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A Mathematical Submodel for the Planktonic Rotatoria in the Ecosystem of the Barther Bodden (Southern Baltic Sea)

key words: functional groups, feeding biology, energy budget, mathematical model

Abstract

Of the rotifers inhabiting the shallow eutrophic Barther Bodden, the pelagic species feeding on fresh detritus comprising dead diatoms and green algae are of particular importance in terms of biological production. The submodel presented here refers only to this functional group (*Filinia longiseta, Brachionus quadridentatus* and *Keratella cochlearis*). The biological situation, the working hypotheses, the equation system, the measured values and coefficients used and the wiring diagram are given. The curves obtained with the model are shown in detail and tested against various criteria. Agreement between the model curves and the measured data is good.

Contents

1. Introduction

The zooplankton of the Barther Bodden (Schnese 1975, 1980) consists of two functionally distinct groups: the copepods and the rotifers. The formerly important cladoceran population started to decline in 1972 and did not become significant again in production terms until 1980.

The chain of shallow waters south of the Darss-Zingst Peninsula consists of four interconnected eutrophic brackish estuarine lakes (Boddens). Their hydrography is governed by nutrient-rich run-off (the Rivers Recknitz and Barthe), water exchange with the Baltic Sea and the wind field of the region. The hydrographic situation results in a constantly varying salinity gradient that decreases from east to west (Fig. 1). The compartments playing the greatest role in the matter and energy flux of the ecosystem "Barther Bodden" are the phytoplankton (diatoms, green algae and, in particular, blue-green algae), the benthic bacteria and the benthic ciliates (Vietinghoff 1982a, b).

The significance of the rotifers for the matter and energy flux in this ecosystem
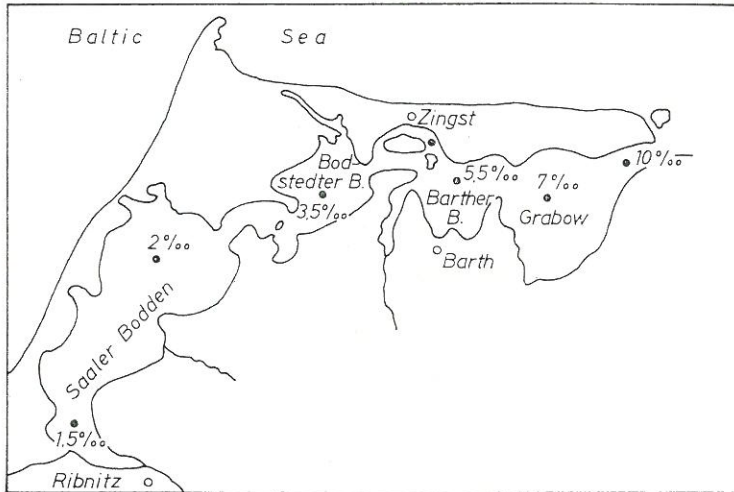
Figure 1.   Map of the western part of the Bodden chain showing the sampling stations and salinities.

is shown by a comparison of the phytoplankton primary production and the uptake of particulate matter by the planktonic rotifers (absolute feeding rate): in June/July, when the rotifers reach their climax, the ratio is 4 : 1.

During the work leading to our model of the Barther Bodden (VIETINGHOFF, HUBERT and SCHNESE 1980, VIETINGHOFF, BALLIN, JOST, HUBERT and SCHNESE 1981, BRINCKMANN, VIETINGHOFF and SCHNESE 1981) the rotifers and copepods were dealt with separately (VIETINGHOFF, HEERKLOSS, HUBERT and SCHNESE 1981) because they differ fundamentally in several important respects (feeding biology, population dynamics, energy balance) and, despite the need for generalization and omission of trivial details, basic biological phenomena and causal chains must be incorporated correctly into the mathematical model in view of its intended use for forecasting.

In the past no articles dealing in depth with the modelling of rotifer populations in natural waters have been published although there can be no doubt regarding their importance for the matter and energy cycle in natural ecosystems (SCAVIA and RO-BERTSON 1979). On the other hand, a wealth of experimental results which, together with the data of the ecosystem that has been investigated, provide a good basis for modelling has been published in recent years, especially at the two international symposiums on the Rotatoria (KING 1977, DUMONT and GREEN 1980).

2. Description of Technique, Data

The most important of the findings and considerations leading to our model approach are shown in Figs. 2 to 4. The essential matter and energy fluxes in the ecosystem are described exclusively on the basis of the amictic females with the high rate of egg production, beginning with the hatching of the resting eggs. For this we use a common first order differential equation, the solution to which is an exponential function. It is evident from the graphical model proposed by EDMONDSON (EDMONDSON 1968, HALBACH 1974) and numerous experimental publications that the use of a continuous exponential approach represents a further permissible degree of abstraction. The sequence of events from hatching, development to mature females, laying of

Fig. 2.1

|	1st group	2nd group	3rd group	4th group
Food	Diatoms and small green algae, (detritus), no blue-greens	Detritus, no diatoms, greens and blue-greens	Blue-green algae,	Nauplii, *Keratella*, *Synchaeta*
Species determining production	*Brachionus calyciflorus* *Keratella quadrata* *Synchaeta* ssp.	*Keratella cochlearis* *Filinia longiseta* *Brachionus quadridentatus*	*Brachionus plicatilis*	Carnivorous *rotifers*: *Asplanchna* ssp.

