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Experiments with controlled carbon flux variations in shallow brackish waters

Introduction

The development of water quality in the Darss-Zingst bodden chain, a tideless estuarine system on the Baltic coast, has been studied for over 25 years. The results show that these waters are becoming increasingly eutrophic, but that ecosystem responses are discontinuous. Grave changes were noted during the early eighties and were accompanied by transition from submersal macrophyte to phytoplankton dominance and an increase in the proportion of seston in the pelagic zone. Complex interdisciplinary experimental analyses of the pelagic system (Pelagic Enclosures = PEKOM series) from 1980 to 1983 revealed the great importance of the microbial food web for the flux of energy and matter in these ecosystemm (SCHIEWER et al. 1986; SCHIEWER & JOST 1991), leading to a fundamental change in concepts concerning their structure and function (Fig. 1). COFFIN & SHARP (1987), HOPKINSON et al. (1989), RIEMANN et al. (1988) and ROMAM et al. (1988) came to similar conclusions following their studies of other estuarine systems. It was therefore necessary to develop new, more accurate models of their buffer capacity and stability for use as a basis on which more realistic restoration and management strategies could be developed.

Further interdisciplinary experimental studies in shallow regions of the bodden chain (Shallow Water Enclosures = FLAK series, 1985 to 1987) were therefore undertaken mainly to investigate the responses of the microbial food web to variations in nutrient loads. A subordinated aim was to trace the development of the microbial food web during the transitional period from late spring to summer under controlled conditions. The characteristic changes in structure and function observed in the control enclosure during the 1986 FLAK experiment will be described and discussed here.

Material and methods

The experiments were carried out in the shallow part of the Kirr Bucht in the Darss-Zingst bodden chain near the Zingst field laboratory of the Department of Biology.
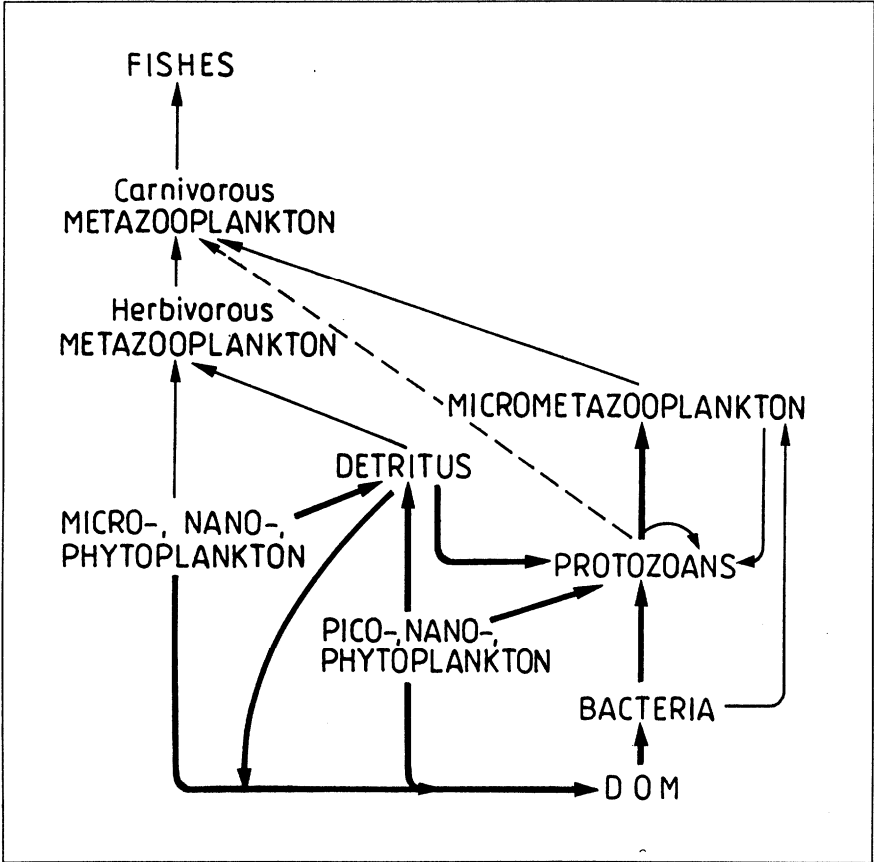
Fig. 1 Simplified model of main pelagic carbon flux routes in the Darss-Zingst bodden chain. Most organic carbon is cycled in the microbial food web.

