

[Re] Chaos in a long-term experiment with a plankton community

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Competing Interests:

The authors have declared that no competing interests exist.

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A reference implementation of

→ Benincà, E., Huisman, J., Heerkloss, R., Jöhnk, K.D., Branco, P., Van Nes, E.H., Scheffer, M. & Ellner, S.P. (2008) Chaos in a long-term experiment with a plankton community. *Nature*, 451, 822–825 DOI: [10.1038/nature06512](https://doi.org/10.1038/nature06512)

Introduction

The original paper describes analyses of fluctuations in the abundance of organisms in a plankton community derived from the Baltic Sea, housed in a laboratory environment. The length of the time series (samples every few days for 2,300 days) allowed for analyses revealing that the observed dynamics exhibited characteristics consistent with chaos produced by non-linear species interactions. The article concludes that stability is not required for persistence of complex food webs, and that long-term prediction of abundances may be fundamentally impossible. The demonstration of chaotic dynamics and limited forecast horizons (sensu Petchey et al. [4]) is important in the field of ecology, since the ability to predict dynamics is an open question with considerable applied importance Petchey et al. [4] Mouquet et al. [3].

Methods

This reproduction started with the raw data (source given below) and used information from the original paper, the supplementary information [the Supplement to the Nature paper](#), and communications with Elisa Benincà, who provided for comparison digitised data from the original article, and Stephen Ellner, who provided code and data used to produce results in the original paper. Use of this data and code in this reproduction is indicated below.

Scope of the reproduction

An attempt was made to reproduce the majority of the results in the original article. Instances where we did not attempt to reproduce a result are detailed below.

The data

The data are available as an Excel file supplement to [an Ecology Letters publication](#) Benincà et al. [2]. The Excel file contains several datasheets. Two were particularly

important, as they are the source of the raw data (one contains original species abundances, the one with the nutrient concentrations). We saved these two datasheets as comma separated value (csv) text files. In the code associated with this reproduction, these data files are read from the associated github repository.

Another datasheet in the Ecology Letters supplement contains transformed variables (we also saved this as csv file, in order to use it in this reproduction). We also received a dataset direct from Steve Ellner, see below for details.

The original species abundance data contained errors (e.g., a few numerical values had a comma in place of a period as the decimal separator) that suggested that this was not the exact version of the dataset used in the original article, or that this was the exact dataset, but with errors corrected.

Reproduction environment

The R language and environment for statistical computing and graphics was used to make the reproduction. Additional R packages required are specified in the code associated with this reproduction.

The code for this reproduction resides in an R markdown document, as well as a source file containing some required functions. Some of the code takes several minutes to run, so an intermediate data file is provided with results from this code.

Results

Population dynamics

The reproduced populations dynamics were at least very similar to those in figure 1b-g of the original publication (figure 1). Note that we plot fourth root transformed values, rather than raw abundances with a y-axis break, as in the original article.

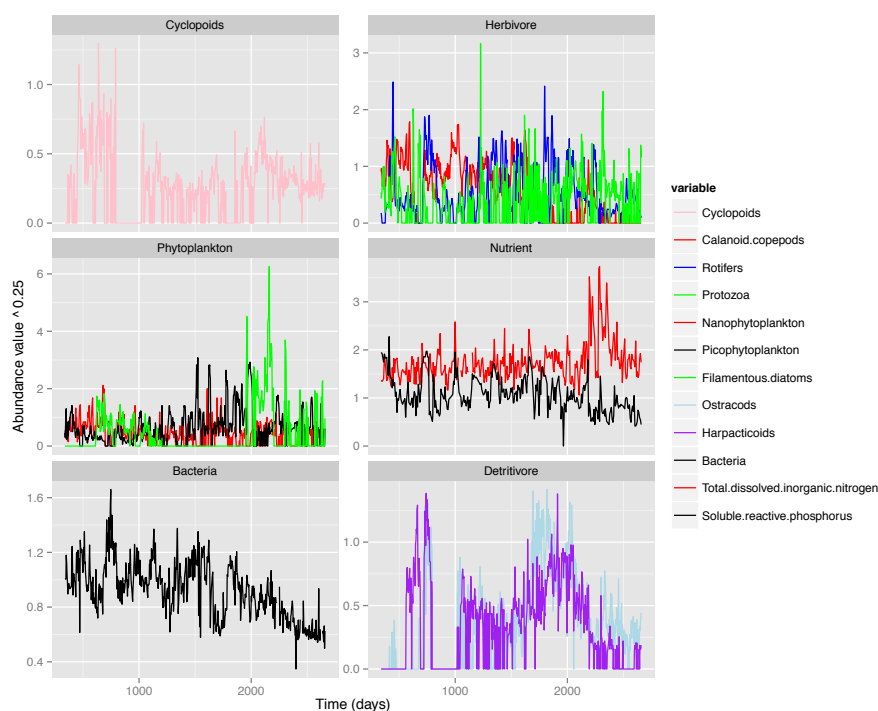


Figure 1: Observed population dynamics.