Fig. 2.2
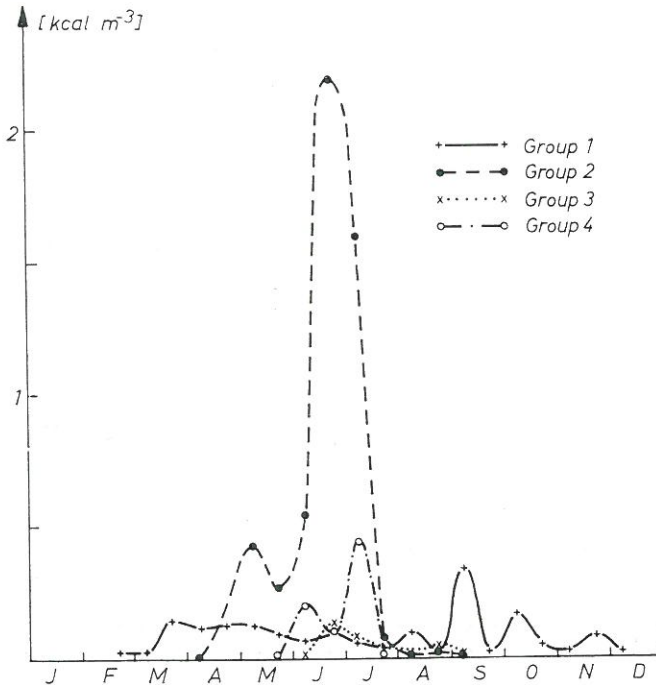
Figure 2.   Classification of rotifers in the western part of the Bodden chain into functional groups on the basis of their food (2.1) and the biomasses of these functional groups (2.2).

	Leimeroth 1980	Doohan 1973	in model (juv. and ad. rotifers)
	juvenile rotifers	*adult rotifers*	
	A: 100 %	A: 100 %	A: 100 %
	P: 58 − 78 %	P (egg production): 57 %	P (egg production): 43 %
	R: 42 − 22 %	R: 40 %	R: 33 %
		♀♀: 790 · 10⁻⁶ cal	M: 24 %
		egg: 500 · 10⁻⁶ cal	

A Assimilation
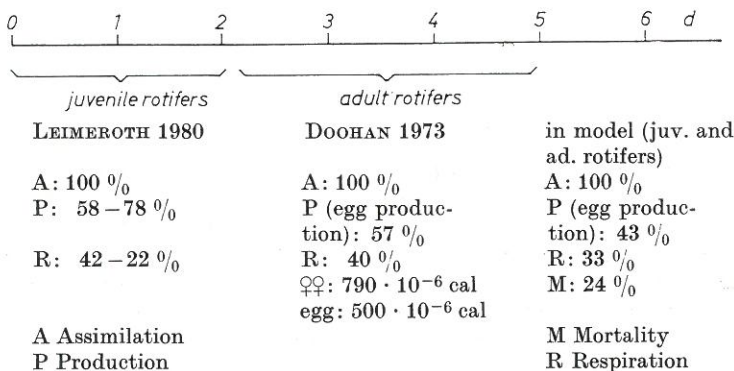P Production

M Mortality
R Respiration

Figure 3.   Estimation of the energy balance of one generation of rotifers.
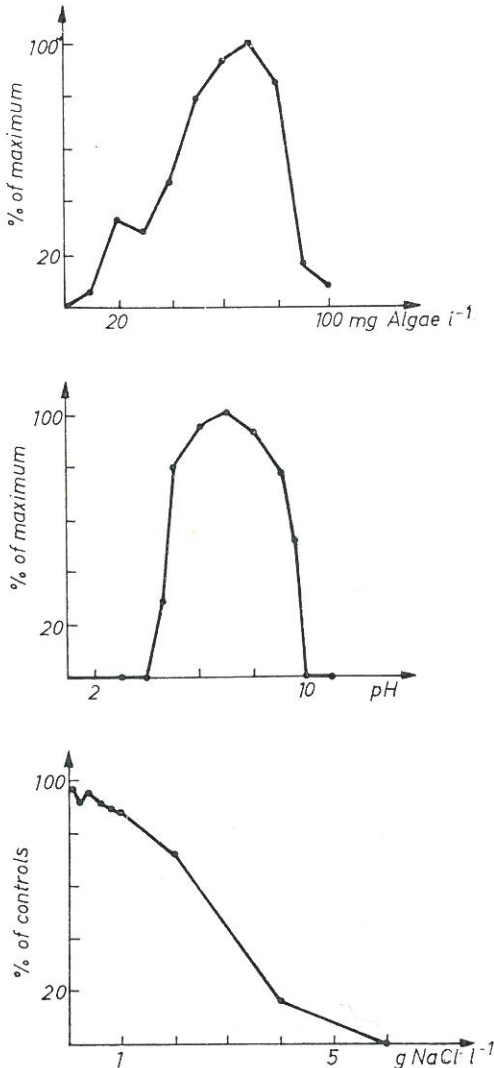
Figure 4. Dependence of growth of *Brachionus rubens* on external conditions (SCHLÜTER 1980).

eggs and death in a single generation is required only for estimation of the energetic balance (ratios between assimilation, respiration, egg production and mortality) of the whole population (see below).