Enclosures with a diameter of 2 m were used to isolate complete water columns with a cross sectional area of about 3 m^2 and a volume of 2.4 m^3 on 30 May 1986. The actual 1986 FLAK experiment started on 3 June, when baseline values were recorded and the additional nutrient loads (NH_4Cl and/or NaH_2PO_4) were introduced. The experiment ended on 25 July. During the experiment, the following parameters were recorded between twice and four days a week: seston, chlorophyll a, phytoplankton abundance and biomass, phytoplankton primary production by the ^{14}C- and O_2- method in situ and in an incubator, bacterial abundance and biomass, bacterial secondary production, protozoans abundance, biomass and grazing rate, and metazooplankton abundances, biomass and grazing rate. Further details are given in SCHIEWER et al. (1986), SCHIEWER et al. (1988) and ARNDT et al. (1990).

Results and discussion

In the ecosystem we studied, detritus and phytoplankton account for the largest fraction of total suspended carbon. During the experiment, the percentage of phytoplankton carbon in the total suspended carbon varied between 11 and 34%. The lowest values were recorded in the 5th and the highest in the 8th week (Fig. 2). The sizes of the detritus and phytoplankton pools varied in the same direction up to the 4th week, but in opposite directions thereafter. The reasons for this were multifactorial. At the beginning of the experiment, the water temperature was relatively low and phytoplankton growth was vigorous, leading to the dominance of the green algae *Crucigenia quadrata secta* (Table 1) which sometimes accounted for over 50% of the
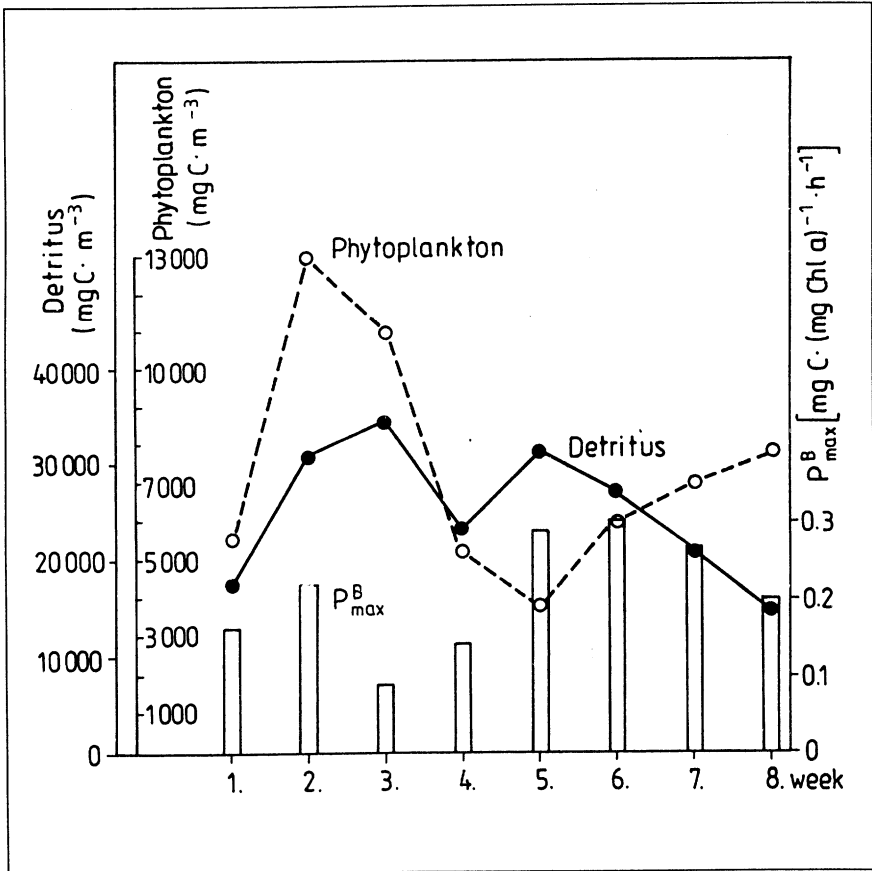

