

## Carbon Flux Dynamics in a Shallow Eutrophic Estuary

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With 3 Figures and 3 Tables

Key words: Eutrophic estuary; Mesocosm; Carbon flux; Microbial loop.

### Abstract

Joint enclosure experiments were performed in Kirr Bucht, a shallow eutrophic bay in the Darss-Zingst estuary. The pelagic community played a major role in the main carbon flux of this ecosystem. Despite constant changes, various states of dynamic equilibrium were identified which were related to nutrient loadings and seasonal periodicity.

The results presented refer to the (N + P)-loaded enclosure from the 1st to 2nd and from the 5th to 6th week of the experiment. The carbon values describing phytoplankton biomass and activity during these two periods are nearly equal, but considerably more detritus was consumed during the second period than during the first. The links and dynamics of the carbon flux are discussed in terms of the principle organism groups or species involved.

### Introduction

The chief characteristic of estuarine ecosystems is the great variability of their structural and functional parameters in space and time. Seasonal rhythms triggered by abiotic factors are also one of their typical features. To understand these rhythms it is essential to know the magnitudes of the different pools and to identify the fluxes between them. The Coastal Research Group of the Department of Biology at Rostock has used the advantages of mesocosm experiments (MENZEL & STEELE 1978; TAKAHASHI et al. 1975) to study the carbon, nitrogen and nutrient fluxes in the course of joint field experiments (SCHIEWER & JOST 1986). The experiments focused on the problem of controlling community structure and function "from below" (MULLIN 1982) by nutrient loading in "bottom-up" experiments. Nutrient loads directly affect the phytoplankton, the main biotic component of the ecosystem we studied. The ultimate aim is to identify possible ways to manipulate this particular estuarine ecosystem and to establish a scientific basis on which biological control technology or ecotechnology can be established.

This paper uses our investigations into the interactions between carbon flux and various ecosystem components to describe our approach. As examples we have selected two quasi-stationary states observed in the (N + P)-loaded enclosure during a long-term experiment (FLAK 86). These two states are characterized by approximately equal phytoplankton and detritus pool sizes, and identical, increasing phytoplankton productivity. They differ with respect to detritus pool size, however, which remained stable during the first period but decreased significantly during the second. We investigated the details of the structural and functional changes associated with these states.

### Material and Methods

The experiments were performed in Kirr Bucht, a shallow region of the boddens south of the Darss-Zingst peninsula (Fig. 1A). Enclosures were used to isolate shallow bodies of water with a mean depth of 75 cm and a surface area of about 3 m<sup>2</sup> from the surrounding water (Fig. 1B). The enclosed water body had a volume of about 2.4 m<sup>3</sup>. The enclosures (FLAK series) consisted of metal rings with a diameter of 2 m and a height of 40 cm which were open at the top and bottom. They were driven 35 cm into the sediment to prevent water exchange at the bottom. A polyethylene cylinder with a height of 95 cm was fastened to each metal ring. Floats at the top of each cylinder provided the necessary buoyancy and also prevented outside water from entering the enclosure during rough weather. The whole structure was protected against wind and wave action by a secondary structure (Fig. 1B).

The experiments began on 30 May 1986 when the enclosures were set up. They ended on 24 July 1986. The water in the enclosure considered here was enriched with NH<sub>4</sub>Cl and NaH<sub>2</sub>PO<sub>4</sub> from 03 June to 21 July 1986 to prevent possible nutrient limitation of phytoplankton development.

The following parameters were measured on at least 2.5 days per week throughout the experiment:

- chlorophyll a concentration by methanol extraction (RIEMANN 1978),
- phytoplankton composition and biomass (UTERMÖHL 1958),
- in situ phytoplankton production by the <sup>14</sup>C-method (SCHINDLER et al. 1972),
- number of bacteria by epifluorescence count (JOST & BALLIN 1980),
- bacterial secondary production by (<sup>3</sup>H)thymidine incorporation into DNA (FUHRMAN & AZAM 1980, 1982),
- ciliate number by discrete counts of live organisms (individuals sorted into size classes for biovolume estimation),
- numbers and feeding rates of rotifers and crustaceans (SCHNESE & HEERKLOSS 1978), and
- detritus content (GEORGI et al. 1980).

The values used for the Figures are means of selected parameters in the (N + P)-loaded enclosure during the 1st–2nd and 5th–6th week. Table 1 presents the changes in phytoplankton biomass and detritus content during these periods.

