cross correlation coefficients, whereas low values suggest bimodality of the frequency distribution. The central tendency is low within the periodic range of r (even with r close to 3.2, where there is a periodic window within the chaotic region).

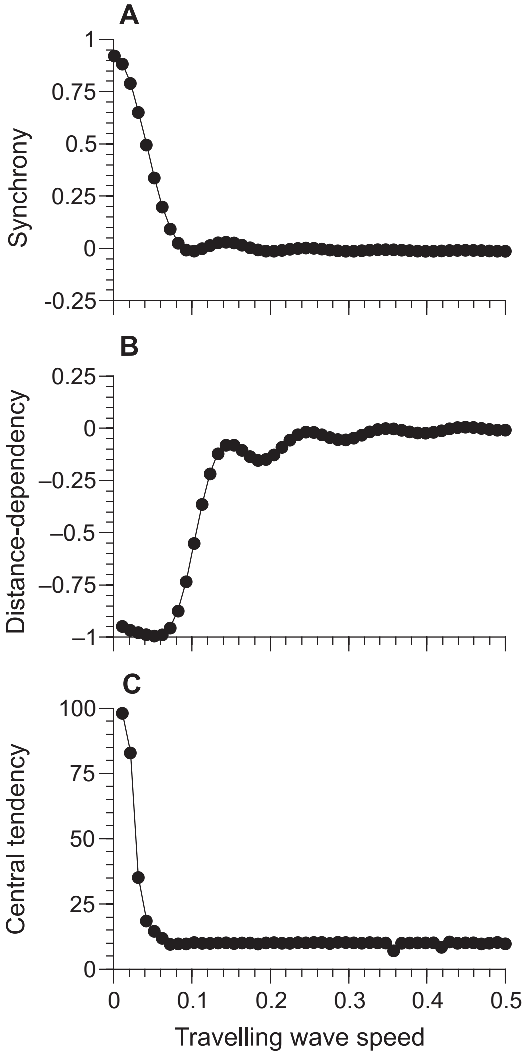

Fig. 4. The three synchrony measures and travelling wave in cyclic dynamics with period length $P = 10$ graphed against the speed of the travelling wave. When the speed is slow (i.e., there is a short distance between wave tops) synchrony is high (**A**), and has a strong negative distance dependency (**B**) and most cross correlations are close to the average cross correlation (**C**). However, when the wave tops spread-out with increasing travel speed of the wave, the average of the synchrony measured goes down because the frequency distribution of the cross correlation coefficients becomes increasingly bimodal (and we also lose the distance-dependency of the synchrony). This is because there begins to emerge two (or more) sets of populations mutually in synchrony, but the different sets being out of phase in their fluctuations.

detecting signatures of extant travelling wave indicated some diagnostic value. First, with a slowly moving wave the average synchrony level is high (Fig. 4A). There is a strong negative correlation between the level of synchrony and the distance among the populations compared (Fig. 4B). Furthermore, the central tendency of synchrony is high, that is, most cross correlation values are associated with the aver-