Fig. 2 Detritus and phytoplankton development. Control enclosure, FLAK-experiment 1986. P^B_{max} = assimilation number.

phytoplankton biomass. This period was marked by the formation of detritus consisting of dying phytoplankton biomass under a low grazing pressure. The transition was caused by a relatively rapid increase in water temperature (increase of > 5 °C during 6 days), as a result of which the sedimentation of phytoplankton, detritus and other ecosystem components increased (SCHIEWER et al. 1988). Previously, specific phytoplankton productivity had declined owing to nitrogen limitation in the control enclosure (Fig. 2, assimilation coefficients). Comparisons with the nutrient loaded enclosures shows that the increase in phytoplankton sedimentation was not causally related to nitrogen limitation. That was a surprising result. In shallow waters, water temperature obviously plays a greater role in regulating ecosystem processes than in stratified lakes (cf. WEISSE 1988, for instance). Later lab microcosm experiments and field observations in the next years confirmed the unexpected influence of fast increasing temperatures on the pelagic community.

Table 1   Phytoplankton composition, FLAK experiment 1986. Percentage of biomass in the control enclosure at different times in the course of the experiment.

Phytoplankton Species	% of Biomass		
	1. Week	5. Week	8. Week
Crucigenia quadrata secta	26.1	39.5	-
Ankistrodesmus sp.	16.0	-	-
Kirchnerella sp.	13.7	-	-
Lyngbya contorta	13.0	7.2	-
Oocystis sp.	7.6	-	5.6
Gomphosphaeria pusilla	5.5	-	11.2
Scenedemus quandricauda	3.3	4.1	3.7
Navicula sp.	-	14.4	-
Rhodomonas minuta	-	7.2	-
Oscillatoria limnetica	-	6.2	35.8
Green flagellates	-	3.9	5.0
Anabaena spiroides	-	-	16.7
Stephanodiscus hantzschii	-	-	4.5
Others	14.8	17.5	17.5
Average water temperature (°C)	14.8	23.8	20.0

A new phytoplankton community dominated by the filamentous summer cyanobacteria *Oscillatoria* and *Anabaena* and the colony-forming *Gomphosphaeria pusilla* developed 1986 after the phytoplankton minimum in the 5th week owing to the high water temperature, the increased grazing pressure of heterotrophs and the consequent improvement of the nutrient situation in the pelagic water.

The most active organisms were those forming a direct part of the microbial food web. The fraction comprising the heterotrophs increase threefold during the experiment (Fig. 3). The most important heterotrophs were bacteria with a mean biomass of 1000 mg C x m^{-3}. With a secondary production of 106 - 1185 mg C x m^{-3} x d^{-1}. These were also the most important secondary producers in the ecosystem. The results reported by COFFIN and SHARP (1987) and ROMAN et al. (1988) for estuarine ecosystems are similar. Since less than 24% of the primary production is released into the water as exudate and is therefore available to the bacteria as dissolved organic carbon in the Darss-Zingst bodden chain (BÖRNER 1984), the additional carbon they need must stem from lysis of algae, detritus import and the feeding activity of heterotrophs.