The rotifers were split into four functional groups (Fig. 2) on the basis of the species (Monogonata) that are biologically important in the Barther Bodden in terms of their production, their measured biomasses (SCHNESE 1980) and their feed requirements as determined in culture experiments and in the field (POURRIOT 1977, NAUWERCK 1963, SPITTLER 1969). The presentation of the biomasses of these four functional groups in Fig. 2.2 shows that only the second group comprising the species *Filinia longiseta* (EHRENBERG), *Brachionus quadridentatus* (HERMANN) and *Keratella cochlearis* (GOSSE) need be modelled, whereas the others can be omitted. This dominant group of rotifers feeds mainly on detritus (POURRIOT 1977, SPITTLER 1969, STARKWEATHER and BOGDAN 1980) or, more specifically, fresh detritus (NAUWERCK 1963, STARK-

WEATHER and BOGDAN 1980, RUTTNER-KOLISKO 1980). Unfortunately it is scarcely possible to measure the quantities of "fresh detritus" or "detritus of diatoms and green algae" experimentally. We estimated this portion of the detritus with the aid of the phytoplankton submodel (VIETINGHOFF et al. 1980) that was computed digitally by B. WIEDEMANN (inpubl.) and fitted to the measured primary production values and, assuming that this portion of the detritus is decomposed and converted into "old" detritus at a relatively high rate ($k = 0.841$ month^{-1}), used it as a forcing function for the rotifer model. (Fig. 5.2).

The food quality was taken into account by using a simple assumption: the three species taken into account by the model feed on fresh detritus from dead diatoms and green algae. Thus, as long as diatoms and green algae are dominant among the phytoplankton, and therefore also among the fresh detritus, the food basis for this group will be very good. When blue-green algae predominate among the phytoplankton
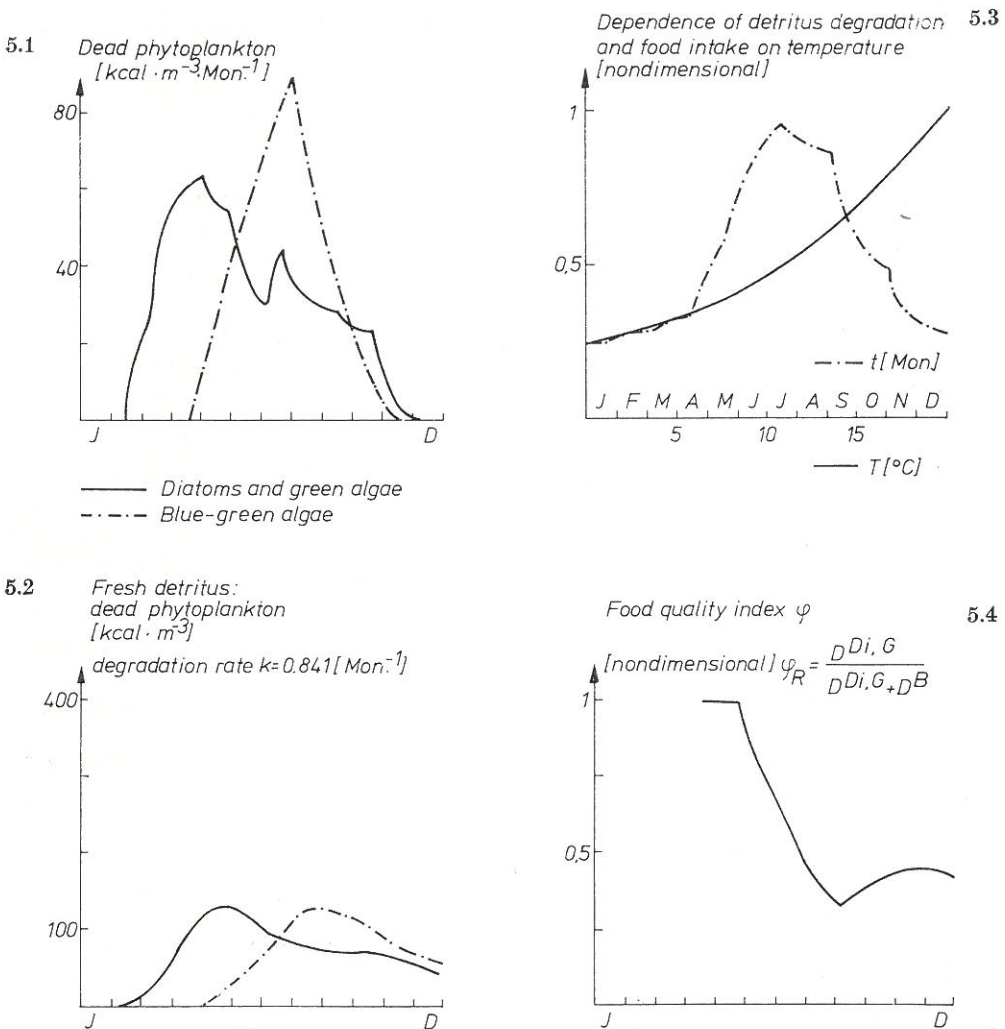

Figure 5.   Input curves for the submodel "Rotifers".

and detritus, however, the food quality will rapidly deteriorate. Mathematically this is formulated in the model by the expression

$$\varphi = \frac{D^{Di+G}}{D^{Di+G+B}} \; ; \qquad 0 < \varphi \leqq 1 \quad \text{(Fig. 5.4)}.$$

The possibility of the rotifers being affected by the blue-greens in other ways (cf. Part 4) than directly via ingestion cannot be excluded at present.