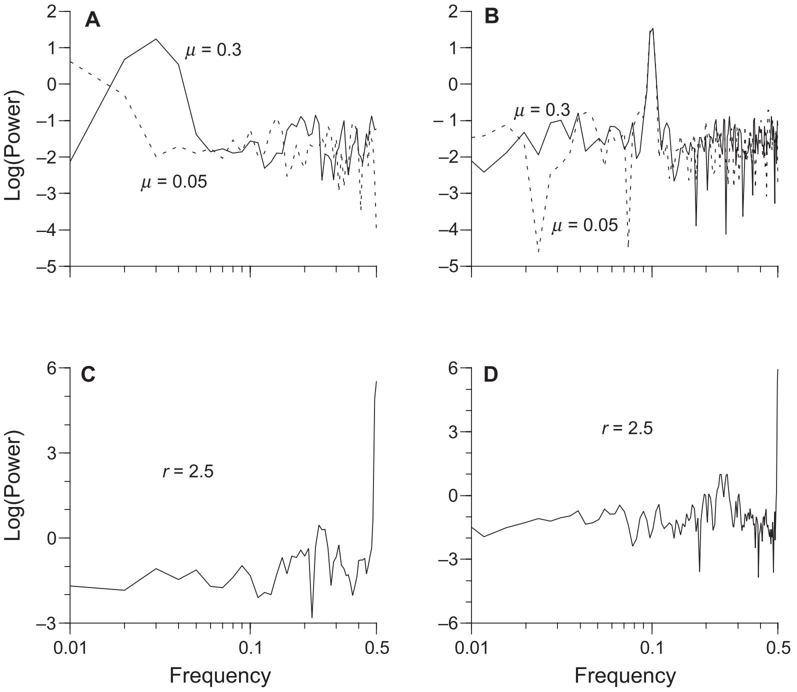

Fig. 5. Spatial and temporal power spectra of the cyclic dynamics, Eq. 1, and the Ricker dynamics, Eq. 2, with different parameter values. — **A**: Note that cyclic dynamics with wave speed μ = 0.05 does not generate travelling wave, whereas μ = 0.3 generates a wave the frequency of which is visible in the spatial power spectrum. — **B**: The ten-year periodicity (P = 10) is clearly visible in temporal spectra for both wave speeds (compare with Fig. 4). The Ricker dynamics (explored with two r values) does generate recognizable peaks with frequency 0.5 both in (**C**) the spatial and (**D**) temporal dynamics. However, with r = 2.8 (close to complex dynamics) the component of the 2 year periodicity is not that clear anymore (compare this with Fig. 3).

age (high) level of synchrony (Fig. 4C). However, when the travel speed of the wave increases both the central tendency and the mean of the cross correlation coefficients goes down, and the distance-dependency of the synchrony disappears (Fig. 4). We have explored the effect of the wave speed on possibilities to find the travelling wave with the cyclic dynamics using various values of P (from 3 to 50) and the major finding, as seen in Fig. 4, holds. That is, with a long-enough period in dynamics and a slow enough travelling speed of the wave, the three indicators reveal the presence of the traveller. Low central tendency, no distance-dependency and low average synchrony are the signatures of a wave that travels in the space.

One may justifiably ask why, with the Ricker dynamics, the two measures, average synchrony and distance-dependency of synchrony failed to identify the travelling wave (Fig. 3). This becomes especially interesting when all the three measures served well in identifying the presence of the wave with the cyclic dynamics (Fig. 4). To address this question we randomly selected one time point and analyzed the power spectrum over all sub-populations, thus covering 100 distance units. With the cyclic dynamics it become apparent that if the wave travels with too slow a speed (μ = 0.05; Fig 5A) the distance between the subsequent tops is so small that the wave periodicity component is not visible. However, with a sufficient travelling speed (μ = 0.3; Fig 5A) there are no problems to identify the presence of the wave with the help of power spectrum analysis. In the Ricker dynamics (r = 2.5) the spatial component of the travelling wave (dominance of the 0.5 frequency in Fig. 5C) is visible. In the temporal spectra both the 10 year cycle (frequency 0.1) and the two-point cycle (frequency 0.5) are clearly visible (Fig. 5B and

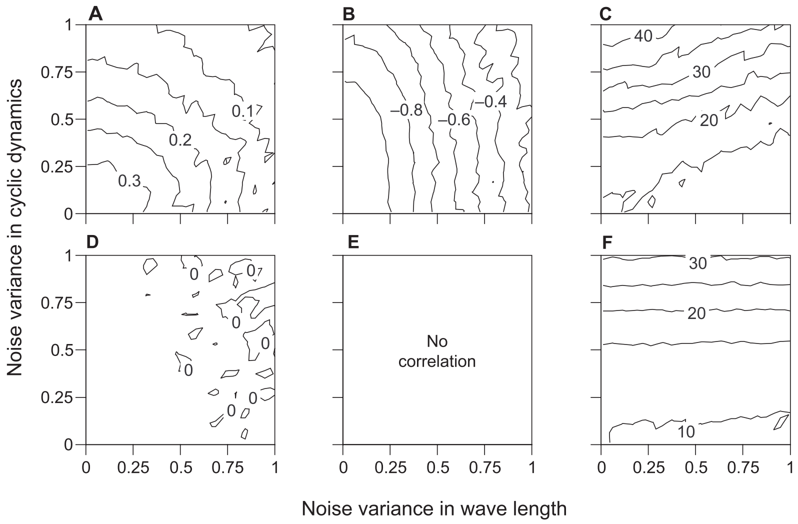

Fig. 6. Isoclines for average synchrony (**A**, **D**), distance dependency of synchrony (**B**, **E**) and central tendency of synchrony (**C**, **F**) in a noisy world with scanty data. The noise is both in the wave speed and in the process generating the cyclic dynamics. The top-row panes are for ten populations over 20 years, while the number of populations is 50 in the bottom row (note that in panel **E** the distance dependency of synchrony was zero for the entire range of the two noises explored).

D). We conclude that the failure of the average synchrony and the distance to recognize the wave is due to the high speed ($\mu = 1$) relative to the two-point cycle created with the r-values from 2 to 2.8 (Fig. 3).