There was no direct link between the development of the detritus pool and that of the bacteria pool. Although they both increased up to the 4th week (Fig, 2 and 3), the size of the bacterial pool fluctuated several times thereafter. Bacterial biomasses,
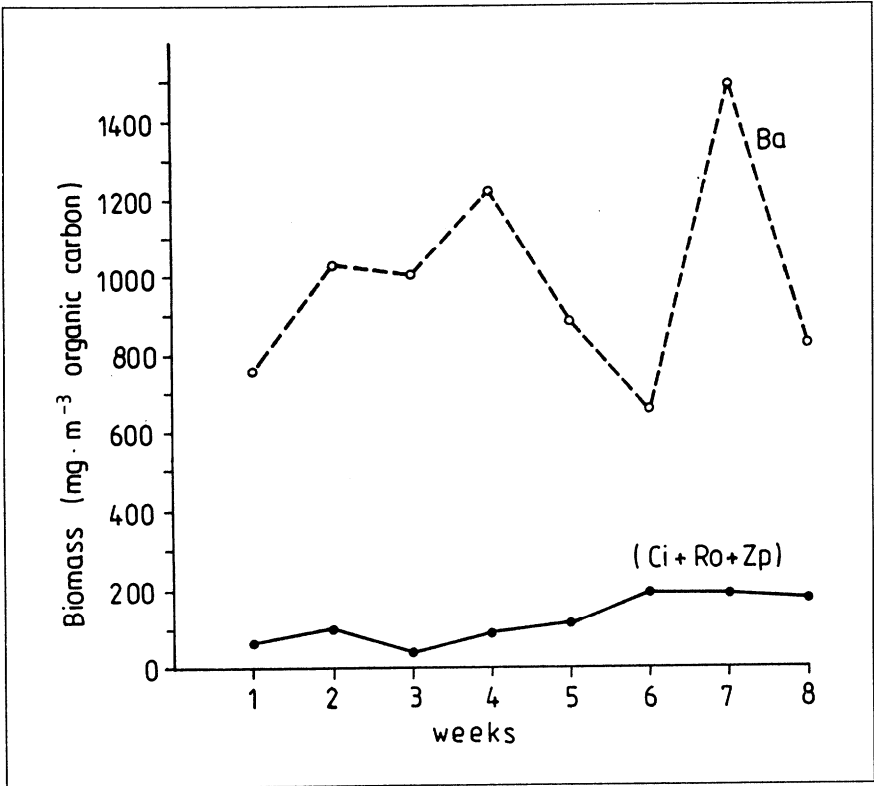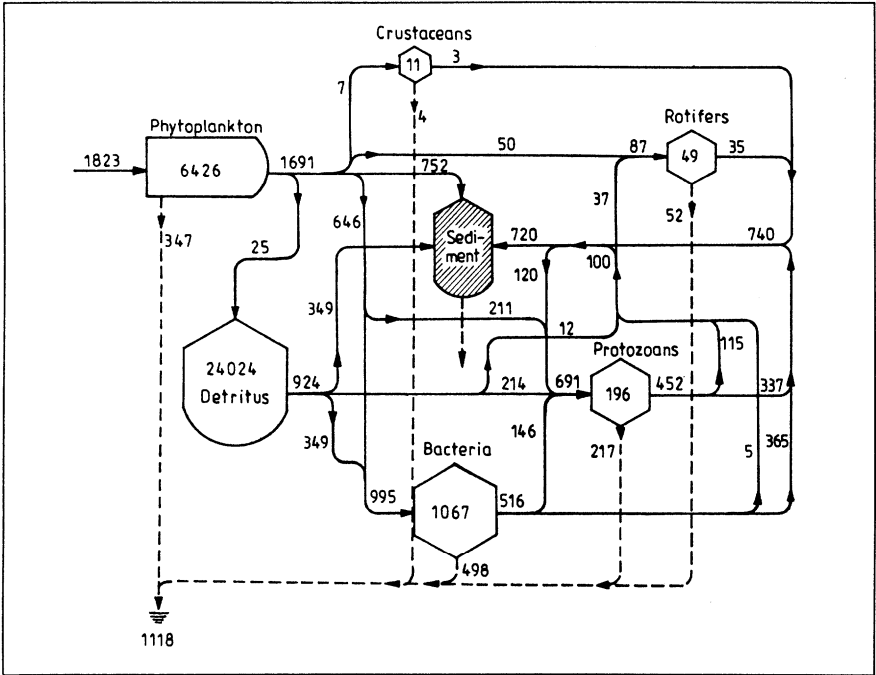

Fig. 3   Pelagic heterotrophs. Development during FLAK 1986, control enclosure.
Ba = bacteria, Ci = ciliates/heterotrophic nanotlagellates, Ro = rotifers, Zo = metazooplankton (crustaceans, cladocers).

which varied by a factor of two, were limited by dissolved organic carbon availability and variations in grazing pressure.