No experimental results were available from the Barther Bodden to permit estimation of the energetic balance of the three species taken into account in the model on account of their production biological importance. Our rough estimate is based mainly on the results published by Doohan and Rainbow (1971), Doohan (1973) and Leimeroth (1980) (Fig. 3), consideration simultaneously being given to the fact that the energy content of a mature female is only about 1—1.5 times that of a single egg and that 1—2 eggs are laid daily for a few days of the life cycle. This implies that during their short life the rotifers assimilate primarily in order to produce eggs! When estimating the energetic balance for the whole population it is necessary to take into account not only the factors mentioned by Leimeroth and Doohan but also the fact that during the decline in rotifer development not only does egg production decline but a larger proportion of eggs and juveniles with their relatively high energy contents die. Although Doohan and Leimeroth give no figures for mortality losses, our calculations make allowances for energy losses due to mortality by slightly reducing the average annual portions of the energy involved in egg production and respiration. These considerations lead to the assumption of the relationship

assimilation : egg production : respiration : mortality
= 100 : 43 : 33 : 24

used for the model.

The investigations undertaken by Lubzens *et al.* (1980) and Pourriot *et al.* (1980) show that the resting eggs obviously hatch after the water temperature and photoperiod have crossed certain thresholds. In agreement with this and with the curves showing the absolute feeding rate and biomass derived from experimental data, the model assumes that the rotifers start to hatch during the first 10 days in April.

Although provision has been made in the wiring diagram (Fig. 7) for the dependence of rotifer growth on external factors (pH, NaCl, NO_3^-) as observed by Schlüter (1980) (Fig. 4) it has not yet been taken into account in the model due to the lack of appropriate data for the three rotifers used in the model.

Time-series for production, feeding rate and biomass are required in order to model the biological components. In this respect we had the following time series at our disposal for the submodel:
- the half monthly biomass means for the rotifer species shown in Fig. 2 for the period 1969—1979 (Schnese 1980) (Fig. 9.6), and
- the monthly means for the absolute feeding rates of the rotifers altogether from 1977 to 1980 (Heerkloss 1980) (Fig. 9.5).

Further input data are given in Fig. 5.1 to Fig. 5.4.

3. Differential Equations and Analogous Circuit Diagram

The whole biological situation described in the preceding section is described by one differential equation (energy flux) (Fig. 6). The corresponding analogous circuit diagram is shown in Fig. 7. This submodel, like those described in earlier reports (Vietinghoff, Holm and Schnese 1975, Vietinghoff, Hubert and Schnese

$$\frac{\mathrm{d}\,\mathrm{Rot}}{\mathrm{dt}} = \begin{cases} k_G^{Rot} \cdot \dfrac{D}{D_1^*} \cdot \hat{T}_G^{Rot} \cdot \varphi_R \cdot \varepsilon \cdot Rot & \text{for } t \geqq 93 \\ 0 & \text{for } t < 93 \end{cases} - \begin{cases} k_R^{Rot} \cdot \dfrac{Rot}{Rot^*} \cdot \hat{T}_R^{Rot} \cdot Rot & \text{for } t \geqq 93 \\ 0 & \text{for } t < 93 \end{cases} -$$

$$- \begin{cases} k_M^{Rot} \cdot \left(1 - \left(\dfrac{D}{D_2^*} \cdot \varphi_R \cdot \hat{T}_G^{Rot}\right)\right) \cdot Rot & \text{for } t \geqq 121 \\ 0 & \text{for } t < 121 \end{cases} - \begin{cases} k_{eggs}^{Rot} \cdot Rot & \text{for } t \geqq 121 \\ 0 & \text{for } t < 121 \end{cases}$$

$$\left[\frac{\mathrm{kcal}}{\mathrm{m^3 \cdot Mon.}}\right] = \left[\frac{1}{\mathrm{Mon.}}\right] \cdot [1] \cdot [1] \cdot [1] \cdot [1] \cdot \left[\frac{\mathrm{kcal}}{\mathrm{m^3}}\right] \qquad - \left[\frac{1}{\mathrm{Mon.}}\right] \cdot [1] \cdot [1] \cdot \left[\frac{\mathrm{kcal}}{\mathrm{m^3}}\right] \quad -$$

$$- \left[\frac{1}{\mathrm{Mon.}}\right] \cdot [1] \cdot \left[\frac{\mathrm{kcal}}{\mathrm{m^3}}\right] \qquad\qquad - \left[\frac{1}{\mathrm{Mon.}}\right] \cdot \left[\frac{\mathrm{kcal}}{\mathrm{m^3}}\right]$$

Figure 6.   Differential equation describing the energy flux in the submodel "Rotifers".

1980), requires several control circuits (cf. quality criteria, Part 4). The purpose of these is to match the curves for the absolute feeding rate and biomass to the differential equations, taking the specified proportions into account, by curve fitting on an analogue computer (2 Meda 81 T) by iteration. The water temperature, detritus biomass and food quality factor curves are put in by means of newly developed function generators (VIETINGHOFF, LÖDE and EBERT 1978). After the model has been established on the analogue computer in this way it is reprogrammed for the ES 1040 digital computer. Further technical details are given in VIETINGHOFF, HUBERT and SCHNESE 1981, BRINCKMANN, WIEDEMANN and TIMM 1981).