The often unavoidable fact with biological time series is that they are short and topped off with noise and often there are not that many available. We shall next turn to these issues. We shall assume that the characteristics of the population dynamics are retained after Eq. 1. We now set $P = 6$ making it possible to achieve three population peaks (with matching number of lows) in 20 years of time. The speed of the wave is $\mu = 0.3$. For brevity, we shall vary only three variables. The number of populations is either $n = 10$ or $n = 50$, while the variance modulating the wave speed μ is drawn from random numbers from normal distribution with $\mu = 0.3$ as mean and the variance taking values from 0.01 to 1. Similarly, ε_t is a random number with zero mean while the variance ranges systematically from 0.01 to 1. We repeated the simulations 100 times for each parameter combination and will report the averages below.

The results are clear-cut. As expected, with limited data set ($n = 10$) the chances to locate a travelling wave are non-existent (Fig. 6A–C). However, with increasing number of populations included there are no problems in finding the signature of the travelling wave (area below the 10% isocline in Fig. 6F). Surprisingly enough, noise variance in wave length is of much lesser importance than noise in the dynamics (isoclines in Fig. 6F are almost parallel to the x-axis). We experimented also by increasing the time span to cover 100 generations but kept $n = 10$. As expected, the outcome is more sensitive to the number of populations examined than to the period covered. Of course, the time span has to be reasonable. With $n = 50$ but only ten generations of data, the isoclines move slightly upwards, without indicating any qualitative change in the results.

Concluding remarks

The current literature on population dynamics indicates an increasing interest in spatial patterns of population dynamics. With good reason we may ask whether there exist patterns in the spatial population dynamics that are essential for population ecology but are not visible in the potentially rich dynamics of single populations or in aggregated data. Further, if such patterns exist, can we detect spatial order from randomness by using analytical and statistical tools, instead of just relying on visual inspection? One possible spatial pattern is travelling wave, which also represents one form of self-organization in population dynamics (Ranta & Kaitala 1997, Kaitala & Ranta 1998).

We have made in this paper an attempt to develop means to uncover travelling waves data by using a set of objective analytical tools. These tools are average synchrony, central tendency of synchrony and distance-dependency of synchrony. We have argued that travelling waves are characterized by the following measures: the mean value of the cross correlation is close to zero, the central tendency of synchrony is low, and there is no distance-dependency in synchrony. It should be noted that as a tool these three measures should be considered as an entity — none of them alone is a strong enough evidence of the presence of travelling wave in the population dynamics.

In addition to the dynamics reported in this paper we also experimented with the second order autoregressive (AR2) model with all possible parameter values. We found the travelling waves every time when the model produced cyclic, periodic, or disturbed damped dynamics. As a whole, a travelling wave in order to be detectable, both visually and using our approach, needs to contain a clear periodical component in the dynamics.

Let us take as an example a spatial setting of random numbers spread over a space. Certainly, we cannot expect to detect any spatial order in this setting. However, the expected value of the cross correlation, averaged over the space, is zero, and there should be no distance-dependency observable in the synchrony. Nevertheless, the central tendency is very high, indicating that the synchrony distribution is concentrated around zero. Thus, it is the central tendency that makes the difference between a spatial wave and random order.

Our conclusions are valid only if the scale of the data is large enough. For too small a scale the mean value of the cross correlation may become positive, and the synchrony may begin to show distance-dependency. However, there is no basis for concluding that if we observe positive average synchrony and distance dependency we are dealing with a part of travelling wave.

Acknowledgements

Many thanks are due to Esa Ranta for his continuous interest in the topic.

References

Bascompte, J. & Solé, R. V. 1995: Rethinking complexity: modelling spatiotemporal dynamics in ecology. — *Trends Ecol. Evol.* 10: 361–366.

Bascompte, J. & Solé, R. V. 1997: Population cycles and spatial patterns in snowshoe hares: an individual oriented simulation. — *J. theor. Biol.* 187: 213–222.

Boerlijst, M. C., Lamers, M. E. & Hogeweg, P. 1993: Evolutionary consequences of spiral waves in a host-parasitoid system. — *Proc. Roy. Soc. Lond.* B 253: 15–18.

Chatfield, C. 1984: *The analysis of time series: An introduction*. — Chapman & Hall, New York.

Comins, H. N., Hassell, M. P. & May, R. M. 1992: The spatial dynamics of host-parasitoid system. — *J. Anim. Ecol.* 61: 735–748.

Hassell, M. P., Comins, H. N. & May, R. M. 1991: Spatial structure and chaos in insect population dynamics. — *Nature* 353: 255–258.

Hassell, M. P., Comins, H. N. & May, R. M. 1994: Species coexistence and self-organizing spatial dynamics. — *Nature* 370: 290–292.