Data transformation

The following transformation steps were used:

1. Time series shortened to remove long sequences of zeros.
2. Interpolation to create equally spaced observations in time series.
3. Fourth root transformation.
4. Detrending of five of the time series.
5. Rescaling to zero mean and unit standard deviation.

The method for selecting the zeros to remove was unclear. In order to reproduce this step, we removed the same data as in the original study, by matching to the transformed data with zeros removed in the Ecology Letters supplement Excel file mentioned above. All remaining transformation steps were performed independently of this dataset. Our reproduction of the transformed data closely matched the published transformed data.

The data received directly from Stephen Ellner was interpolated, but without zeros removed. Our interpolated data, without zeros removed, matched closely this data.

Correlations among species abundances

Correlations among species abundances presented in Table 1 of the original article closely matched our reproduced correlations, calculated from the transformed data with zeros removed (figure 2). Deviations between the original and reproduced correlations are relatively small (less than 0.072 units) and infrequent.

Highlighted in the text of the original paper were: negative correlations of picophytoplankton with protozoa, and of nanophytoplankton both with rotifers and calanoid copepods, positive correlation of picophytoplankton with calanoid copepods, negative correlation between bacteria and ostracods, and positive correlation between bacteria and phosphorus. All of these correlations were qualitatively reproduced.

Spectral analyses

Spectral analyses in the original paper were presented graphically in figures S3 (raw spectrograms) and S4 (Welch periodograms). These graphs were, apparently, visually inspected to reveal: “fluctuations covered a range of different periodicities”, and “picophytoplankton, rotifers and calanoid copepods seemed to fluctuate predominantly with a periodicity of about 30 days.” It is unclear how these conclusions were derived from figures S3 and S4 of the original article. Our reproduced spectra (not shown here, but code provided) were not quantitatively identical to the spectra in the original article.

Lyapunov exponents by direct method

Reproduced divergence rates (figure 3) and Lyapunov exponents (figure 4) were somewhat different from those in the original article.. The original article states: “the distance between initially nearby trajectories increased over time, and reached a plateau after about 20–30 days”. The reproduced results appear not inconsistent with this statement, except for one group of species (Harpacticoids). The original article also stated that the analyses “yielded significantly positive Lyapunov exponents of strikingly similar value for all species (Fig. 3; mean exponent = 0.057 per day, s.d. = 0.005 per day, $n = 9$)”. Reproduced exponents had very similar mean value, but had about four times greater standard deviation (mean = 0.055 and s.d. = 0.019).