4. Results and Discussion

The results of the model calculations are shown in Figs. 8 and 9. The list of coefficients is given in Table 1. Other important parameters and criteria in addition to the biomass model curve and its agreement with the measured biomass curve should be used when assessing these model curves, such as

1. the biomass values,
2. the absolute feeding rates,
3. the relative proportions of the shares in the balance equation (i. e. assimilation : respiration : egg production : mortality = 100 : 33 : 43 : 24),
4. the estimation of the error caused by simplification,
5. the agreement of important values yielded by the model with those given in the literature, and
6. the degree to which the hypotheses are supported by experimental data.

The agreement between the curves yielded by the measured values and the model for biomass and absolute feeding rate can be considered good. This assessment takes into account the fact that the confidence intervals about the means of ecological parameters are generally rather large. The biomass curve based on measurements contains only the biomasses of the three rotifer species used in the model; the model curve is shifted slightly in time, but the area beneath it is the same as that beneath the curve based on measured values. The curve yielded by the measurements of the absolute feeding rate is based not only on the feeding rates of the three rotifer species used in the model but also the feeding rates of the other three functional groups. Although the curve yielded by the model for the absolute feeding rate is rather smaller,
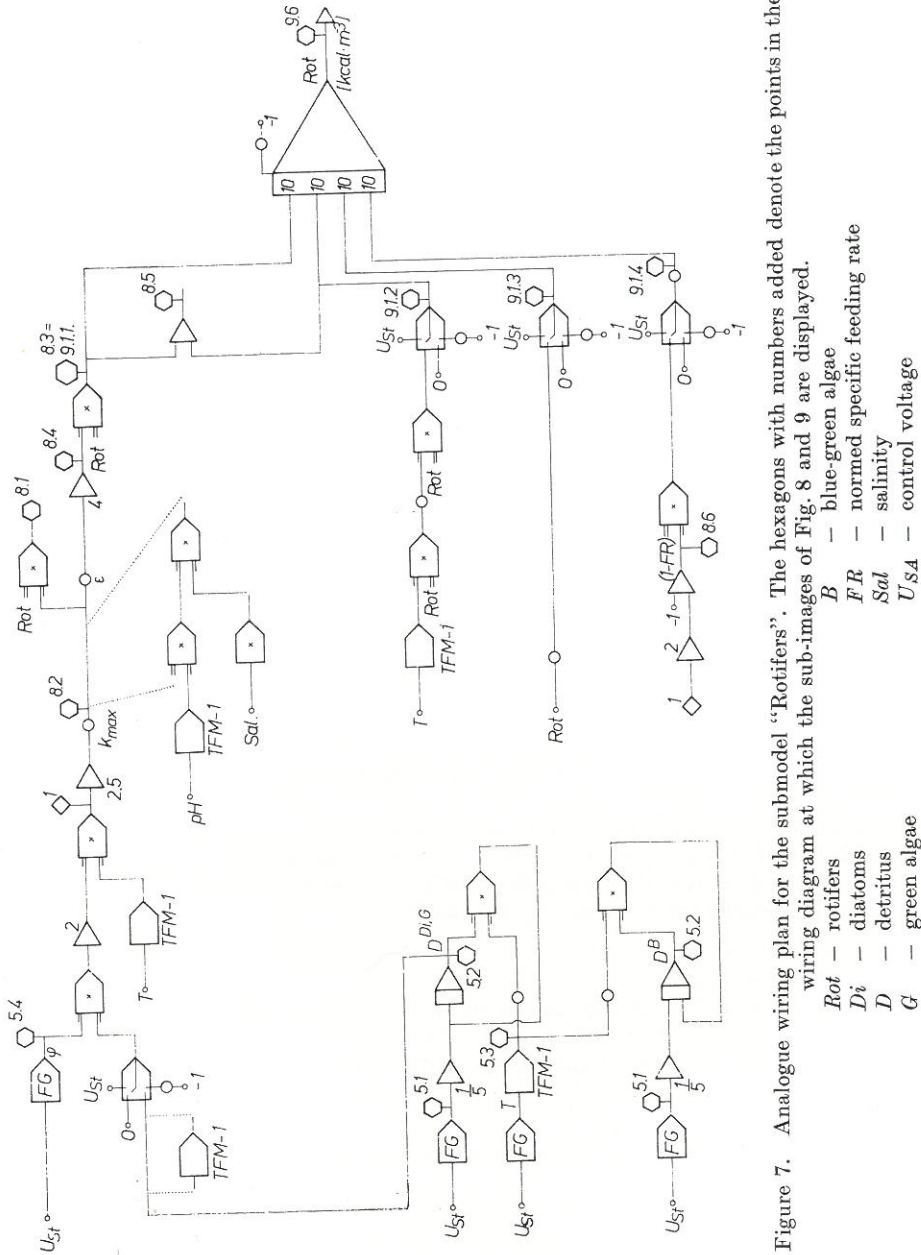
Figure 7.   Analogue wiring plan for the submodel "Rotifers". The hexagons with numbers added denote the points in the wiring diagram at which the sub-images of Fig. 8 and 9 are displayed.

