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Chaos far away from the edge of chaos: A recurrence quantification analysis of plankton time series

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ABSTRACT

Population abundance exhibits large fluctuations over time. Whether these irregular oscillations are driven by random environmental factors or a suite of deterministic mechanisms is an unsettled question in theoretical ecology. In this connection, one prevalent view is that at least part of the apparent disorder, which is known as deterministic chaos, is caused by deterministic interactions between species and/or some external periodic forcing. Disentangling this chaotic dynamics from environmental noise in field data remains problematic, however. Recent attempts to find chaos in the wild resulted in the conclusion that a great majority of populations live at a boundary between chaotic and regular dynamics, i.e. on the edge of chaos. Parallel to that result, we report here that chaos is an inherent dynamic phenomenon, which can emerge far away from the edge of chaos in a natural population. We have observed that the plankton dynamics in the Naroch Lakes, Belarus, exhibit chaos with the horizon of predictability of around 2.5 months, and the corresponding dominant Lyapunov exponent equals approximately 0.4, thus laying out of the narrow interval between −0.1 and +0.1 characteristic of living at the edge of chaos. Furthermore, we have found that the second order Renyi entropy can be considerably greater than the values of the dominant Lyapunov exponents. It implies that the plankton dynamics can be characterized by at least two physical degrees of freedom, and the qualitative description of irregular changes in plankton abundance requires a four- or higher-dimensional phase space. In other words, interspecific interactions across trophic levels can significantly contribute to the emergence of chaos far away from the edge of chaos.

1. Introduction

"Is chaos a mathematical artifact or ecological reality?"—A prevalent unresolved question in ecology is weakening the link between non-linear dynamics and population ecology (Sherratt et al., 1997). Detection and characterization of chaotic dynamics or near-to-chaos dynamics in natural populations is, therefore, a thriving area of contemporary ecological research. Many attempts have been made to identify chaotic oscillations (see Turchin, 2003; Solé and Bascompte, 2006 and references therein). Chaotic population dynamics specifically characterized by positive values of the dominant Lyapunov exponent, which quantifies the sensitivity of the dynamics to initial conditions (Ott, 2002), were found to be rare in nature (Berryman and Milstein, 1989; Thomas et al., 1980; Ellner and Turchin, 1995; Higgins et al., 1997). Analysis of a large number of population time series allowed hypothesizing that the majority of wild populations live at the edge of chaos, i.e. at a boundary between chaotic and regular dynamics (Ellner and Turchin, 1995). The boundary is characterized by the values of the dominant Lyapunov exponent close to zero. Living at the edge of chaos implies that small changes in parameters can cause the population dynamics to switch between regular and chaotic behavior. Alternatively, continual transitions in and out of chaos may also arise as a result of competition between coexisting regular and chaotic attractors at the same set of parameter values (Kaitala et al., 2000; Medvinsky et al., 2001). Switching between

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regular and chaotic dynamics may cause adaptation of populations to environmental changes. In a broader context, it has been argued that living systems can evolve towards the edge of chaos by natural selection (Kauffman, 1993; Levin, 1998).

The role of chaotic dynamics in shaping the population dynamics can be better understood by a combination of theoretical approaches and analysis of field observations (Medvinsky et al., 2002; Rogers et al., 2013). However, field observation data are often collated at relatively very short periods of time, which undermines ecological investigations of the role of chaos in a wild population. In order to analyze typically short time series, methods to assess the dominant Lyapunov exponent by means of mathematical models, directly fit to time-series data, were developed (Ellner and Turchin, 1995; Turchin and Ellner, 2000). These methods enabled detection of chaos with realistic amounts of available data. In particular, it was shown that the vole population dynamics in northern Fennoscandia were characterized by chaos alternating with non-chaotic oscillations. Specifically, the global Lyapunov exponent, which characterizes the long-term behavior of a system under study, was found to be statistically undistinguishable from zero while the values of the local Lyapunov exponent, which measure the sensitivity to perturbations in different parts of the state space, turned out to be significantly positive (Turchin and Ellner, 2000).

Nevertheless, the as yet unanswered question whether chaotic populations can persistently function far away from the edge of chaos calls for further investigation. A persistent discrepancy between theoretical predictions and field observations resulted in contemporary ecological investigations seeking explanations for the rarity of chaos in wild populations and revealing the actual roles of chaos in maintaining the population dynamics (Ellner and Turchin, 1995; Costantino et al., 1997; Gibson and Wilson, 2013). For example, chaos may be structurally unstable due to a deep nest of periodic windows within chaotic domains, which are exhibited in bifurcation diagrams (Kaneko and Tsuda, 2000). As a result, even a small variation in a bifurcation parameter can change the dynamics from chaotic to periodic. One common reason why chaotic dynamics are hardly observable in nature could be maladaptiveness of chaos. Indeed, one can see from bifurcation diagrams that chaotic oscillations of population numbers can be close to zero. As a result, small environmental fluctuations could cause the population to extinct (Berryman and Milstein, 1989; Drake and Griffen, 2010; Roques and Chekroun, 2011). On the other hand, it was demonstrated theoretically that chaos may reduce, rather than promote, extinction of populations in metapopulation systems (Allen et al., 1993).