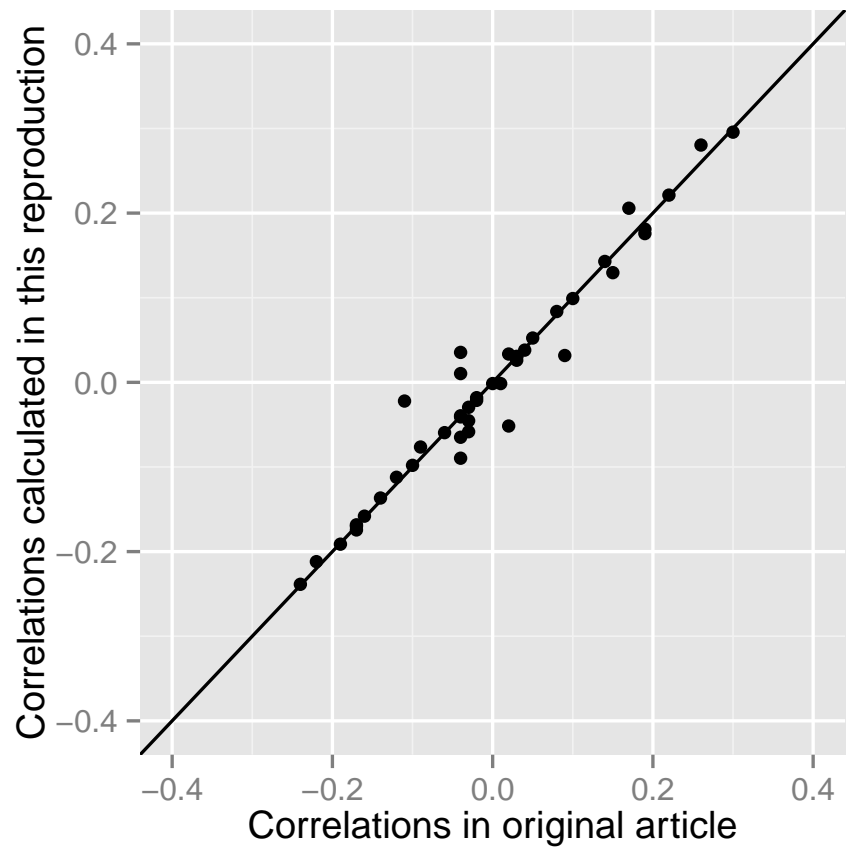


Figure 2: Comparison of calculated correlations among species abundances in the original article and this reproduction.

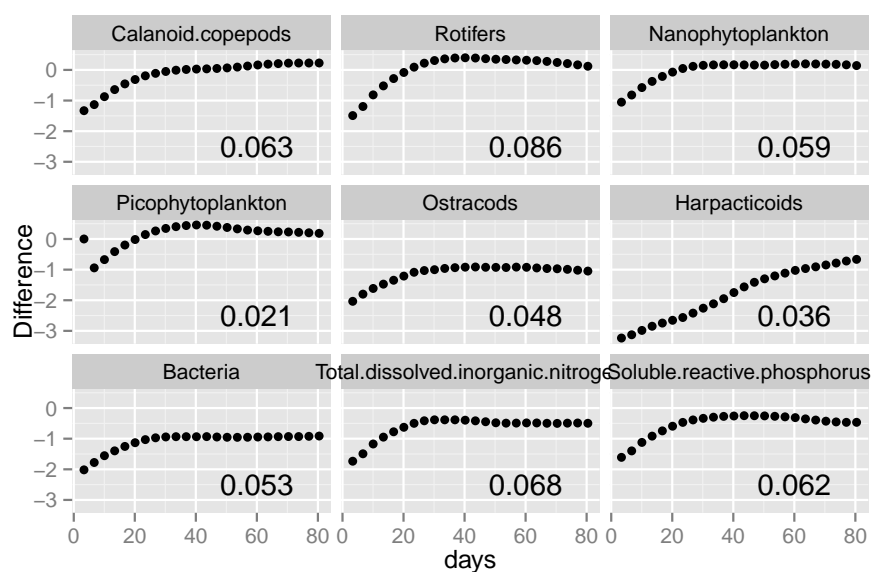


Figure 3: Reproduced divergence rates and Lyapunov exponents (figure 3 in the original article).

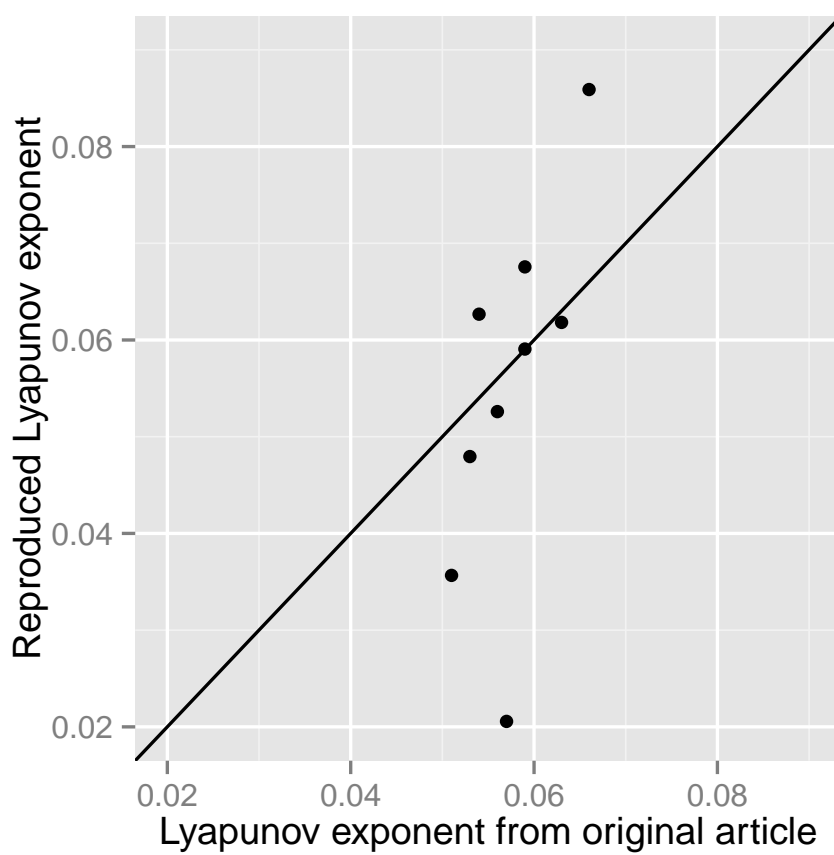


Figure 4: Comparison of Lyapunov exponents, estimated by direct method, in the original article and this reproduction.