Fig. 4   FLAK 86, control enclosure: biomasses and fluxes between the biotic components and detritus of the pelagic zone.
Numbers in the symbols: measured biomasses and detritus carbon in mg C x m^3.
Numbers on the solid line arrows: measured or tentative calculated flux rates between the trophic levels in mg C x m^{-3} x d^{-1}.
Numbers on the broken line arrows: respiration rates in mg C x m^{-3} x d^{-1}.
Means of the 6 to 7th week.

The potential bacterial grazers were protozoans (heterotrophic nanoflagellates, ciliates) and rotifers (Fig. 4). Grazing pressure on the bacteria was exerted primarily by heterotrophic nanoflagellates and the bacterivorous and detritivorous ciliates (Table 2). These were represented mainly by *Mesodinium* species and cf. Enchelys. It was particularly high during the 5th and 6th weeks, but then decreased considerably. The ciliates (Table 2) were the main consumers of the nano- and picophytoplankton.

Table 2   Functional groups of protozoans, FLAK experiment 1986. Percentage of grazing rates in the control enclosure at different times in the course of the experiment.

Functional groups	% grazing rate		
	1. Week	5. Week	8. Week
Bacterivorous/detritivorous	62.9	78.4	59.4
Herbivorous	37.1	6.4	40.6
Raptors	-	15.2	-

The influences of the copepods and cladocerans were very slight during the study period. Thus the final consumers in the pelagic zone were the rotifers (Table 3). However, their biomass and feedind activity is substantially lower than that of the ciliates. Although their activity increaced towards the end of the experiment, their overall influence on carbon turnover was slight and probably affected mainly the phytoplankton and detritus.

Table 3   Metazooplankton groups, FLAK experiment 1986. Changes in biomass and grazing rates in the control enclosure at different times in the cour- se of the experiment.

Metazooplankton groups	Biomass (mg C $\cdot$ m^{-3})			Grazing rate (mg C $\cdot$ m^{-3} $\cdot$ d^{-1})		
	1. Week	5. Week	8. Week	1. Week	5. Week	8. Week
Rotifers	19.4	23.7	46.5	17.7	21.6	42.5
Copepods	0.3	-	-	0.1	-	-
Cladocers	-	1.5	6.1	-	0.9	3.6

Our studies show that the microbial food web plays an important role in shallow tideless estuaries on the Baltic coast. Approaches for the development of effective restoration and management strategies for such waters must therefore consider this point. It high turnover rates led to high remineralization rates inducing a remarkable self-eutrophication of the pelagic ecosystem. Owing to the limited biomass and per- formance of the metazooplankton, there are limitations to the flux of matter via the traditional grazing food chain to higher trophic levels. Besides the phytoplankton, the protozoans are obviously also an important regulating factor because the can act as both a sink and a link (SHERR & SHERR 1988).

Summary

The carbon flux in tideless shallow eutrophic estuaries of the Darss-Zingst bodden chain is linked mainly to the microbial food web. The control enclosure used during the FLAK field experiment (2 June to 25 July) yielded the following conclusions:

– Detritus and phytoplankton accounted for most of the supended organic carbon during the whole experiment. The sizes of both pools varied in the same direction during the 1st to 4th weeks, but in opposite directions during the 5th to 8th weeks.

– The differences were a result of changes both in environmental factors and in the structure and function of the microbial food web.

– The collapse of the 1st phytoplankton bloom was caused by the relatively rapid increase in water temperature. Increased heterotroph biomass and activity, particularly of ciliates, were important prerequisites for the 2nd phytoplankton bloom.

– Comparable processes, although modified by the rather better supply of inorganic nutrients for the algae, take place in the surrounding open water of Kirr Bucht.

– Effective restoration and management strategies for such waters can only be developed and implemented if activities of the microbial food web are taken into account.

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