Kaitala, V. & Ranta, E. 1998: Travelling wave dynamics and self-organization in a spatio-temporally structured population. — *Ecol. lett.* 1: 186–192.

Koenig, W. D. 1999: Spatial autocorrelation of ecological phenomena. — *Trends Ecol. Evol.* 14: 22–26.

Lambin, X., Elston, D. A., Petty, S. J. & MacKinnon, J. L. 1998: Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. — *Proc. Roy. Soc. Lond.* B 265: 1491–1496.

Mackinnon, J. L., Petty, S. J., Elston, D. A., Thomas, C. J., Sherrat, T. N. & Lambin, N. 2001: Scale invariant spatio-temporal patterns of field vole density. — *J. Anim. Ecol.* 70: 101–111.

May, R. M. 1976: Simple mathematical models with very complicated dynamics. — *Nature* 261: 459–467.

Moss, R., Elston, D. A. & Watson, A. 2000: Spatial asynchrony and demographic traveling waves during Red Grouse population cycles. — *Ecology* 81: 981–989.

Murray, J. D. 1993: *Mathematical biology*, 2nd edition.

— Springer-Verlag, Heidelberg.

Perry, D. A. 1995: Self-organizing systems across scales. — *Trends Ecol. Evol.* 10: 241–244.

Powell, T. M. & Steele, J. H. (eds.) 1995: *Ecological time series*. — Chapman & Hall, New York.

Ranta, E. & Kaitala, V. 1997: Travelling waves in vole population dynamics. — *Nature* 390: 456.

Ranta,E., Kaitala, V. & Lindström, J. 1997a: External disturbances and population dynamics. — *Ann. Zool. Fennici* 34: 127–132.

Ranta, E., Kaitala, V. & Lindström, J. 1997b: Dynamics of Canadian lynx populations in space and time. — *Ecography* 20: 425–431.

Ranta, E., Kaitala, V. & Lindström, J. 1998: Spatial dynamics of populations. — In: Bascompte, J. & Solé, R. V. (eds.), *Modelling spatiotemporal dynamics in ecology*: 47–62. Springer Verlag, Berlin Heidelberg.

Ranta, E., Kaitala, V. & Lindström, J. 1999: Spatially autocorrelated disturbances and patterns in population synchrony. — *Proc. Roy. Soc. Lond.* 266: 1851–1856.

Ranta, E., Kaitala, V. & Lundberg, P. 1997c: Population variability in space and time: the dynamics of synchronous population fluctuations. — *Science* 278: 1621–1623.

Ranta, E., Lindström, J. & Lindén, H. 1995a: Synchrony in tetraonid population dynamics. — *J. Anim. Ecol.* 64: 767–776.

Ranta, E., Kaitala, V., Lindström, J. & Helle, E. 1997d: Moran effect and synchrony in population dynamics. — *Oikos* 78: 136–142.

Ranta, E., Kaitala, V., Lindström, J. & Lindén, H. 1995b: Synchrony in population dynamics. — *Proc. Roy. Soc. Lond.* B 262: 113–118.

Ranta, E., Lindström, J., Kaitala, V., Kokko, H., Lindén, H. & Helle, E. 1997e: Solar activity and hare dynamics — a cross-continental comparison. — *Am. Nat.* 149: 765–775.

Ricker, W.E. 1954: Stock and recruitment. — *J. Fish. Res. Bd. Can.* 11: 559–623.

Rohani, P. & Miramontes, O. 1995: Host-parasitoid metapopulations: the consequences of parasitoid aggregation on spatial dynamics and searching efficiency. — *Proc. Roy. Soc. Lond.* B 260, 335–342.

Shigesada, N. & Kawasaki, K. 1997: *Biological Invasions: theory and practice*. — Oxford University Press, New York.

Solé, R.V., & Valls, J. 1991: Order and chaos in a 2D Lotka-Volterra coupled map lattice. — *Phys. lett.* A 153: 330–336.

Solé, R.V., Valls, J. & Bascompte, J. 1992: Spiral waves, chaos and multiple attractors in lattice models of interacting populations. — *Phys. lett.* A 166: 123–128.

Stenseth, N. C., Chan, K.-S., Tong, H., Boonstra, R., Boutin, S., Krebs, C. J., Post, E., O'Donoghue, M., Yoccoz, N. G., Forchhammer, M. C. & Hurrell, J. W. 1999: Common dynamic structure of Canada lynx populations within three climatic regions. — *Science* 285: 1071–1073.

Tilman, D. & Kareiva, P. (eds.) 1997: *Spatial ecology: The role of space in population dynamics and interspecific interactions*. — Princeton University Press, Princeton.