Table 1. Changes in the phytoplankton and detritus pools (mg · m<sup>-3</sup> · C) during the selected periods (1st–2nd and 5th–6th week) of the FLAK-experiment. (N + P)-loaded enclosure

Period	Phytoplankton	Detritus
1. period		
02. 06. 1986	9747	19985
14. 06. 1986	18199	18199
mean	13937	
2. period		
30. 06. 1986	5572	19291
11. 07. 1986	23891	12364
mean	14732	

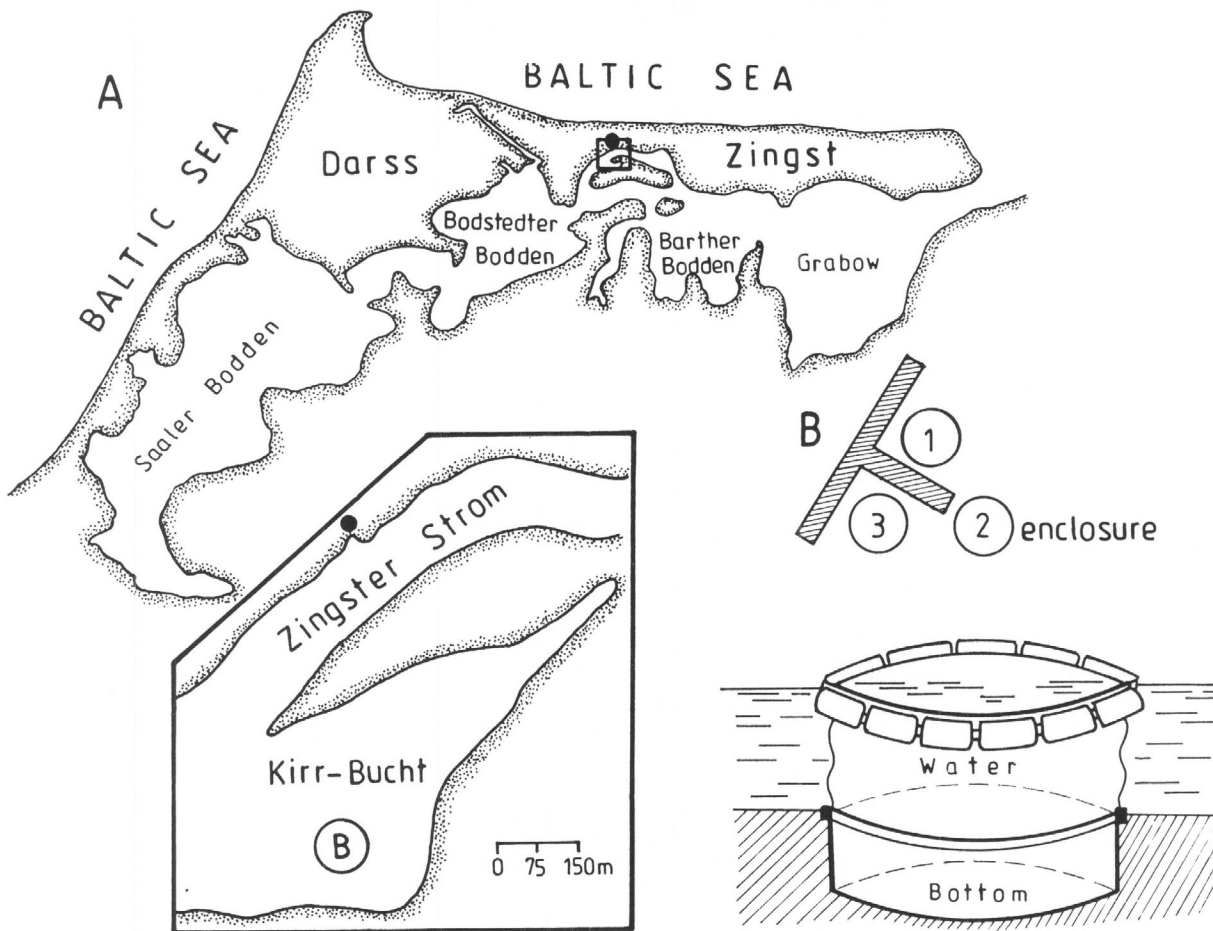


Fig. 1. Investigation area and mesocosm design.  
 A. Chain of boddens south of the Darss-Zingst peninsula.  
 B. Laboratory station Zingst, Kirr Bucht; mesocosm and enclosure design

## Results

The ecosystem we studied is brackish and eutrophic. The food web is predominantly microbial in the pelagic zone ("microbial loop"). Large invertebrates (meiofauna, macrofauna) are important consumers only in the benthic zone. Figs. 2 and 3 show the measured pool sizes, input and output rates and the calculated fluxes between system components.