Chaotic dynamics are characterized not only by a sensitivity to perturbations but also by an aperiodic behavior. The aperiodicity implies that the state variables never return to their previous values. However, they can recur very closely to the previous values. In order to visualize the recurrences of dynamical systems, a method of recurrence plots was put forward in the late 1980s (Eckmann et al., 1987); see Section 2 for more details. The recurrence quantification analysis allows linking the recurrences to dynamical invariants, such as the correlation dimension and correlation entropy (Marwan et al., 2007). We use the recurrence quantification analysis in order to analyze the data of long-term monitoring of irregular fluctuations in the plankton abundance in the system of Naroch Lakes, Belarus. We demonstrate that the plankton time series show evidence of chaos far away from the edge of chaos.

2. Materials and methods

2.1. Sampling and sample analysis

The sampling and the measurements, which resulted in the time series presented in Fig. 2, were carried out in 1993–2013.

Samples were collected monthly at monitoring points during the vegetative season (from May to October) using a two-liter Ruttner sampler. The samples were collected from six different depths (0.5, 3, 6, 8, 12 and 16 m) in Lake Naroch, from four depths (0.5, 4, 7 and 9 m) in Lake Myastro, and from three depths (0.5, 3 and 5 m) in Lake Batorino. The water samples from all the depths were mixed in such a way that the water volume of each level (depth) in the mixed sample was proportional to the fraction of the level in the total water volume in each of the lakes according to bathymetry. Samples of 0.5 liters for phytoplankton measurements and 10 liters for zooplankton measurements were taken from each of the mixed samples. Phytoplankton samples were fixed with Utermöhl's solution (Mikheyeva, 1989). Then the samples were sedimented in total darkness for no less than one week. These samples were concentrated very thoroughly up to 100–150 ml by pouring off all excess water using a silicon or rubber siphon covered with a two-layer silk sieve with a 77 μm mesh. The resulting concentrate was poured into plankton bottles and allowed to settle for no less than 2–3 days. Then extra water was drawn off using a medical syringe with a thin vinyl tubule at the end. The final sample volume was 15–30 ml depending on the sediment thickness.

A Zeiss Axiolab light microscope was used to analyze phytoplankton samples. The phytoplankton abundance is expressed in cell number (number of one-celled species, number of cells in filaments and colonies) per liter. A Fuchs–Rosenthal chamber 3.2 mm^3 in volume was used to count small phytoplankton individuals. Larger phytoplankton such as *Ceratium*, *Asterionella*, *Melosira*, *Aulacoseira*, *Tabellaria*, *Fragilaria*, *Microcystis*, *Coelosphaerium*, *Anabaena* and some others were counted using a 1 ml chamber while large colonial organisms (*Gloeotrichia echinulata, Volvox*) were counted using a Bogorov chamber.

Phytoplankton biomass was estimated by the method of true volumes (Kiselev, 1969). In this method, the volumes of a cell or an organism are calculated for each species by applying a solid geometric shape (ellipsoid, sphere, rod, cone, *etc.*) most closely matching their shape. The relative density of phytoplankton was set to 1. The total biomass of phytoplankton was calculated by taking the sum of the biomass for each isolated individual. Fluctuations of the total phytoplankton biomass (in mg of fresh mass per l) are given in Supplementary information (Table SI1).

Zooplankton samples were filtered using an Apstein plankton net of 64 μm mesh size. The resulting sediment of 150 ml in volume was poured into a plastic bottle filled with 4% formalin and allowed to settle for 10 days. Then, the sample volume was reduced to 50 ml by decanting the top layer without stirring-up the sediment. A silicon siphon covered with a 55 μm mesh net was used for decanting. A 2–6 ml amount of the sample was taken by a pipette dispenser and analyzed. Zooplankton species were counted and identified in two repeats using Zeiss Axiolab and Zeiss Stemi 2000 microscopes. The number of zooplankton individuals was counted in a 40 mm Petri dish with the grid pattern on the back. Zooplankter sizes were measured by means of an ocular micrometer. The body mass of *Cladocera* and *Copepoda* was determined using the equations describing the exponential dependencies between length and body volume (Balushkina and Vinberg, 1979). The body shapes of *Rotifera* were compared with the defined geometric figures. The body volume was determined according to geometric equations (Balushkina and Vinberg, 1979). The relative density of zooplankton was set to 1. The total biomass of zooplankton was calculated by summing up the biomasses of all isolated individuals. Fluctuations of the total zooplankton biomass (in mg of fresh mass per l) are given in Supplementary information (Table SI2).

The final dataset was prepared to construct the time series shown in Fig. 2. The time series were obtained as a result of