Rot — rotifers B — blue-green algae
Di — diatoms FR — normed specific feeding rate
D — detritus   *Sal* — salinity
G — green algae U_{SA} — control voltage

this is not contrary to our expectations. The relative proportions between the factors in the balance equation (third quality criterion) are exactly identical to those yielded by the initial calculations (see above).

When estimating the error introduced by simplification (fourth quality criterion) it is necessary to take into account the error caused by omitting the mictic females and the three other functional groups. The error caused by the former is 5–10 % (King and Snell 1980) and is therefore negligible. In the latter case, however, it is
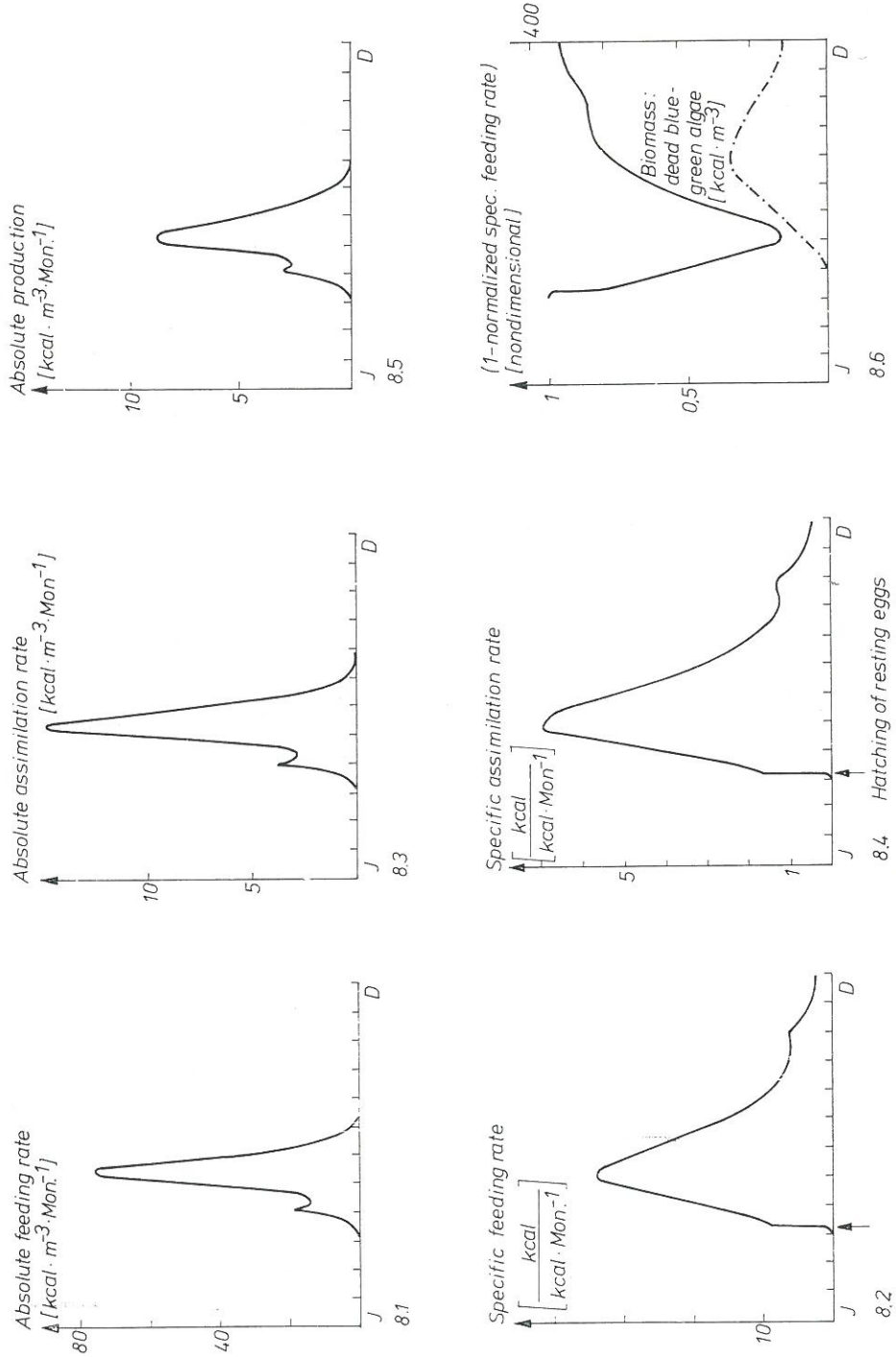
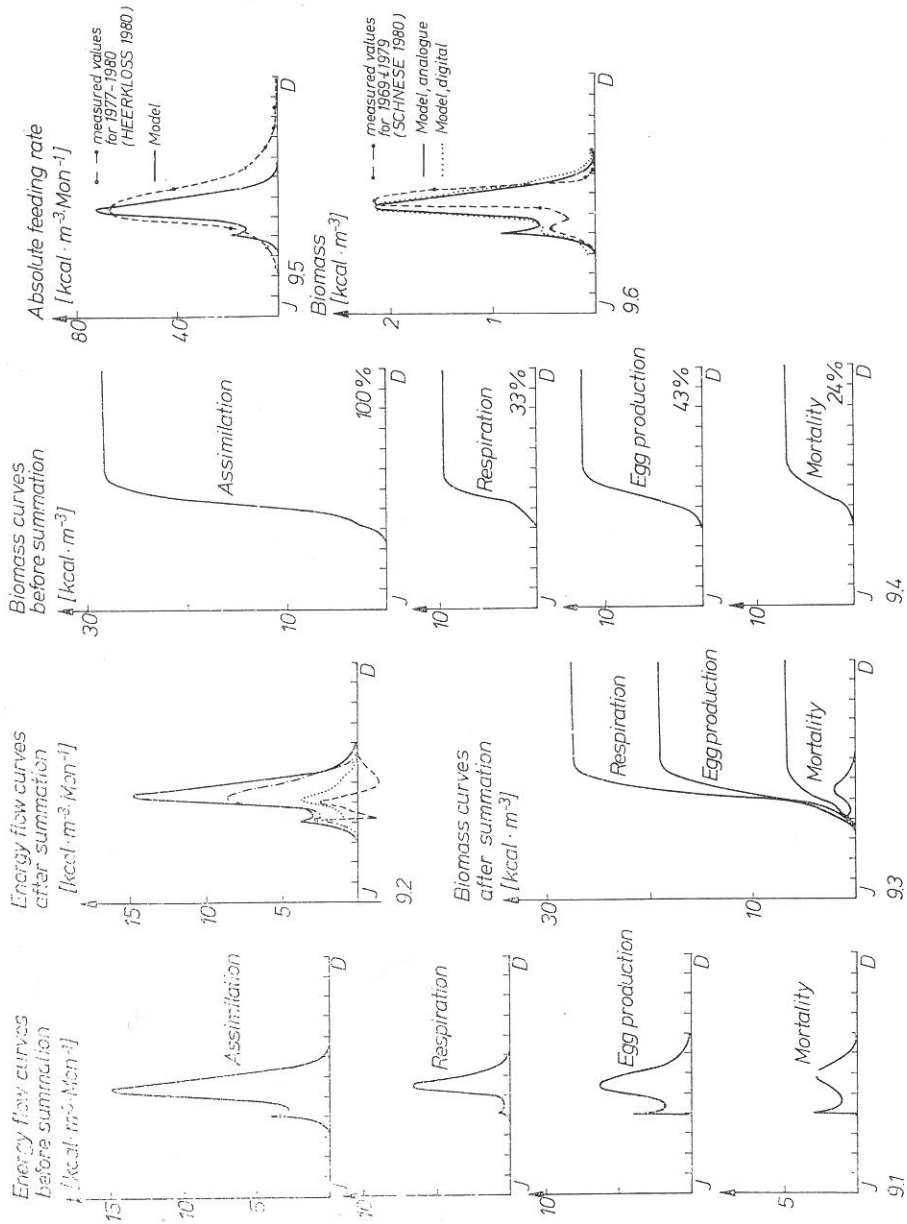Figure 8. Result curves (I) obtained from the submodel "Rotifers".