The detritus and phytoplankton pools are largest. The bacteria pool is significantly smaller. The sizes of these pools remained approximately constant during both periods. However, the turn-over rates of the detritus and bacteria pools were much higher during the second period than during the first. The pools comprising the other heterotrophic organisms varied considerably, but in all cases they were larger during the second period than during the first.

The crustaceans have virtually no influence on the turnover of matter. Small heterotrophic organisms are responsible for most of the carbon flux. This accelerates recycling within the ecosystem. The carbon flux to the sediment during the first period differs qualitatively from that during the second: sedimentation of phytoplankton predominated during the first, but the detritus pool, phytoplankton and heterotrophs metabolism contribute almost equally to this flux during the second.

The fluxes of matter between the various ecosystem components and the ways in which they can be in-

fluenced must be known if the processes taking place in the ecosystem are to be understood. We therefore analyzed the structural and functional variations in the different groups of organisms in order to elaborate a corresponding web.

## Phytoplankton

Phytoplankton development was definitely nitrogen-limited when the experiment began. Loading with

Table 2. Phytoplankton species and percentage biomasses during the selected periods. (N + P)-loaded enclosure.

Period	% Biomass
1st—2nd week	
<i>Crucigenia quadrata</i> var. <i>secta</i>	46.9
<i>Lyngbya contorta</i>	17.6
<i>Gomphosphaeria pusilla</i>	14.8
<i>Scenedesmus quadricauda</i>	6.5
<i>Oocystis</i> spec.	2.5
others	11.7
5th—6th week	
<i>Scenedesmus quadricauda</i>	16.0
<i>Oscillatoria limnetica</i>	12.9
<i>Chroococcus limneticus</i>	12.9
<i>Synedra</i> spec.	11.9
<i>Crucigenia quadrata</i> var. <i>secta</i>	11.3
others	34.9

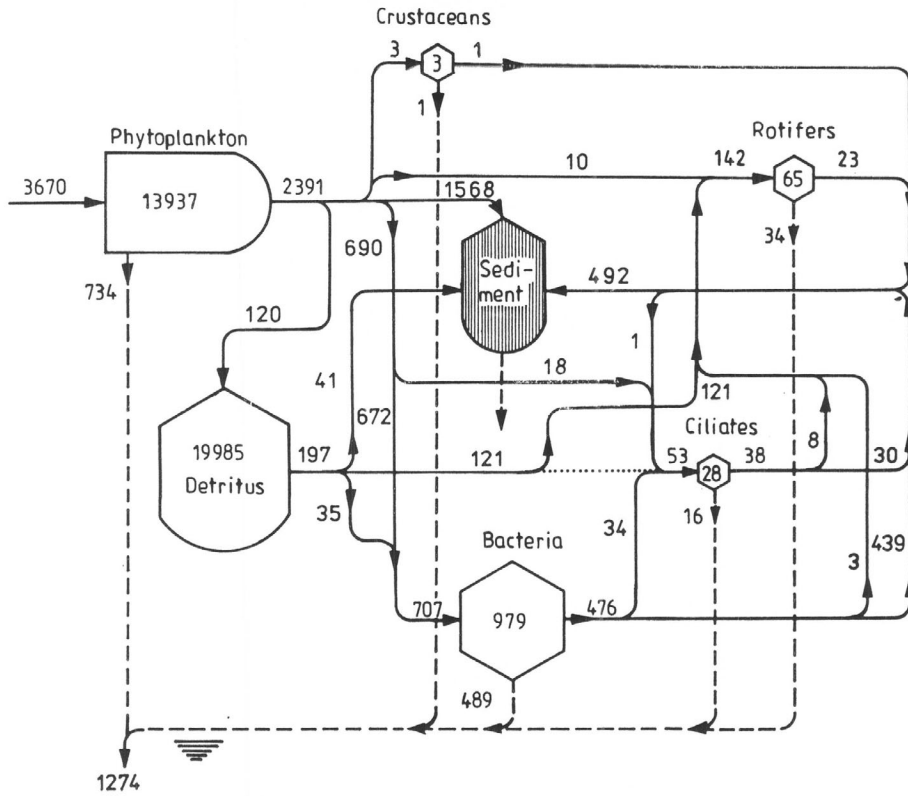


Fig. 2. Carbon pools and fluxes in the (N + P)-loaded enclosure, 1st-2nd week of the FLAK-experiment 1986.