Lyapunov exponents by indirect method

The original paper reported global Lyapunov exponent calculated via two modelling approaches (neural network and generalised additive models [GAMs]). Only the GAM approach was reproduced, with the assistance of code donated by Stephen Ellner. The original article obtained a global Lyapunov exponent of -0.08 day⁻¹. The reproduced value was 0.04. We did not reproduce the bootstrapping used to give confidence intervals around this estimate.

Predictability decay

The article stated: “For short-term forecasts of only a few days, most species had a high predictability of $R^2 = 0.70 - 0.90$ (Fig. 2). However, the predictability of the species was much reduced when prediction times were extended to 15–30days.” The reproduced predictabilities, which were calculated from the GAMs, were consistent with these qualitative statements, though were quantitatively different (5). We did not reproduce the predictability estimates for linear models.

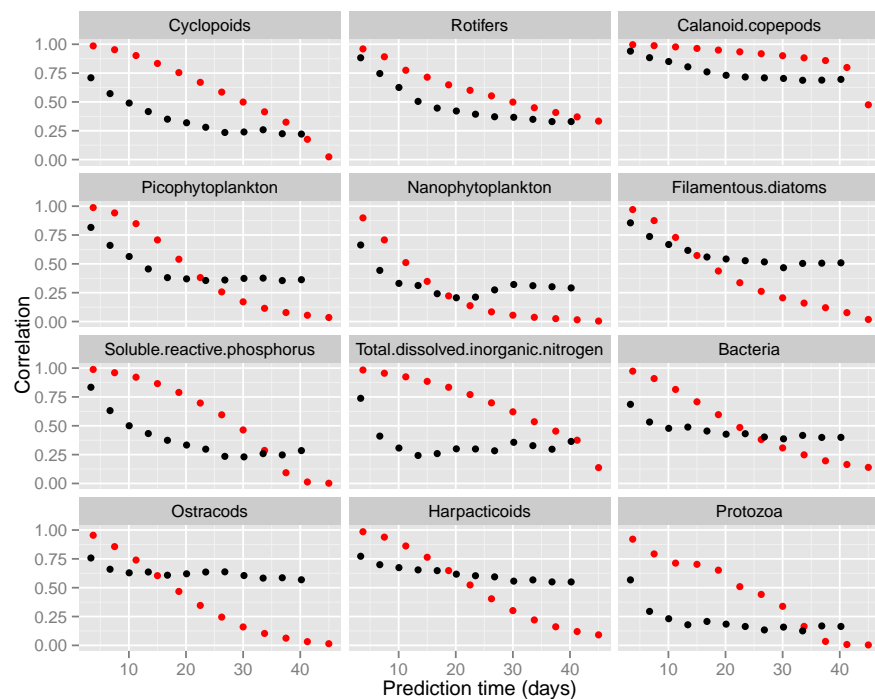


Figure 5: Predictability (correlation between predicted and observed abundances) and prediction distance (days) (figure 2 in the original article). Reproduced data in red, and data from original publication in black.

Conclusion

Although we were not able to make a quantitatively accurate reproduction of all results of the original article, the qualitative results were largely identical. For example, all Lyapunov exponents estimated by direct method are positive, as in the original article, consistent with chaotic dynamics. Quantitative differences may have resulted from difference in algorithms used. For example, the original used the [Tisean software](#) to calculate Lyapunov exponents. As this was available from CRAN [until mid 2014](#) and

since it is a bit less well integrated with R, we instead use the `tseriesChaos` package Antonio and Narzo [1], which in any case was largely inspired by the TISEAN project. In addition, there may have been some difference in algorithm parameters, as not all parameters required by the functions we used were reported in the original ms. There may also have been some difference in data used for specific analyses, e.g., data with zeros removed or not, as it was not always possible to be totally sure the reproduction used exactly the same data as the original article.

In conclusion, this reproduction supports the general scientific conclusions of the original article, but also shows how difficult can be an accurate quantitative reproduction, even in the presence of the extensive methodological details provided alongside the original article.

Acknowledgements

This reproduction was made as part of the Reproducible Research in Ecology, Evolution, Behaviour, and Environmental Studies (RREEBES) Course, lead by Owen Petchey at the University of Zurich. More information about the course [here](#) on github.

References

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