Figure 9. Result curves (II) obtained from the submodel "Rotifers".

some 30 % (Figs. 2 and 9.6), and our approach therefore needs some explanation: errors of this order are within the error limits associated with numerous ecological parameters, and it is far from unusual to omit, without affecting accuracy but greatly increasing the efficiency, rare species from the calculation and to compensate for this by increasing the values (displacement volume, biomass, etc.) calculated for the principal species by an estimated percentage (van Heusden 1972, Hobro and Willén 1974, and others). This could also have been done in our submodel. But it is more important to consider the contribution of the three groups not included in the model

Table 1.   List of coefficients used in the submodel "Rotifers"

Symbol	Parameter	Value[1]
k_G^{Rot}	maximum feeding rate	25.0
ε_{Rot}	assimilation efficiency	0.2031
$k_G^{Rot}\dfrac{Rot}{Rot^*}$	respiration rate	2.4854
k_M^{Rot}	mortality rate	4.1978
k_{eggs}^{Rot}	egg production rate	2.0
$Rot\ (t=0)$	initial value	0.0778
Rot^*	assumed maximum rotifer biomass	2.0
D^*	assumed maximum detritus biomass	400.0

[1] Dimension as in Fig. 6

in relation to the matter and energy flux in the ecosystem as a whole, and this accounts for only a few percent. Moreover, the simplifications and their consequent errors also seem justified in view of the foreseen optimization calculations, for which it was necessary to keep the size of the model within certain limits.

With regard to the fifth criterion, the agreement between the parameters yielded by the model with those given in the literature, we would like to discuss in particular the temperature dependence, the assimilation efficiency and the maximum feeding rate. Not only the different species used in the model but also their parameters (food intake, growth, development, etc.) can exhibit varying dependence upon temperature (BAKER 1979, EDMONDSON 1965, NAUWERCK 1963, RUTTNER-KOLISKO 1980, PREISSER and SPITTLER 1977, HALBACH 1970). The different temperature functions were weighted and averaged for use in the model (the curves for the dependence of the summary parameter "growth" on temperature were taken more into account than those for the feeding rate or development), although only the temperature range from 10 to 20 °C is of importance. The temperature function used (Fig. 5.3) is thus a compromise.