Numbers in geometric symbols: carbon contents in  $\text{mg} \cdot \text{m}^{-3}$  in the phytoplankton, detritus, crustacean, bacteria, ciliate and rotifer pools. Solid arrows: carbon fluxes in  $\text{mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$  between the different pools. Broken arrows: respiration losses in  $\text{mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$  carbon and total loss. Estimated values: pools, input and output; calculated: fluxes between the pools (see text). The sediment is considered as a sink only. All values are means for the 1st period

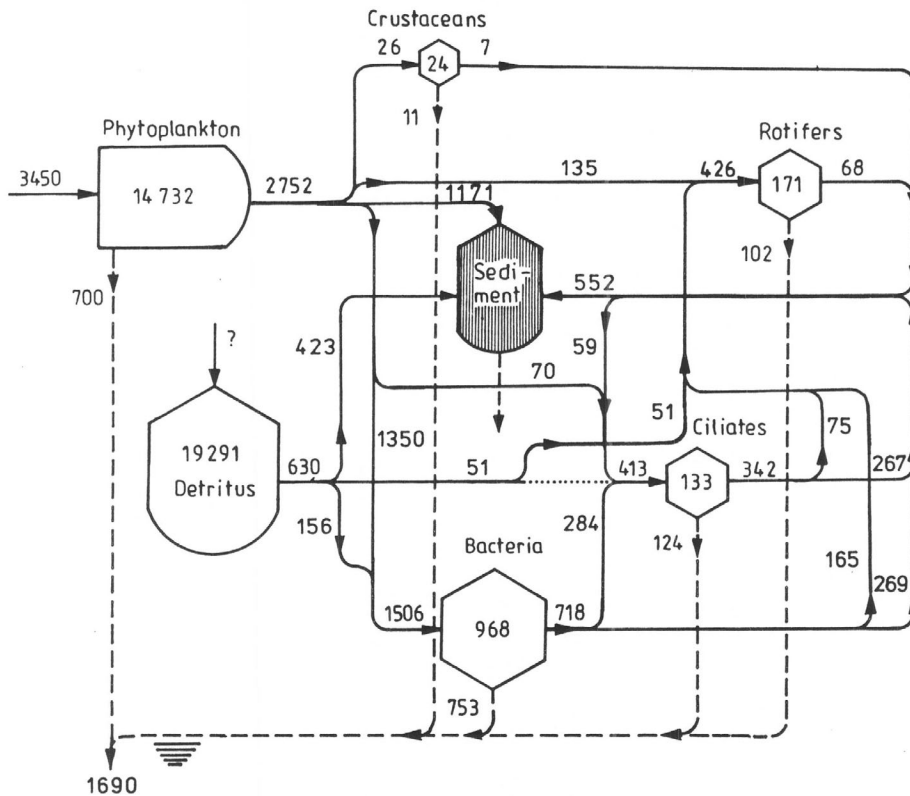


Fig. 3. Carbon pools and fluxes in the (N + P)-loaded enclosure, 5th-6th week of the FLAK-experiment 1986. (cf. Fig. 2 for further details)

(N + P) encouraged primary production and led to a larger, stable phytoplankton pool. Comparison of the two periods (Table 2) shows that the carbon pools and fluxes remain almost constant although the community structures change completely. During the 1st and 2nd week the green algae, particularly *Crucigenia*, predominate. On account of their high growth rate they out-compete the other algae. This and their relatively high sedimentation rate increases the flux of algae into the sediment.

During the second period the phytoplankton consisted of about equal biomasses of at least five algal species. Their co-existence indicates that growth conditions were about equally suitable for them all on account of their different growth and/or loss rates.

