Biodiversity of plankton by species oscillations and chaos

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Background

Main Question: The Paradox of the Plankton

- **Competition**: an interaction between species in which both require the same limited supplied resources, which affects both negatively
- **Competitive exclusion principle**: 2 species that compete for the same resources cannot stably coexist — species less suited to compete for resources must either adapt or die out
- **Reality**: a wide variety of plankton species can coexist in the relatively stable and homogeneous environment of the open water column in lakes and oceans
- **Circumvention**: Hutchinson and others suggest that ecological and environmental factors continually interact such that the planktonic habitat never reaches an equilibrium for which a single species is favored

Introduction

- **Model**: Competitive Model Nonlinear First Order ODE
- **Assumptions**: No external factors such as selective predation so we can assume m_i accounts for all mortality of species i, homogeneous distribution of resources. Therefore, we can focus only on the competition factor's influence on plankton biodiversity.
  Moreover, this constant environment assumption allows the usage of the Monod equation for the growth rate of the plankton, which is non-linear

Variables

- **n**: Number of Species
- **k**: Number of Resources
- $\boldsymbol{N_i}$: Population Abundance of species i – the number of individuals in a population per unit of area
- $\boldsymbol{R_j}$: Availability(current accessible amount) of resource j
- $\boldsymbol{m_i}$: specific Mortality rate of species i
- **D**: System's turnover rate - at which a resource is replenished or replaced
- $\boldsymbol{S_j}$: Supply concentration of resource j
- $\boldsymbol{c_{ji}}$: The rate of consumption of resource j in species i

Equations

$$\frac{dN_i}{dt} = N_i(\mu_i(R_1, \ldots, R_k) - m_i), \quad i = 1, \ldots, n$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} c_{ji}\mu_i(R_1, \ldots, R_k)N_i, \quad j = 1, \ldots, k$$

Here $\mu_i(R_1, \ldots, R_k)$ represent the specific growth rate of species i
We can simplify the two equations above into:

$$\frac{dN}{dt} = N(\mu - m)$$

$$\frac{dR}{dt} = D(S - R) - c \cdot rN(1 - \frac{K_s}{K_s + R})$$

Equations

$\mu_i(R_1, \ldots, R_k)$ is assumed to be following the Monod equation and the Law of the Minimum:
$\mu_i(R_1, \ldots, R_k) = \min(\frac{r_i R_1}{K_{li}+R_1}, \ldots, \frac{r_i R_k}{K_{ki}+R_k})$

- $\boldsymbol{r_i}$: the Maximum specific growth rate of species i
- $\boldsymbol{K_{ji}}$: the half-saturation constant for resource j of species i – an indicator of the affinity of microorganisms for the resources: a lower K_{ji} means a faster growth rate at low resource concentrations, hence a stronger competitive advantage

The dynamics of the model

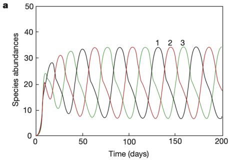
Competition theory

It claims that the number of species cannot exceed the number of limited resources, i.e. $n \leq k$

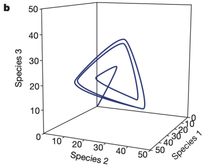
However, under the assumption of a constant and homogeneous environment, the resource competition model suggests:

- $n = 2$:
  1. If all species are limited by the same resource, the strongest competitor dominates and leads to a monoculture equilibrium.
  2. If different species are limited by different resources, stable coexistence between two species can occur.

- $n = 3$: Extending the competition model to three species and three resources reveals sustained oscillations when species displace each other cyclically.



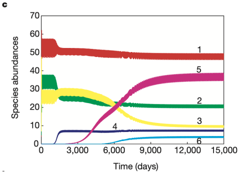
Time course of the abundances of three species competing for three resources



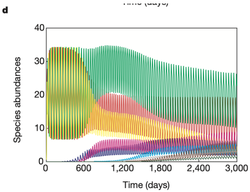
The corresponding limit cycle

Oscillations on three resources

- Oscillation amplitudes vary based on parameter settings.



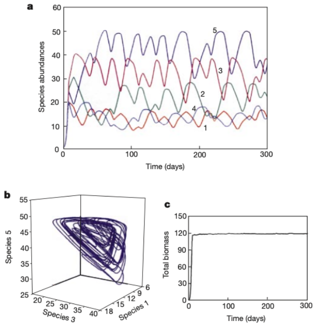
Small-amplitude oscillations of six species on three resources



Large-amplitude oscillations of nine species on three resources

Oscillations on three resources

- n=5:
  1. Irregular Divergence: unpredictable, non-repeating fluctuations with diverging but bounded abundances.
  2. Stable Biomass: fluctuations coexist with stable total biomass.



Chaos on five resources.

Experiment

- Find K experimentally and store this in a matrix where K_{ij} is the half-saturation constant of resource i for species j
- The chemostat is a device that creates a steady-state environment
- for each species growth dominates or competition dominates depending on K

Experiment

- Both K and C are stored in stoichiometric matrices
- Resource content is also found experimentally C and stored in a matrix where Cij is the content of resource i in species j
- These values can both be obtained by experimentation with the chemostat
- Two parameters were fixed in the making of the species over time trajectories, m and D, turnover, and mortality which were set at .25

- In the case of 5 resources and 5 species if $K_{41} < .2$, then species 1 is a strong competitor for resource 4 and the other 4 species die out. But $K_{41} > .4$ means species 1 is a weak competitor and there is oscillation and coexistence
- Being an intermediate competitor with $.24 < K_{41} < .35$ leads to chaos

1. **Passivity of Competition**: it is not necessarily a destructive force. The oscillations and chaos may allow the persistence of a great diversity of competitors on only a few limited resources
2. **Biodiversity Insight**: Enhances understanding of species coexistence and ecosystem stability
3. **Climate Change Research**: Helps in modeling and mitigating climate change through a better grasp of carbon cycling by plankton
4. **Algal Bloom Management**: Improves prediction and management of harmful algal blooms to protect water quality and marine life.‘

Potential Improvements

1. **Integration of External Drivers** (Hutchinson, G. Evelyn. "The paradox of the plankton."): Enhance the model by incorporating external factors like nutrient availability, weather conditions, and predation pressures to capture the complexity of real-world ecosystems.
2. **Multi-Trophic Interaction Incorporation**: Expand the model to include interactions with other trophic levels, such as zooplankton and predators, for a holistic view of ecosystem dynamics.
3. **Resource Limitation Switching**: Consider the switching that occurs as a species changes from being growth-rate limited by one resource to being limited by another.
4. **Possible Linear Case:** Plankton populations may initially follow a linear growth pattern when resource limitations and density-dependent factors are minimal, with growth rates proportional to population size.

Works Cited

- Huisman, Jef, and Franz J. Weissing. "Biodiversity of plankton by species oscillations and chaos." *Nature* 402.6760 (1999): 407-410.
- Hutchinson, G. Evelyn. "The paradox of the plankton." *The American Naturalist* 95.882 (1961): 137-145.