The values given in the literature for the assimilation efficiency, ε, range from 0.19 to 0.78 (GALKOVSKAYA 1963, 1971, cited in DOOHAN 1973, LEIMEROTH 1980). LEIMEROTH (1980) reported values between 0.49 and 0.20 for *Brachionus calyciflorus*, stating that the value declines as the food concentration increases. H. ARNDT (unpubl.) found a value of 0.2 for the same species. The value used in the model was $\varepsilon = 0.203$.

The maximum specific feeding rate of $f_{max} = 22.82 \left[\dfrac{\text{kcal}}{\text{kcal} \cdot \text{month}} \right]$[1] used in the model is also within the range of experimental data: according to STARKWEATHER et al. (1979) the specific feeding rate of *B. calyciflorus* varies between 0.864 and 31.68 $\left[\dfrac{\text{kcal}}{\text{kcal} \cdot \text{month}} \right]$. At food concentrations similar to those in the Barther Bodden values between 20 and 30 $\left[\dfrac{\text{kcal}}{\text{kcal} \cdot \text{month}} \right]$ can probably be expected.

As to the sixth criterion, the degree to which the hypotheses used are supported by experimental data, we shall explain how we formulated our food quality index and the mortality rate.

According to POURRIOT (1980) and other authors (RADWAN 1980, SPITTLER 1969, STARKWEATHER and BOGDAN 1980, NAUWERCK 1963), *Keratella cochlearis*, *Filinia*

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[1] $f_{max} = 25 \left[\dfrac{\text{kcal}}{\text{kcal} \cdot \text{month}} \right]$ for the digital submodel

longiseta and *Brachionus quadridentatus* are able to utilise detritus and bacteria very well. Diatoms, green algae and blue-green algae are not ingested, although the rarer groups of algae form a certain proportion of the food intake that is probably more qualitative than quantitative. DUMONT (1977), NAUWERCK (1963), RADWAN (1980) and other authors report that mainly fresh detritus is ingested (better C/N ratio, lower Fe^{+++} and Ca^{++} concentration, etc). But the rapid drop in the absolute feeding rate and the sudden disappearance of the population at the end of July and beginning of August (HEERKLOSS 1980, SCHNESE 1980) cannot be explained alone by the curves showing the measured temperature variations and the biomass of the "fresh detritus" from all three of the main phytoplankton groups. A satisfactory explanation can only be given by assuming a third factor, and this seems to be related to the mass appearance of blue-green algae. As Figs. 8.6 and 9.6 show, there is a striking correlation between the collapse of the populations of the three rotifer species used in the model and the mass development of blue-greens in July. In Lake Erken the mass development of blue-green algae in July coincided with a minimum in the occurrence of *Keratella cochlearis* during exactly the same period (NAUWERCK 1963). Other authors have also described the same phenomenon and have discussed possible causes (DUMONT 1977, for instance). According to POURRIOT (1977) the rotifer species being considered here fail to reproduce in cultures if blue-greens are present. We have attempted to take this phenomenon into account mathematically by introducing the food quality index φ, which is a fully legitimate way of including the various possible causes for the collaps of the rotifer population (reduction in the diversity of species or excretion of toxic substances) in the model. As yet no experimental investigations regarding this problem have been performed in the area under consideration, but they will be started on account of this work.

The idea on which our formulation of the mortality rate is based was originally published by LEHMAN, BOTKIN and LIKENS (1975), and we have applied it in modified form for almost all biological components (phytoplankton, microorganisms, copepods). In the present case the mortality rate is proportional to the product of (1 − normalized specific feeding rate) and the rotifer biomass (Fig. 8.6). This assumes that the mortality rate is low when the feeding rate is high and, conversely, mortality increases when the feeding rate declines. This is expressed in Fig. 8.2. and Fig. 8.6. The dependence between the mortality rate and the biomass is easy to formulate mathematically with a fair degree of accuracy. It would, of course, be more accurate to make the mortality rate proportional to the biomass some 6—14 days earlier (mean lifespan of the rotifers), but this would be impossible in the case of analogue computers and would entail too great an effort in the case of digital computers (optimization). The chief purpose of our formulation was to take into account both the mortality among the juveniles when food conditions deteriorate and among the adults due to ageing.

A further conceivable criterion—checking of the model by means of an independent data set—has not yet been applied. We have averaged all data at our disposal in order to adapt our model to these long-terms means. This accentuates important aspects of rotifer development while suppressing trivial phenomena. This sixth criterion will, however, be applied in future work.

In summary it can be stated that we have checked the submodel for rotifers against several criteria and have found that it agrees satisfactorily with the natural situation. We believe that it is absolutely necessary to check the different submodels against the largest possible number of criteria even in the case of complex ecosystems.

5. Summary

A submodel for the energy flux through the rotifer compartment of a shallow eutrophic brackish coastal inlet (the Barther Bodden) is described. The model takes only the amictic females of the species responsible for the greater part of the production (*Keratella cochlearis*, *Filinia longiseta* and *Brachionus quadridentatus*) into account.

The model is based on biomass values (samplings fortnightly to monthly) for 12 years (SCHNESE 1980) and feeding rate measurements for four years (HEERKLOSS 1980). The accuracy of the submodel is assessed on the basis of the following criteria: biomass, feeding rate, relative proportions of the shares in the balance equation, and agreement between important data yielded by the model with data given in the literature.

6. Acknowledgements

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