### Bacteria

The structure of the bacterial populations was not analyzed. The different turnovers despite equal bacterial biomasses raises the question of the regulating mechanisms involved. There is evidently no direct link between either input rates or bacterial secondary production and phytoplankton biomass or productivity. This is contrary to the findings reported by FUHRMAN et al. (1980) for marine ecosystems and by HAGSTRÖM & LARSEN (1984) for Baltic biotopes. The range of phytoplankton species and/or the detritus are obviously more important in the eutrophic brackish waters we studied.

### Ciliates

Ciliates are always an important component of the ecosystem we studied (ARNDT 1986). The number of ciliate species it contains and the rapid changes in the composition of species are considerable (ARNDT et al. 1988). To avoid the complexity this would normally entail, we have split the ciliates into the three most important functional groups (Table 3). This also facilitated quantification. The bacterivorous and detritivorous group always had the highest feeding rate. The substantial decline in the algivorous group during the 5th–6th week was accompanied by growth of the omnivorous group.

### Rotifers

A distinct change in dominance took place among the rotifers during our investigations (Table 3): *Filinia longiseta* was replaced as the dominant species by smaller rotifers. The other species played only a minor role. *Filinia longiseta* is a typical detritivour, and its loss of dominance was accompanied by a shift towards increased consumption of the bacteria by the smaller rotifers.

### Crustaceans

Several crustacean species are found in the ecosystem although their total biomass is small. The copepods predominated initially, but cladocerans became more abundant later (Table 3). This change had no real impact on the ecosystem, however, because the potential turnover of the latter group is very small.

The above information regarding dominance and feeding rates was used to calculate the carbon fluxes between

Table 3. Functional groups of ciliates, species of rotifers and crustaceans and their percentage biomasses and feeding rates in the (N + P)-loaded enclosure during selected periods. FLAK-experiment 1986

	1st–2nd week		5th–6th week	
	Biomass (%)	Feeding rates (%)	Biomass (%)	Feeding rates (%)
<b>Ciliates</b>				
Bacterivores	33.8	64.6	66.5	68.8
Algivores	58.8	34.2	4.0	16.9
Omnivores	7.4	1.2	29.5	14.3
<b>Rotifers</b>				
Small rotifers (100 µm; <i>Trichocerca</i> , <i>Synchaeta</i> etc.)	1.5	1.7	79.9	82.0
<i>Filinia longiseta</i>	85.3	85.0	2.4	2.2
<i>Brachionus urceolaris</i>	5.3	5.3	8.0	7.2
<i>B. quadridentatus</i>	5.4	5.4	0.4	0.4
<i>B. angularis</i> , <i>Keratella tecta</i> and others	2.5	2.6	9.3	8.2
<b>Crustaceans</b>				
Copepods	100.0	100.0	68.2	58.7
Cladocera	0.0	0.0	31.8	41.3

the different compartments of the community. The sediment was considered only as a sink (Figs. 2 and 3). The respiration rate of the sediment as measured by the O<sub>2</sub> method was only about one third that of the pelagic zone. The ciliate population of the sediment increased 10-fold from the 1st–2nd week to the 5th–6th week. It consisted at all times mainly of bacterivorous and detritivorous. The meiozoobenthos, particularly the oligochaetes and harpacticoids, declined during the same interval. These changes were caused by increased organic inputs owing to the greater productivity of pelagic phytoplankton and accelerated the turnover of matter in the sediment.

During the 1st–2nd week only about a third of the phytoplankton production was used by pelagic heterotrophs, which were mainly bacteria. The remainder sedimented to the bottom. For ciliates the main food source is bacterioplankton, whereas the rotifers feed mainly on the detritus pool. With turnover times of 1.9 · d<sup>-1</sup> (ciliates) and 2.2 · d<sup>-1</sup> (rotifers) these two groups have considerable biomass turnover rates.

The carbon flux through the bacteria compartment was twice as high during the 5th–6th week. The larger amounts of dissolved organic matter needed for such an increase are probably released partly from the detritus and partly a result of increased biomass turnover by the ciliates and rotifers. The greater phytoplankton diversity probably also enhances bacterial metabolism by increasing the range of utilizable dissolved organic matter available. The increase in the proportion of omnivorous ciliates increases the density of the carbon flux web in the ciliate compartment. Bacteria and small phytoplankters constitute the main food of the rotifers during the second period of our study. The turnover time had increased for both the rotifers (2.5 · d<sup>-1</sup>) and ciliates (3.1 · d<sup>-1</sup>).

