7.1 Critical Consideration of Chemostat Experiments

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7.1.1 Introduction

The use of chemostats in rotifer culture was first proposed by Droop (in Conover 1970) who regarded this technique as a promising approach for ecophysiological studies. He referred to, and later described in more detail (Droop 1976), a two-stage system in which the second-stage rotifer chemostat is supplied by a steady-state algal culture. This has been the most widely used system since then, and the following considerations essentially apply to it. Other continuous culture techniques, such as one-stage chemostats, turbidostats, or semi-continuous cultures (see other chapters in this volume), differ in important aspects.

In theory, the chemostat is thought to hold important advantages: It receives a known input of food algae in a defined physiological state, and as a self-regulating system it sustains time-invariant populations with a constant age structure, that essentially have lost their previous history. Most importantly, due to these characteristics, metabolic rates and efficiencies can be deduced from state variables that are easily measured (see Part 4).

The aim of this chapter is to check critically the above ideas. The assumption of time-invariant populations will be examined theoretically and compared with empirical data. Furthermore, I will give evidence that the assumption of a defined nutritional base may be erroneous and that this may lead to certain misinterpretations when determining functional and numerical responses from chemostat steady states.

7.1.2 The Occurrence of Oscillations

Periodic oscillations are known for laboratory populations of Daphnia (Pratt 1943) and of rotifers (Halbach 1970). Population cycles have also been reported for zooplankton in the field (McCauley and Murdoch 1987). They may thus be a widespread phenomenon rather than a mere laboratory artifact. This kind of population dynamics can be modeled by modifying the logistic equation to
incorporate a time lag in the density-dependent term (Hutchinson 1948):

\[
\frac{dN(t)}{dt} = r_{\text{max}} N(t)[1 - N(t-T)/K],
\]

(7.1.1)

where

- \( N \) = population density
- \( K \) = equilibrium population density
- \( r_{\text{max}} \) = maximal growth rate
- \( T \) = time lag.

The dynamic behavior of the model depends on the parameters \( r_{\text{max}} \) and \( T \) (May 1981):

- \( r_{\text{max}} \cdot T < e^{-1} \) exponential approach to \( K \)
- \( e^{-1} < r_{\text{max}} \cdot T < \pi/2 \) damped oscillations
- \( r_{\text{max}} \cdot T > \pi/2 \) stable limit cycles

Generally speaking, if the expression \( r_{\text{max}} \cdot T \) surpasses a certain value, oscillations can be expected, the magnitude of which increases with \( r_{\text{max}} \cdot T \).

The applicability of the time-lagged logistic has especially been demonstrated for rotifer populations (Halbach and Burkhardt 1972). There was a reasonable agreement between the dynamic behavior of simulations using empirically determined parameters and laboratory population dynamics.

Time lags are due to the fact that it necessarily takes a certain time to convert food taken up into offspring. The length of this time span is largely temperature dependent (Halbach and Burkhardt 1972) and can therefore be regarded as invariable for a given clone of rotifers growing under stable laboratory conditions. The probability and magnitude of oscillations under these circumstances depends on \( r_{\text{max}} \). When considering the stability of steady states in a rotifer chemostat, however, \( r_{\text{max}} \) has to be substituted by the "highest apparent growth rate" \( r'_{\text{max}} \).

\[
r'_{\text{max}} = r_{\text{max}} - D.
\]

(7.1.2)

From this, it follows that oscillations can particularly be expected in rotifer chemostats running at low dilution rates and that the potential for fluctuations decreases as the dilution rate, \( D \), approaches \( r_{\text{max}} \). The occurrence of oscillations, however, means that the assumption of time-invariant populations with a constant age structure may not be given.

Since most work with rotifer chemostats aims at information deducible from steady states, the population dynamics are seldom described in the literature. However, some examples for the occurrence of oscillations in continuous

Fig. 7.1.1 a-d Examples of population dynamics that show oscillations in continuous culture: a Brachionus calyciflorus (after Boraas 1980); b B. angularis (after Walz 1983b); c B. rubens (Rothhaupt, unpublished in data); d B. rubens (dots) and B. calyciflorus (circles) in "rotating culture" competition experiments (After Rothhaupt 1988)