### Discussion

Despite the virtual absence of large invertebrates as consumers, in the shallow pelagic zone 34% (1st–2nd week) and 55% (5th–6th week) of the net phytoplankton production were consumed during the experiments. This emphasizes the great importance of the “microbial loop” (AZAM et al. 1983) in this ecosystem. Compared

with the 80% reported by OVERBECK (1983) and SIMON & TILZER (1987) for the top 5 m and 20 m of the pelagic zone in lakes, these turnover rates are amazingly high for a water depth of only 75 cm.

In the ecosystem we studied the decisive heterotrophic component is the bacterioplankton. According to JOST & BALLIN (1980) it consisted mainly of free bacteria and accounted for 38% and 45% of the total pelagic respiration in the first and second period of investigation respectively. Secondary bacterial production during these period totaled 20% and 26% respectively of the net primary production and resulted from a bacterial population of about  $10^7$  individuals per ml. This "summer plateau" (JOST & BALLIN 1980) was extremely stable and could not be influenced appreciably even by experimental manipulation. Bacterial growth therefore seems to be closely linked to corresponding loss processes. This view is supported by the increased bacterioplankton turnover during the 5th–6th week, which is accompanied by an increase in grazing pressure by ciliates and rotifers from 4% in the 1st–2nd week to 46%.

Dissolved organic carbon is the most important carbon source for the bacterioplankton. Excreted organic carbon can account for between 5% and 95% of that fixed by phytoplankton (cf. JENSEN 1985). However, since this can only be partly utilized, a considerable proportion of the carbon they need, at least during the 5th–6th week, must enter the water through the lysis of phytoplankton or be liberated as a result of the grazing activity of ciliates and rotifers. It seems likely that some also enters the water from the sediment, but this was not checked experimentally. In this case aerobic decomposition in the top few millimetres of the sediment would doubtless represent an important source.

The ciliates play an important, but imperfectly understood (cf. PORTER et al. 1985) role in the ecosystem described here. Present in about 50 species (ARNDT et al. 1988), they are obviously capable of forming complex substructures. The ciliate community includes all of the functional groups identified by PRATT & CAIRNS (1985). The groups shown in Table 3 were important during our studies. Owing to its considerable structural and functional variability, the ciliate community represents an important regulatory component of the ecosystem, enabling it to respond quickly to perturbations and thus ensuring its stability. Since population sizes are regulated "internally" by omnivorous species, they are less dependent upon regulation by other grazers. On the other hand, this only makes the overall system more difficult to understand. Microcosm experiments (CARON et al. 1985; ANDERSEN et al. 1986) have shown that ciliates play an important role in the recycling of nutrients. Bacteria, in contrast, compete with algae for nutrients (CURRIE et al. 1986).

The rotifers have some regulatory effect on the ciliates. Since crustaceans play no significant role, the rotifers can be regarded as the final link of the food web in the pelagic zone. Interacting with the bacteria and ciliates, they govern the relationships between the heterotrophic and photoautotrophic microorganisms. Our experiments show that control by biomani-pulation from above through the top grazers is impossible in this ecosystem. The most promising approach for control appears to be through phytoplankton, although regulation through heterotrophic organisms may be possible in the case of ciliates. However, this will not be known definitely until our knowledge of these interesting organisms has increased.

## Conclusions

1. The "microbial loop" is of decisive importance in the brackish eutrophic pelagic system we studied in the chain of boddens south of the Darss-Zingst peninsula.
2. Although the carbon pools and fluxes in the phytoplankton compartment were identical during both periods of investigation, the carbon pools, carbon fluxes and population structures of the heterotrophic compartments varied.
3. The variations were not governed by nutrient availability for phytoplankton since neither phosphorus nor nitrogen was a limiting factor. Temperature and light are the obvious factors causing seasonal changes.
4. The stability of the ecosystem is maintained quite generally through changes in fluxes, changes in biomass playing a relatively minor role.
5. The bacterial compartment is characterized by stable numbers of individuals and carbon pool, but flux rates in this compartment can vary considerably.
6. Considerable variability in carbon pool sizes and flux rates are characteristics of the ciliates and rotifers. Crustaceans are of minor importance. The ciliates evidently play an important regulatory role.
7. Structure and function are closely related. The functional redundancy is anchored largely in the species composition of the biotic components.

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